Effects of food web construction by evolution or immigration

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We present results contrasting food webs constructed using the same model where the source of species was either evolution or immigration from a previously evolved species pool. The overall structure of the webs are remarkably similar, although we find some important differences which mainly relate to the percentage of basal and top species. Food webs assembled from evolved webs also show distinct plateaux in the number of trophic levels as the resources available to system increase, in contrast to evolved webs. By equating the resources available to basal species to area, we are able to examine the species-area curve created by each process separately. They are found to correspond to different regimes of the tri-phasic species-area curve.

PACS numbers: 87.23.Cc
Keywords: Species area relation, Food webs, Trophic levels, Individual-based model

I. INTRODUCTION

Models of food web structure fall into several distinct classes. Early models tended to be either static, where links were assigned between species according to some rule, or dynamic, but where the dynamics consisted of population dynamics on a random network. Examples of the former are the cascade [1, 2] and niche [3] models, and of the latter the work of [4, 5]. More recent approaches have incorporated longer time scales, allowing for the introduction of new species through immigration or speciation and for species extinction. This allows the web structure to build up over time; the structure of the web emerges rather than being put in by hand. The two ways of doing this have been through assembly models, which introduce new species into the community from a species pool [6], and evolutionary models, which introduce new species through modification of existing species – speciation [7]. The purpose of this paper is to unify these two approaches by constructing a species pool through an evolutionary dynamics and then using this to assemble communities.

Assembly and evolutionary models both have two, separated, time-scales. On the ecological time-scale the population sizes of the species in the community change according to the equations of the population dynamics until they eventually reach a fixed point or some other attractor. On a longer time-scale species are introduced through immigration (assembly models) or by speciation (evolutionary models). The new species then competes with the existing species following the equations of the population dynamics until the system again reaches equilibrium. If the new species does not immediately go extinct, it may either coexist with those species present at its introduction, or may cause one or more extinctions, potentially resulting in its own extinction. The population dynamics takes the form of differential equations for the population numbers (using, for instance, Lotka-Volterra, Holling type II, or ratio-dependent functional responses) and so the extinction threshold has to be specified. Typically this is set to be such that if the population of any particular species falls below 1, it is deemed to be extinct.

Assembly models usually consist of species pools of tens of species which are labelled as “plants”, “herbivores”, “carnivores”, etc. The interactions between these various trophic levels are typically assigned by some rule with a large amount of randomness built in, but body-size considerations may also be used to decide the predator-prey relationships. Early work used numerical integration of Lotka-Volterra equations, combined with the criterion of local stability [8, 9, 10], although this had some problems [11], and other methods of deciding whether a particular community is stable have been used [12, 13]. Species assembly models are capable of generating reasonably-sized food webs [6] through immigration, although the species pool is made up of species which are randomly assigned rather than having co-evolved, and as such it is very artificial. Moreover, only very simple population dynamics have been investigated, underlining the overall lack of realism of this approach.

Evolutionary models have been developed during the last decade or so. Species and their interactions may be specified by traits which define phenotypic or behavioural characteristics [14, 15, 16, 17], or the strength of interaction between species may be described through matrices [18, 19]. Additional mechanisms, such as adaptive foraging, may be included and may add stability to the system [18]. The evolutionary approach starts from a small number of species and, through the modification of existing species, is capable of generating large webs. The choice of population dynamics seems to be important [20], with the simplest types of population dynamics, such as Lotka-Volterra, being unable to lead to communities with large stable webs. A disadvantage of evolutionary models is that it is not clear what community is being constructed; it seems to be one in which immigration has
played no part. A more consistent viewpoint would be to use the community constructed through the evolutionary approach as a species pool in the sense of the assembly model, and then use these co-evolved species to create food webs which would be more analogous to those for which data is collected. This will be the point of view we adopt here.

The idea of using a pool of species as a source of immigrants for colonisation goes back many years and was the central feature of the theory of island biogeography developed in the 1960s \cite{21, 22, 23, 24, 25}. There the pool was called the "mainland" and the community of interest the "island", and this is the terminology we will adopt here. That theory was an equilibrium theory; it assumed that immigration and local extinctions were in balance, although with continual overturn of species. Although there have been calls for this theory to be updated and extended \cite{26, 27}, there has been little work trying to do so using recent developments in modelling tools and techniques. A notable exception is the work of Hubbell \cite{28} which uses the mainland/island picture to formulate a neutral theory of biogeography and biodiversity. One way to view the work we describe here is as a generalisation of these ideas to predator-prey interactions, incorporating many other aspects and leading to food webs with several trophic levels.

In the following section we reiterate the Webworld mathematical model presented in \cite{14}, which was used to generate the simulation results presented in this paper. In previous papers \cite{15, 29} this model has been used to construct food webs through evolution of the species present. We discuss the modifications used to study the effect of food web construction through immigration. In our main results section we examine typical measures of food webs structure in terms of the resources available to the system, and in terms of the number of species present. We then focus on the species-area relation as a composite measure of food web behaviour, and examine our results in terms of power-law fitting. We conclude with a discussion of the results we have obtained and possible directions for future work.

