We study the evolution of the network properties of a populated network embedded in a genotype space characterised by either a low or a high number of potential links, with particular emphasis on the connectivity and clustering. Evolution produces two distinct types of network. When a specific genotype is only able to influence a few other genotypes, the ecology consists of separate non-interacting clusters in genotype space. When different types may influence a large number of other sites, the network becomes one large interconnected cluster. The distribution of interaction strengths — but not the number of connections — changes significantly with time. We find that the species abundance is only realistic for a high level of species connectivity. This suggests that real ecosystems form one interconnected whole in which selection leads to stronger interactions between the different types. Analogies with niche and neutral theory are also considered.

Keywords: ecosystems; networks; species abundance distribution; neutral and niche theory; evolution and self-organisation.

1 INTRODUCTION

An important characteristic of an ecosystem is the total set of interactions between the various individuals. Organisms may influence each other in many ways and it is difficult to monitor and quantify all possible interactions except the most direct, such as simple trophic relations. The development of the set of interactions over evolutionary time scales is even more difficult to measure because of random mutations and the resulting adaptations. Gaining an understanding from observations is also problematic since laws may very well only be recognisable at the level of averages, see Loreau and Hector, 2001, Yedid and Bell, 2002. Here, we approach these issues within the framework of a simple model of ecosystem assembly and evolution Christensen et al., 2002, Hall et al., 2002, di Collobiano et al., 2003.

We compare early and late time connectivity and cluster properties of ecosystems evolving in two differently connected spaces: genotypes influence either a small or a large number of others. Clearly, the actual number of interactions experienced by a site depends on which of all the possible mutations and adaptations have occurred, i.e. the network is dependent on its history. It turns out that the interaction strengths change significantly with time, whilst the degree (number of active interactions) distribution remains close to what would
be expected if genotypes were occupied at random. The species abundance curve takes a log-normal form only for spaces where the genotypes are linked to many others. Our model is neutral in some aspects but also draws on concepts from niche theory.

2 METHODS

We briefly describe the structure and dynamics of the TangledNature model. Details can be found in [Christensen et al., 2002, Hall et al., 2002]. An individual is represented by a vector $S^\alpha = (S_1^\alpha, S_2^\alpha, \ldots, S_L^\alpha)$ in the genotype space $S$, where the “genes” $S_i^\alpha$ may take the values $\pm 1$, i.e. $S^\alpha$ denotes a corner of the $L$-dimensional hypercube. In the present paper we take $L = 20$. We think of the genotype space $S$ as containing all possible ways of combining the genes into genome sequences. Many sequences may not correspond to viable organisms. The viability of a genotype is determined by the evolutionary dynamics. All possible sequences are made available for evolution to select from. The number of occupied sites is referred to as the diversity.

For simplicity, an individual is removed from the system with a constant probability $p_{\text{kill}}$ per time step. A time step consists of one annihilation attempt followed by one reproduction attempt. One generation consists of $N(t)/p_{\text{kill}}$ time steps, which is the average time taken to kill all currently living individuals. All references to time will be in units of generational time.

The ability of an individual to reproduce is controlled by a weight function $H(S^\alpha, t)$:

$$H(S^\alpha, t) = \frac{1}{cN(t)} \left( \sum_{S \in S} J(S^\alpha, S)n(S, t) \right) - \mu N(t),$$

where $c$ is a control parameter, $N(t)$ is the total number of individuals at time $t$, the sum is over the $2^L$ locations in $S$ and $n(S, t)$ is the number of individuals (or occupancy) at position $S$. Two positions $S^a$ and $S^b$ in genome space are coupled with the fixed random strength $J^{ab} = J(S^a, S^b)$ which can be either positive, negative or zero. This link is non-zero with probability $\theta$. There is no self-interaction, so $J^{aa} = 0$. The present paper compares the three cases $\theta = \frac{1}{1000}$, $\theta = \frac{1}{200}$ and $\theta = \frac{1}{4}$. The non-zero values of $J^{ab} \neq J^{ba}$ are determined by a deterministic but rapidly varying function of the two positions $S^a$ and $S^b$ [Hall et al., 2002].

The conditions of the physical environment are simplistically described by the term $\mu N(t)$ in equation (1), where $\mu$ determines the average sustainable total population size, i.e. the carrying capacity of the environment. An increase in $\mu$ corresponds to harsher physical conditions. Notice that genotypes only adapt to each other and the physical environment represented by $\mu$. We use asexual reproduction consisting of one individual being replaced by two copies. Successful reproduction occurs with a probability per unit time given by

$$p_{\text{off}}(S^\alpha, t) = \frac{\exp[H(S^\alpha, t)]}{1 + \exp[H(S^\alpha, t)]} \in [0, 1].$$

We allow for mutations in the following way: with probability $p_{\text{mut}}$ per gene we perform a change of sign $S_i^\alpha \rightarrow -S_i^\alpha$, during reproduction.

