



Comparison of food webs constructed by evolution and by immigration

Craig R. Powell*, Alan J. McKane

Theory Group, School of Physics and Astronomy, University of Manchester, Manchester M13 9PL, UK

ARTICLE INFO

Article history:

Received 19 February 2008
 Received in revised form 16 December 2008
 Accepted 5 January 2009
 Available online 11 February 2009

Keywords:

Species–area relation
 Food webs
 Trophic levels
 Individual-based model

ABSTRACT

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.

© 2009 Elsevier B.V. All rights reserved.

1. 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 (Cohen and Newman, 1985; Cohen, 1990) and niche (Williams and Martinez, 2000) models, and of the latter the work of May (1972, 1974). 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 (Law, 1999), and evolutionary models, which introduce new species through modification of existing species–speciation (Drossel and McKane, 2003). 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 specia-

tion (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 (Post and Pimm, 1983; Drake, 1988, 1990), although this had some problems (Morton et al., 1996), and other methods of deciding whether a particular community is stable have been used (Law and Morton, 1996; Morton and Law, 1997). Species assembly models are capable of generating reasonably sized food webs (Law, 1999) 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

* Corresponding author. Tel.: +44 161 2754192; fax: +44 161 3064303.
 E-mail address: craig.powell@manchester.ac.uk (C.R. Powell).

define phenotypic or behavioural characteristics (Caldarelli et al., 1998; Drossel et al., 2001; Yoshida, 2003; Rossberg et al., 2006), or the strength of interaction between species may be described through matrices (Lässig et al., 2001; Kondoh, 2003). Additional mechanisms, such as adaptive foraging, may be included and may add stability to the system (Kondoh, 2003). 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 (Drossel et al., 2004), 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 (Preston, 1962; MacArthur and Wilson, 1963, 1967; Simberloff, 1974; Pielou, 1979). 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 (Lomolino, 2000; Brown and Lomolino, 2000), 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 (2001) 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 Drossel et al. (2001), which was used to generate the simulation results presented in this paper. In previous papers (Drossel et al., 2001; Quince et al., 2005b) 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.

2. Model

The Webworld model was introduced by Caldarelli et al. (1998) to link ecological modelling of food web structure with evolutionary dynamics of species creation. A refinement to the population dynamics was introduced by Drossel et al. (2001), and it is this model, described in detail below, which we adopt. The long-term behaviour of the model, identified by Drossel et al. (2001), 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 anti-symmetric matrix m is randomly generated to indicate the relative score of pairs of attributes; the relative score of two species is defined by

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

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 environmental 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

$$\dot{N}_i = \lambda \sum_j g_{ij} N_j - \sum_j g_{ji} N_j - d N_i, \quad (2)$$

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 λ 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 (e.g. Pimm, 1982). 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

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

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 Drossel et al. (2001), 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

Download English Version:

<https://daneshyari.com/en/article/4372755>

Download Persian Version:

<https://daneshyari.com/article/4372755>

[Daneshyari.com](https://daneshyari.com)