## II. MODEL

The Webworld model was introduced by \cite{14} to link ecological modelling of food web structure with evolutionary dynamics of species creation. A refinement to the population dynamics was introduced by \cite{15}, and it is this model, described in detail below, which we adopt. The long-term behaviour of the model, identified by \cite{15}, is for a continual overturn of species to occur with relatively well defined mean values of such quantities as the number of species present.

The Webworld model constructs food webs from species defined by a set, $A$, of ten different attributes which represent phenotypic and behavioural characteristics pertaining to survival. Initially an antisymmetric matrix $m$ is randomly generated to indicate the relative score of pairs of attributes; the relative score of two species is defined by

$$S_{ij} = \frac{1}{L} \max \left( 0, \sum_{\alpha \in A_i} \sum_{\beta \in A_j} m_{\alpha \beta} \right),$$  \hspace{1cm} (1)$$

where $L = 10$ is chosen to give scores $S_{ij} \sim 1$. If $S_{ij} > 0$ then species $i$ is capable of feeding on species $j$. The utility of this system of defining species is that incremental evolution can occur by changing one attribute of a member of a selected species to form a new species, whose scores will be similar to those of the parent species. Species are numbered such that $1 \leq i \leq S$, where $S$ is the number of species present. Each species has population $N_i$ subject to the population dynamics. One special species is created, denoted as species zero, whose population is fixed at $N_0 = R$. This species represents the environment, the basic food source supplying the whole food web. The value $R$ is the effective population of the environmental resources, which provides a persistent food source for the food web as a whole. A value of $R = 10^6$ was chosen to grow a source community with approximately 100 species, and hence this value of $R$ is an approximate upper bound for models utilising this source community. The maximum value of $R$ used for evolving communities was prescribed by computational resources.

In the evolutionary model, the first species is created with a random set of attributes such that its score against the environment species is non-zero. Were this not the case, the first species would go extinct, being unable to feed. Subsequent species are introduced by taking one extant species as the parent, and altering one attribute to create a daughter species of population 1. No attribute is allowed to repeat within a single species. The food web is constructed by repetition of this speciation mechanism, with extinctions determined by the population dynamics described below. The decision to introduce new species with population 1 is arbitrary except that this is the smallest population which does not lead to immediate extinction.

The population dynamics is described by a balance equation for the numerical gains and losses of each species. This is written as

$$\dot{N}_i = \lambda \sum_j g_{ij}N_j - \sum_j g_{ji}N_j - dN_i,$$  \hspace{1cm} (2)$$

where the three terms on the right-hand side correspond respectively to gains from foraging, losses to predation, and losses to natural death. The factor $\lambda$ between losses to a prey species and gains to its predator reflects the ecological efficiency of the system, and we adopt a value of $\lambda = 0.1$ consistent with empirical data \cite[e.g.][]{30}. We assign the scaling factor of natural death, $d$, to be unity for all species, thus fixing the time-scale of the model. The remaining term, $g_{ij}$, comprises the functional response. We adopt a ratio-dependent functional response that relates to a foraging strategy; $f_{ij}$ is the fractional effort...
species $i$ puts into potential prey $j$, where $\sum_j f_{ij} = 1$. The functional response is given by

$$g_{ij} = \frac{f_{ij}S_{ij}N_j}{bN_j + \sum_k \alpha_{ik}f_{kj}S_{kj}N_k}, \quad (3)$$

for very small predator populations this is approximately

$$g_{ij} = \frac{f_{ij}S_{ij}}{b}, \quad (4)$$

so $b$ can be seen to restrict the feeding rate with high prey availability. A value of $b = 0.005$ has been adopted from [15], where it was found to give suitably realistic food webs. The sum in the denominator reflects the effect of competition. Competition is maximal between members of the same species, for which $\alpha_{ii} = 1$ for all $i$. Competition with other species is weaker, indicating the greater ability to extract resources from a prey species given by a diversity of feeding techniques. The formula for $\alpha$ we also adopt from [15] as

$$\alpha_{ik} = c + (1-c)q_{ik}, \quad (5)$$

where $q_{ik}$ is the fraction of attributes shared by $i$ and $k$. It can therefore be seen that $\alpha$ has a minimum value of $c$ for two dissimilar species; we adopt the value of $c = 0.5$, which has been shown to produce reasonable food webs. [15] show that there exists an evolutionarily stable strategy for $f$ given by

$$f_{ij} = \frac{g_{ij}}{\sum_k g_{ik}}, \quad (6)$$

which we therefore take to yield the strategy for each species at all times.