Initially, we place $N(0) = 500$ individuals at randomly chosen positions. Their initial location in genotype space does not affect the dynamics. A two-phase switching dynamic is seen consisting of long periods of relatively stable configurations (quasi-Evolutionary Stable Strategies or q-ESSs) interrupted by brief spells of reorganisation of occupancy which are terminated when a new q-ESS is found, as discussed in [Christensen et al., 2002].
3 RESULTS

a Parameters

As mentioned previously, the only parameter that is changed in this paper is the connectivity, $\theta$. The values used throughout are $L = 20$, $c = 0.005$, $\mu = 0.01$, $p_{kill} = 0.2$ and $p_{mut} = 0.015$. This selection provides several transitions between different q-ESSs for each run, see [Hall et al., 2002; di Collobiano et al., 2003]. We consider three $\theta$ values: 0.001, 0.005 and 0.25, which we will refer to as very low, low and high $\theta$ respectively. These correspond to below, near and above the percolation threshold. That is, the point where there is a non-zero probability that all living sites are connected in one dominant cluster [Albert and Barabási, 2002]. A realistic species abundance curve was only obtained above the threshold. We will be contrasting results at $t = 500$ (primal time), $t = 5000$ (early time) and $t = 500000$ (late time). Early time is well outside the system’s initial transient search for a quasi-stable configuration in genotype space. The low and high $\theta$ ensembles consist of 500 realisations. Each run uses a different random number seed but, for any given run, only $\theta$ is changed between the two ensembles.

Each figure in the paper, apart from figure 4, shows two sets of data: one labelled simulation (which are the results generated by the dynamics of the model) and the other random. In the random case, rather than evolving the network, for any specified time we read in the diversity and number of individuals alive in the simulated run. The individuals are then thrown on to the network of $2^{20}$ genotypes at random with the constraint that the diversity is the same as the simulation. Thus, random data is not dependent on the history of the network, but has the same global properties (diversity and population size) as the simulations. This provides a very useful null model. Comparisons with this procedure will reveal whether the network is really evolving, or the results are just by-products of increasing diversity. Simulated data is always shown as a dotted line and random as a continuous line.

b Connectivity

We study the temporal evolution of the network connectivity in the space of occupied positions for different $\theta$ values. Note that the hard-wired configuration of couplings $J(S^a, S^b)$ between all $2^{20}$ positions in genotype space is determined at $t = 0$ and remains constant. The network of occupied sites will nevertheless change with time. The degree distributions in figure 4 show the number of genotypes having $x$ active interactions.

The leftmost pair of curves represents primal time, the next, early time and the rightmost late time. Considering only the simulation data for now, a clear shift to a greater number of active links is seen in the high $\theta$ case, whilst a slight change occurs for low $\theta$. The difference between early and late time is bigger than that between early and primal time. The degree of a site is equal to the number of direct interactions it has with all other occupied sites. This explains why any particular site in the low $\theta$ runs only has at most nine and usually only one or two direct interactions. The data is integrated over each ensemble. How much of this shift is due to a genuine change in network connectivity? For high $\theta$, the null model data shows that there is very little difference between evolving the network and throwing down individuals randomly. Low $\theta$ appears to show a change. However, any site that does not interact with any others will die very quickly in a simulation. If for any instant in time genotype positions are chosen by chance, such a low connectivity will give a disproportionate
number of isolated genomes that would be forbidden by the dynamics. There is no fair way to simulate this effect, but it can be seen that the differences between the time curves in the random and simulated runs is similar and thus the network connectivity does not evolve for either value of $\theta$.

c  Interaction strength

For both $\theta$ values, the diversity gradually increases with time. What is causing this? It turns out that the strength of the interaction between sites is crucial to the ability of the network to support larger numbers of individuals. Figure 2 shows the distribution of interaction strengths between each living site and all other living sites at a given time. Interaction strengths are assigned at random and are not necessarily symmetric [Hall et al., 2002]. For example, $J(S^{18}, S^{59}) = 0.3$, but $J(S^{59}, S^{18}) = -0.2$. For all times and both values of $\theta$, the distribution for the random data is a sharply pointed, symmetrical curve peaking at $J = 0$. This makes sense because there is no bias in the ratio of positive to negative links when the links are assigned to the “bare” network at $t = 0$.