To maintain a limited size community, and in particular to give meaning to the system size parameter $R$, species are removed from the community if their population falls below unity. From [8] it can be seen that all values of $g_{ij}$ are unchanged if all populations $N_i$ are changed by the same factor. As such, if all $N_i$ are zero, [2] shows that this will still be the case after scaling all $N_i$. Hence all dynamics of the food web are unchanged if both $R$ and the extinction threshold are scaled by the same factor, and the arbitrary choice of unity population for extinction is of no consequence. In the absence of a non-zero extinction threshold no extinctions ever occur, since populations will at worst exponentially decay towards zero.

### A. Comparative models

The source community, from which species are drawn for immigration into island communities, was built using the model described above, with $R = 10^6$. At the time at which the evolution run was stopped, after 50 000 evolutionary events, 103 species were present, and the food web was in a steady state configuration where the number of species does not change systematically over long time intervals. The exact number of species would change on short timescales as evolution and extinction events balance only on average. This size of web was chosen to give a reasonably large set of species for immigration without taking excessive computational time to reach the steady state.

To construct an island community, the model was initialised with the same matrix $m$ and environment species as the source community, but a value of $R$ that was in general different. Species were introduced from the source community in a random order; the speciation mechanism by which new species are introduced in the mainland model is not used, so the number of species that can co-exist on any island is limited by the number of species in the source community. The parameter $R$ was used as the independent variable to investigate the effect of resource availability on the nature of the food web constructed.

For comparison with the effects of $R$ on the nature of the food web constructed through immigration, mainlands were created for a range of values of $R$ by the same process as the source community, using the same matrix $m$ and environment species. Different mainlands were isolated in the sense that the species subject to population dynamics were unrelated between mainland instances.

A second line of comparison comes from taking the source community and performing population dynamics

| Name                  | Symbol | Definition                  |
|-----------------------|--------|----------------------------|
| number of species     | $S$    | $\sum_i 1$                 |
| population            | $N$    | $\sum_i N_i$               |
| abundance             | $p_i$  | $N_i / \sum_j N_j$         |
| Shannon index         | $H$    | $-\sum_i p_i \ln p_i$      |
| Simpson index         | $D$    | $\sum_i p_i^2$             |
| Fisher index          | $\alpha$ | $S = \alpha \ln (1 + N/\alpha)$ |
| Shannon equitability  | $E$    | $H / \ln S$                |
| trophic levels        | $\Lambda$ | $\max_i \Lambda_i$        |
| mean species level    | $\Lambda_S$ | $\sum_i \Lambda_i / S$    |
| mean individual level | $\Lambda_N$ | $\sum_i p_i \Lambda_i$    |
| links per species     | $l$    | $\sum_i l_i / S$           |

TABLE I: Summary of community measures used in this paper. Each species $i$ has population $N_i$, trophic level $\Lambda_i$, and $l_i$ links to other species, counting both predators and prey. A discussion of diversity measures can be found in [32], who denotes the Shannon index $H'$. Definitions of $H$ sometimes use $\log_{10}$ or $\log_2$, and hence will differ in their results by a constant factor.
while gradually reducing $R$ from its initial value. There is no stochasticity in the result since the population dynamics are deterministic and we are not introducing species, so a single sequence of webs is produced. We call this sequence the reduction sequence, and for any value of $R$ refer to the food web in the reduction sequence corresponding to resources $R$ as the reduced food web of $R$.

III. RESULTS

The results presented in this paper will cover only some of the aspects of food web examination, and in particular will concentrate on the variation with system size of measurements summarising food web characteristics. Equivalent figures are shown for measurements taken from each of the mainland, island and reduction versions of the model. Table I summarises the community measures used, where $N_i$ is the population of the $i$th species, $\Lambda_i$ is its trophic level, and $l_i$ is its total number of prey and predators.

A. Island food webs

In order to obtain meaningful averages over discretised quantities such as the number of trophic levels in a food web, the results plotted in figure 1 are the mean of measurements taken from 100 simulation runs. Continuously varying quantities, such as the total population of all species, were found to rapidly converge on this mean as the number of runs increased, implying a statistical similarity of the food webs generated. Results are shown for the range of resources $100 \leq R \leq 10^6$; the lower bound was chosen because typically only one or two species were found in the resultant food web, with very small total populations. The behaviour of food webs under formation as they approach the limit in which only one species is supported, and that near extinction, is of little interest; in any case a model using non-stochastic population dynamics is inappropriate in this regime. The upper limit of the resource range is determined by the number of species in the source community; as resources in the immigrant community increase, the number of species present approaches that of the source, and the other measured characteristics saturate also. Saturation also occurs in time, measured by the number of immigration events that have occurred, and the samples examined were taken after 500 immigration events. For the largest values of resources there was some systematic change at later times as the last few species were assimilated into the food web.

In figure 1a) we plot the simplest measure of success in assembling a food web from immigrant species, which is the number of those species simultaneously present at the moment of measurement. As $R$ increases, almost all species are able to invade the island, which suggests that the process of assembling a community in this way is quite efficient. A second simple feature to calculate from a known food web is the number of trophic levels, plotted in figure 1b). Here we use strictly defined trophic levels equivalent to counting the number of feeding links in the shortest route from each species to the environment on which all basal species feed. Thus all species feeding on the environment – basal species – are in trophic level 1, species which feed on basal species but not directly on the environment are in trophic level 2, and so forth. The number of trophic levels in any particular web is a measurement of the highest single species, and thus is an integer. The solid line in figure 1b) shows the mean value of this quantity over simulation runs, and hence is not necessarily integer. It can immediately be seen that the formation of food webs with multiple trophic levels does occur when species are supplied by immigration from a previously evolved food web. We note that the increase in the number of trophic levels with $R$ is not smooth, and that for certain ranges of resources, essentially all webs have the same number of trophic levels. For example, in

![FIG. 1: Food web measures taken from immigrant communities grown with various values of $R$. The three vertical bands correspond to ranges of $R$ where the number of trophic levels changes, influencing other measures. a) Number of species present, $S$; b) solid line – number of trophic levels, $\Lambda$; dashed lines – top, species average level, $\Lambda_S$, bottom, individual average level, $\Lambda_N$; dotted line – $\Lambda_N$ against right hand axis; c) Total population of all species, $N$, divided by $R$; d) solid line – fraction of basal species; dashed line – fraction of unpredated species; e) number of feeding links (in plus out) per species, $l$; f) solid line – Shannon index, $H$; dashed line – Fisher’s $\alpha$ index; g) solid line – Simpson’s $D$ index; dashed line – equitability, $E$.](image-url)
the range $200 < R < 2000$ the mean number of trophic levels is almost exactly 2, and a similar plateau occurs at a mean trophic level of 3. The transition from a single trophic level to two is particularly sharp, with the onset of higher trophic levels being spread over a larger range of resources. Vertical bands in figure 1 mark the periods of transition between trophic levels, and the first transition can be seen to correspond to a rapid increase in the number of species present. Examination of individual food webs suggests that this occurs when ‘herbivores’, which feed on the basal ‘plants’, enter the system. A herbivorous species reduces the success of the plants on which it feeds, which in turn allows other plants to compete for resources effectively. The Webworld model thus displays predator-mediated coexistence. For slightly larger $R$ figure 1k) shows a plateau in the number of species present before an approximately power law increase in $S(R)$ sets in.

Figure 1d) also plots, as dashed lines, the average trophic level. The upper dashed line indicates the mean trophic level of a species in the food web, which increases more smoothly than the number of trophic levels. A new trophic level is founded by a single species; as the population of the species on which it feeds increase, it becomes possible to support a greater number of species on the top level, and hence the mean trophic level increases while the number of distinct levels is constant. The lower dashed line indicates the mean trophic level of individuals in the food web, and is lower than the mean by species since the population of species tends to decrease with increasing trophic level. To examine this curve more closely it has been re-plotted as the dotted line against the right-hand axis. Here it can be seen that there is a maximum in this quantity immediately after the onset of the second trophic level. Thereafter the population of basal species increases more rapidly than for other trophic levels, and $\Lambda_N$ decreases asymptotically. This is related to the result plotted in figure 1e), which shows that after the onset of the second trophic level, the number of individuals summed over all species is nearly a constant fraction of $R$. Considering the case of a single species feeding on the environment, we can identify its population by setting the time derivative in (2) to zero and substituting $f = 1$ in (3). For a given value of $S$, this can be used to deduce the population of the species to be

$$\frac{N_{\text{basal}}}{R} = \lambda \left( \frac{1}{d} - \frac{b}{S} \right),$$  \hspace{1cm} (7)

and hence cannot exceed 0.1 for our value of $\lambda$. The larger value of $N/R$ seen at the left of figure 1b) corresponds to the presence of multiple basal species, where the reduced inter-specific competition allows a larger total population. The steady value of $N/R$ for multiple-trophic level webs seems to be an effect of food web regulation.

Figure 1f) shows the fraction of species that are basal (solid line), and the fraction that are unpredated (dashed line). The fraction of basal species falls steadily as resources increase and more species are able to find niches at higher trophic levels. The fraction of top species, i.e. those that are unpredated, has a remarkably different behaviour, dropping to an almost constant level as soon as trophic structure exists. As new species find a niche in the food web they have small population and are likely to be unpredated, but at the same time typically find that niche by feeding on a species that was previously unpredated. As $R$ increases, all species present typically increase in population, and at some point a top species becomes an exploitable prey. The fluctuations in the fraction of top species, $T$, suggest this quantity emerges from food web regulation, and we do not expect a simple explanation for structure in $T$ as a function of $R$.

Figure 1g) indicates that the complexity of the food web increases with increasing resources in terms of the number of feeding links associated with each species. To better interpret the structure in such plots we present, in figure 2 the same plots as in figure 1 but plotted against $S$. Features in the previously discussed quantities seem better understood in terms of resource availability, but figure 2l) suggests that the food webs produced by this model have a typical connectance increasing almost proportionally to log $S$. The connectance of these food webs decreases with $S$, but on average species become more

![Figure 2](image)
The remaining plots, figure 1f) and g), corresponding to figure 2e) and f) respectively, show measures of diversity in the food web. Diversity indices each summarise the species abundance distribution (SAD) of an ecosystem as a single number, and note that different indices will not provide consistent ranking among ecosystems because they each measure a different aspect of diversity. Where one food web is unambiguously more diverse than another we expect to see similar trends in each of the diversity indices, but differences between them are also expected, reflecting the changing SAD. The first diversity index we show is the commonly used Shannon index as determined from our simulations is $1 < H < 2.5$, indicating a lower diversity and/or equitability. For comparison we calculate $H$ from the data set for tree abundances on Barro Colorado Island (BCI), Panama in 2005 [33]. For the full set of 299 tree species with non-zero population, the Shannon index has a value of nearly 4. To match $H$ as determined from our simulation results, the abundance distribution must be truncated after 35 species. An important difference between the BCI data and our simulation results is that the former comprises a single trophic level. The food supply available to a ‘herbivore’ in our model is approximately the total population of all species, which figure 1c) shows to be approximately $0.08R$. We expect the herbivore population to be reduced by a corresponding factor. To model this, we sort the BCI data by abundance, and except for the first $x$ species reduce the abundance of each species by a factor of 0.08. For $x \approx 10$ we obtain $H \approx 2.5$. This is similar to our simulation results with a similar number of basal species. The sudden increase in $H$, and drop in the Simpson index $D$, during the formation of the second trophic level correspond to the increasing number of basal species which partition the total basal population. Further species additions tend to occur at higher trophic levels, and hence have a much smaller population, contributing diminishing amounts to the Shannon index as the total number of species increases. The form of the species abundance distribution (SAD), which is summarised by the diversity indices, will be examined in a future paper.

Fisher’s $\alpha$ diversity index [e.g. 32] is often favoured as a diversity index which does not depend on sample size [e.g. 34], being unaltered as increasingly rare species are sampled from an underlying distribution. The fact that $\alpha$ increases as a function of $R$ therefore indicates that the underlying distribution is changing; it is not an adequate description to suppose that the species present are those whose population in some static distribution lies above a threshold which decreases with increasing $R$.

FIG. 3: Food web measures taken from mainland communities grown with various values of $R$. The outer vertical bands correspond to the first two bands of figure 1; the middle band is described in the text. a–g) as figure 1. Marked points connected by dotted lines correspond to averages over ten runs; other data are averaged over 100 runs.

B. Mainland food webs

Whereas island communities reach a steady state after only a few hundred immigration events, tens of thousands of evolution events are required to reach the corresponding steady state; here we use results from runs of length 50,000 evolutions. As such the computational demands of mainland ecosystems are far greater than those of islands, and we have not been able to calculate statistical results for such a wide range of resources. A further factor increasing computational complexity is the fact that as $R$ becomes large there are more species on mainlands than on islands, where $S$ cannot exceed that of the source community. Averages in figure 3 are over one hundred runs for the solid lines, as with the island results, but are averages over only ten runs for the dotted lines corresponding to larger $R$. It was noticed that the results of averaging over even one hundred simulation runs were particularly poor in the range of resources marked by the central vertical band in figure 3, which manifests itself as a large variation in most quantities plotted within this range. This effect can be seen most clearly in figure 3g), the Simpson index $D$, which appears to be in transition between two values marked by dotted lines. The main cause of these fluctuations is related to the number of webs possessing different number of species, with $S$ for
an individual mainland web in the range $1 \leq S \lesssim 10$ for $R = 700$.

The most obvious difference between the results for a food web grown through evolution when compared to the island food webs is that there are no longer distinct boundaries corresponding to the onset of trophic levels. When plotted against boundaries corresponding to the onset of trophic levels, the island food webs is that there are no longer distinct food web grown through evolution when compared to $R \rightarrow \infty$. In the Webworld model is far larger at $\sim 60$. On the right vertical bands in figure 3 mark the onset of the second and third trophic levels respectively in island food webs, and mainland food webs do not begin to attain those levels until the right-hand edge of the corresponding band. We hypothesise that for small $R$, where island communities support more species than mainlands, the effect of species adapting to their predators and prey makes it more difficult to attain high trophic levels. Prey species in island communities cannot adapt to evade predators in our model, so predators can succeed more easily.

As remarked, for $R \lesssim 3000$ an island community supports more species than a mainland; the dashed line in figure 3a) repeats the curve for islands shown in figure 1b). As species evolve to become better at feeding on their prey and avoiding their predators, they tend to reduce the population of those species until they in turn evolve. As such, for small $R$ it is easier for one species to eliminate another from the food web, and the steady state number of species is smaller. As $R$ increases, the availability of new species to an island diminishes, whereas for a mainland the amount of novelty possible increases with $S$ leading to a potentially unbounded value of $S$ as $R \rightarrow \infty$. Certainly the total number of species possible in the Webworld model is far larger at $\sim 10^{20}$ (for the particular parameter values we have adopted here) than the number simultaneously present in any web created, and the dotted line in figure 3b) appears to continue the trend of an approximately power law increase in $S$ with $R$, $S \propto R^{0.63}$.

A striking difference between island and mainland food webs appears in the fraction of top species, shown in figure 3a) as the dashed line. For island food webs the fraction of top species is small and nearly constant for food webs of multiple trophic levels, whereas for mainland communities it decreases gradually toward zero from a higher starting point. This probably reflects the potential for new species to enter the food web specialising in previously unpredicted species, while in the island community species are constrained by their existing abilities. The fraction of basal species, shown as the solid line in the same plot, is somewhat higher in the mainland community, but with a similar trend to decrease with $R$. Examination of figure 3a) shows that for $S \lesssim 6$ island and mainland communities behave similarly, but for larger $S$ the fraction of basal species in island communities starts dropping more rapidly. This is not obviously associated with the number of trophic levels, which is not seen to increase significantly in figure 3a) for island food webs at $S \simeq 6$. Conversely it is at about $S \approx 6$ that the total population of island and mainland communities as a fraction of resources, shown in figure 2i), converge. For smaller $S$ island communities have a higher total population, and both settle to a similar value for larger $S$, with islands having slightly lower abundance.

In comparing the number of links per species between island and mainland food webs, it is found that the differences shown in figure 3b) are neither large nor systematic. As such it seems that the number of feeding links a species possesses is primarily dictated by the number of species in the ecosystem as a whole, with relatively minor contributions from probable influences such as the trophic structure and direct consequences of assembly. Diversity indices $H$ and $D$, shown in figures 2c) and 2d) respectively, also show a behaviour that is largely similar for island and mainland communities. There is an initial increase in diversity which is nearly linear in terms of $H$ versus log $S$, turning down for $S \gtrsim 20$. This later decrease in the derivative is probably related to the fact that species are increasingly added at higher trophic levels where the population is automatically smaller: $H$ is maximised by a uniform distribution. The strongest difference between the diversity of island and mainland communities occurs at $S \simeq 6$, where there is an anomalous excess in $H$ for islands. The maximum difference

![FIG. 4: Comparison of selected quantities between island and mainland food webs, as a function of $S$. Solid lines indicate mainland data and dotted lines island data repeated from figure 2. a) number of trophic levels, $\Lambda$; b) Total population of all species, $N$, divided by $R$; c) fraction of basal species; d) number of feeding links per species, $l$; e) Shannon index, $H$; f) Simpson’s $D$ index.](image-url)
coincides with the sharply emerging difference in the fraction of basal species shown in figure 4), and is presumably related. For \( H \) to be higher in island communities when most species are basal indicates that there is a more even distribution of population between those basal species. The rapid increase in the fraction of species on the second trophic level diminishes \( H \) by the previously noted effect of population decreasing with level, restoring equality between island and mainland food webs.

C. Reduction food web

The number of species in the single reduction process from the island source community necessarily starts at 103 for \( R = 10^6 \), corresponding to the source community itself. For this value of resources the island community does not generally reach the full compliment of species, and the mean value is considerably lower. As shown in figure 5a), as resources decrease species drop out of the reducing food web gradually rather than triggering catastrophic losses, and the number of species in the reducing food web is larger than the number in the immigrant community for all \( R \) despite the limitation that species cannot be reintroduced. The limitation that we have only one possible history to examine means that there is an integer number of trophic levels for all \( R \) in the reduction model (non-integer values plotted in figure 5b) lie between sample points), so plateaux are an inevitability. These plateaux roughly correspond to the ranges for which plateaux are seen in the corresponding results for island food webs, shown in figure 1b). Figure 5h) shows that the island communities tend to have more trophic levels for the number of species than the reduction model, although as mentioned they have fewer species for a given \( R \).

In general the trends seen in the reduction model are very similar to those seen in the island food webs. The fraction of basal species in the island and reduction webs approach each other for large \( S \); for small \( S \) this fraction tends to unity more rapidly as \( R \) decreases for the reduction model, possibly reflecting a tendency to preferentially remove non-basal species. The difference seems to relate to the trophic structure shown in figure 5b), and might be removed if reintroduction of species were allowed in the reduction model. Measurements of \( N \) and \( l \) shown in figures 6(a) and 6(f) respectively are less smooth for the reduction model due to the absence of averaging, but are otherwise consistent. The small increase in the Shannon index of the reduction model over islands, shown in figure 6b), is probably related to a preference for removing species of higher trophic level, thus making the average species more like a basal species in population and increasing uniformity. This increase in diversity is also shown in the Simpson index in figure 6f).

IV. SPECIES-AREA RELATION

One of the most studied features related to the effect of size on food web structure is the species-area relation (SAR), because this is relatively easy to sample for real systems. We model the SAR by equating area to resources, \( R \), with which we supply basal species, and examine the equilibrium number of species for food webs grown with different values of \( R \). Several distinct types of SAR can be formed depending on the sampling method; that applicable to our data was labelled as the Type IV species-area curve by 35, corresponding to sampling of physically distinct regions (islands or other isolated units) of differing area. 36 prefer to reserve the term "species-area curve" for just this case, but see 37 and 38 for further discussion. Although a monotonic increase in \( S \) with area is intuitive for any SAR, it is not a necessary consequence of the Type IV sampling method; large islands may in principle have fewer species than smaller islands.

Some of the effects found in real ecosystems which influence the shape of the SAR are not applicable to the data we collect on Webworld. In particular, 34 discusses three reasons to expect more species in a larger sample area. Firstly, a larger sample area may imply a larger number of collected individuals, giving a more complete sample. For Webworld we have complete population information at any time in the simulation, and in particular can distinguish with accuracy whether a
species is present or absent. The second effect relates to diversity of habitats; a larger area in a physical system is likely to contain heterogeneous regions to which different species are better adapted. The Webworld model has only a single habitat type independent of the ‘area’ we attribute to that system, and additional niches only arise through the existence of exploitable populations of other species. The third factor discussed in complicating SARs measured from real data is the existence of biogeographical provinces; a very large system may contain areas which could be occupied by the same set of species except for historical exclusion. Examples abound of apparently identical niches being filled by different species in isolated regions. Since the Webworld model we use is only implicitly spatial, no such geographical barriers exist to maintain diversity, and this explanation for an increase in species count with area can also be excluded.

[34] contests the findings of [39] that the number of species increases with area for a homogeneous environment, indicating that Fisher’s diversity index, $\alpha$, does not systematically depend on area for their samples. As shown in figures [1], [3] and [5], our results show a significant trend in $\alpha$ with area. We conclude that in our results the increase in species number with area is not merely due to changes in the cut-off population of otherwise similar distributions. For the smallest food webs this is particularly obvious in the food web structure, since the coexistence of basal species (‘plants’) is strongly promoted by the presence of a single ‘herbivorous’ species.

The method of immigration we have used in the context of the Webworld model is similar to the premise of the theory of island biogeography by [21]. However, the population dynamics in Webworld is deterministic, so between the introduction of species the population of each species settles to a steady value, and hence the rate of extinction becomes zero. As such, extinctions are related to the displacement of species by new arrivals rather than through fluctuations per se. It is still the case that those species driven extinct are those unable to adopt a feeding strategy that will support an equilibrium population above our extinction threshold.

In figure 7 we show log-log plots of the SAR of islands, mainland and the reduction sequence in a), b), and c) respectively; in [4] we plot for comparison against a linear y-axis (Gleason plot). In this case it can be seen that only for the reduction sequence is a linear regression a reasonable approximation across any of the range. For at least the island and mainland models, a power law fit to the data is acceptable for all $R$ greater than some threshold, indicated by arrows in figure 7. The behaviour of $S$ with area for small $R$ is discussed in the results section.

Power law indices for the immigration and reduction models are similar, whereas the evolution model has a rather steeper power law. [34] attributes the degree of fitting of observed SARs to the form $S = k_1 + k_2 \log A$ for constants $k_1$, $k_2$ and area $A$ to sampling effects in small food webs; [40] note that the SAR including large islands is only well fitted by a power law, despite their conclusion that a logarithmic increase is a better description overall.

The shape of the SAR identified by [41] is tri-phasic; $z$ is larger for both small and large areas than for the range of area between. Although we see anomalous behaviour for small areas in the Webworld results, we cannot associate a power law with these results since we do not see a straight line in the log-log plot. [42] collect examples of typical power law indices in their Table 1, which have the approximate range $0.15 \leq z \leq 0.5$, consistent with our results for the island and reduction models, which have $z = 0.39$ and $z = 0.36$ respectively. The power law index we find for the mainland model exceeds this range somewhat, at $z = 0.63$. [28] describes the part of the tri-phasic curve corresponding to the largest areas as the ‘continental’ scale, where diversity is attributable to evolutionary processes. Values for $z$ as high as unity are possible for intercontinental scales; $z = 1$ would be found if two sample areas of equal size and no overlap in species were considered. [34] cites examples of data from which species-area curves with $z = 1$ can be extracted, corresponding to large length scales.

A different context within which a high power law index $z$ is found for the species-area relation was identified by [43] who study the changing SAR during stages of succession on Mount St. Helens following volcanic sterilisation. [43] found that the power law index of the SAR decreased with time as species became re-established, and in their figure 2 present the SAR of Abraham Plains for 1988 in which $z = 0.69$. We hypothesise that the large value of $z$ we find for mainland data may be due to

![FIG. 6: Comparison of selected quantities between island food webs and the reduction sequence, as a function of $S$. Solid lines indicate reduction data and dotted lines island data repeated from figure 2. a–f) as figure 3.](image-url)
internal disruption caused to the food web structure by the overturn of species, noting that in small food webs one effect of this overturn is to remove specialised predators whose prey becomes replaced. A system in which evolution and immigration were both allowed to play a part would be expected to display a power law index intermediate between those found for our immigration and evolution models, and be consistent with the concept of lessened disruption.

V. DISCUSSION AND CONCLUSIONS

In this paper we make use of the Webworld model introduced by [14] and [15] to examine food web assembly through immigration. Previous work on this topic, in particular assembly models [6], have drawn immigrant species from a randomly assigned species pool, and as such their results may not reflect the properties of a natural ecosystem. Instead we create the species pool itself by evolution, and draw species from this stable community to construct ‘island’ food webs, where in this discussion we use the term ‘island’ to relate to ecosystems constructed solely by immigration. Food webs constructed solely through evolution in situ we designate ‘mainland’. In order to compare our results with measurements of real ecosystems we equate the resources supplying the Webworld model to physical area, noting that not being explicitly spatial, Webworld can only represent systems without geographical barriers.

It is of interest to study food webs assembled through immigration not only because these correspond to most of the real world ecosystems for which data is available, and especially to any experimental set-up which could be created, but also because from a modelling point of view the assembly of food webs through immigration is much more repeatable than the evolutionary scenario, in which the identity of the species is necessarily a chance occurrence. For each food web grown through evolution we can in shorter time examine the statistical properties of the family of island communities which can be grown from it.

One of the clearest differences between island and mainland food webs is the power law index of the species-area relation. For our islands we find this to be, at $z = 0.39$, within the range found for natural ecosystems, typically $0.2 \leq z \leq 0.4$. For our mainland results we find the steeper power law of 0.63, and note that a steeper power law in nature is associated with the very largest length scales, where evolution is more important than immigration due to the presence of substantial geographical barriers. It is difficult to obtain a species-area relation for real ecosystems in which only evolution played a role because these would need to correspond to regions sufficiently small to promote complete mixing and sufficiently remote to avoid immigration from a continent, yet numerous enough to provide good statistics for essentially similar environments. We note that a high power law may also be associated with a strongly perturbed system, e.g. [43], and that the continual turnover of species through evolution may provide such a disturbance.

A second significant difference between island and mainland food webs is found in the fraction of basal and of top species. For island food webs the fraction of top (unpredated) species does not change systematically over a large range of system size, or equivalently a function of the number of species. For mainlands with a large number of species ($S > 10$) there are far fewer top species than on islands. Conversely islands have a smaller fraction of basal species than mainlands in our results. Considering the progression of food webs from small area to large, we observe that islands show distinct plateaux in the number of trophic levels, with all islands having the same number of levels for large ranges of area. Mainland food webs may show a weaker tendency toward this phenomenon, but we cannot exclude a smooth increase in the mean number of levels with area across realisations.

Despite these important differences, much of the behaviour of the model is essentially similar whether immigration or evolution supplies the species. In particular the number of trophic levels is close for islands and mainlands of similar area, and the number of feeding links per species is also very similar, implying statistical similarities between the food webs constructed. Such similarities are reflected in the Shannon index of the system, which increases nearly linearly in $S$ for small food webs, with a

![FIG. 7: Species-area relations for the three model variants; a) immigration, b) evolution and c) reduction. Dotted lines mark power-law fits to data to the right of the corresponding arrow. Power law indices are 0.39, 0.63, and 0.36 respectively. d) Gleason plot of the above data. Solid line – reduction data and fit of data right of the arrow ($S = 35\log R - 112$); dotted line immigration; dashed line evolution.]
decrease in the gradient for $S > 10$. The Shannon index is associated with the distribution of population sizes, which we will examine in a future paper.

Several avenues of future work are suggested by the results we have found. We have performed preliminary work in which immigration takes place along a chain of islands, with immigration to one island only being possible from its predecessor in the chain. Our results to date suggest that this induces changes in the nature of the food webs several links down the chain, with a ‘filtering’ effect precluding the transmission of species which can be easily displaced. Similar scenarios reminiscent of real archipelagos may provide interesting comparison with real systems.

Another change to bring our model more into line with real systems would be to interpolate between the pure evolution and pure immigration models by allowing both to take place concurrently to different degrees. Of particular relevance is the case in which a small degree of evolution is allowed, to determine whether this has a significant effect on the island properties we have identified in this paper.

All of the islands for which results are presented in this paper were grown from a single source community. Beside confirming that the results are not significantly altered depending on the course community used, we are in principle able to examine the behaviour of an island where immigration occurs from two or more independent mainlands. A related complexification of the model which may relate to real ecosystems is to introduce multiple environment species to simulate the presence of different habitats. This work may require a spatially explicit model for which computational resources are not yet available.

Finally we note that one of the most important food web characteristics which we have not examined is the species abundance distribution (SAD). This is related to the various diversity measures in that they provide different scalar measures of this distribution. The species-area relation is also related to the dependence of the SAD on area. The examination of the SAD requires substantial detail, and our results for this will be presented in a future paper.

Acknowledgements

We wish to thank the EPSRC (UK) for funding under grant number GR/T11784.
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