For reasons of clarity, the simulation results are only shown for primal and late time. Clearly, a significant change takes place for high $\theta$ between $t = 0$ and primal time. Some weight is taken in the fall of the peak at $J = 0$ and the drop in negative $J$ values, and redistributed into positive strengths i.e. the curve shifts right. This comprises a significant shift in the probability density. The move from primal to late time is smaller — but still noticeable — since the large number of reorganisations of genotype space in the early generations drops to occasional punctuation of q-ESSs later in the run. (Typically, there are only one or two transitions from early time onwards.) Despite this, the curve continues to drift to the right. On first inspection, the low $\theta$ runs seem to have changed dramatically from the initial configuration. However, nothing particularly interesting is happening here: it is simply an effect of the structure of clusters in the low $\theta$ space and is explained below.

d  Clustering

The indirect connectivity or clustering (how sites are linked to each other through other sites) is another useful network measure. For high $\theta$ we find that at any given time, all occupied sites in genotype space belong to one and the same cluster. Thus the cluster size for high $\theta$ simply follows the diversity. In contrast, we observe the formation of distinct clusters for low $\theta$. The rest of this section will deal solely with low $\theta$.

The overall structure of the clusters does not seem to change much with time. This is the first indication that the clustering is not an evolving property of the network. As would be expected, one-clusters are transient. They are born on a new site as mutants from a parent but are isolated from other sites and so are extremely unlikely to reproduce. (Since $\mu = 0.01$ and the average total population is about 2700, $p_{off} \approx 10^{-12} \ll p_{kill} = 0.2$ so an isolated site is much more likely to be killed than multiply when chosen.) These sites are simply flashing in and out of existence.

Simulations indicate that the building blocks of larger groups are two-clusters. These tend to be two very old sites that have mutually positive links. Large clusters are formed mainly from very old two-clusters joined together by a mutant. The continual background of mutants flitting in and out of the network plugs these building blocks together. However, the
entire cluster is rarely long lived, whereas the two-clusters are formed early in any particular run, quickly build up their population and are very persistent since their occupation is high.

Clusters do indeed generally increase in size with time. There are, however, large fluctuations in the record size which gives an indication of how unstable these large clusters are, see figure 3. The largest recorded cluster in any run at any time contained 281 sites. It is revealing to compare the results from the null model, where the maximum cluster size is much smaller but just as variable. When individuals are thrown down at random, two-clusters are no longer the building blocks of the large clusters and any long string of connected sites is determined purely by chance and hence the biggest cluster will always be smaller than that produced by the dynamics. The temporary nature of the large clusters is further borne out by time and ensemble averaging the cluster sizes. The number of clusters of a particular size $S$ is stored at intervals of 5000 generations from early to late time for each of the 500 runs and the time and ensemble average is then calculated. As expected, there are many one-clusters and fewer large clusters.

The distribution follows the functional form $n_s \sim s^{-5/2}e^{-(p-p_c)^2}e^{-2s}$ anticipated for the cluster size distribution on a random graph of $D (\approx 195)$ nodes. (See equation (36) in [Albert and Barabási, 2002].) The percolation threshold $\theta_D$ is very close to the considered connectivity $\theta = 0.005$. A comparison with the random data shows that this scale-independent distribution is not due to the dynamics of the system, the only difference being the appearance of larger record clusters in the simulation, as shown in figure 3. This is perhaps the most compelling piece of evidence that the low $\theta$ regime does not show any emergent structure. We also ran simulations for very low $\theta$ ($0.001$) and found that the cluster sizes were exponentially distributed as would be expected below the percolation threshold.

Figure 2 (low $\theta$) can now be easily explained. Unconnected sites die extremely quickly in the first few generations leaving behind two-clusters and other sites with positive interactions. The slight increase in sites with $J > 0$ for late time is caused by well established positive-positive two-clusters. So what looked like an interesting result initially proves to be due to the fairly constant microscopic structure of the network.

e Species abundance

The Species Abundance Distribution or SAD is important in characterising ecosystems. It is the proportion of species that contain $\rho$ individuals. We define a species as one site in genotype space. Ideally, we would like to use a coarse-grained definition more likely to reflect real ecologies, where species are defined as groups of points in genotype space echoing the genotypic cluster species definition introduced by Mallet [Mallet, 1995]. Since the maximum number of genotypes in our model is only around $10^6$ anyway, the single site species approach is more appropriate. We have been able to extend the initial results obtained in [Hall et al., 2002] and can consider the evolution of the SAD for high and low $\theta$ integrated across all 500 runs, as seen in figure 4. The larger ensembles allow enough statistics for illuminating conclusions to be drawn. Note that the null model is absent since when individuals are sprinkled randomly across the living sites, there is no tendency for accumulation on any particular site, so the individuals follow a multinomial distribution.

The key result of this paper is that only high $\theta$ leads to a SAD similar to those observed in nature. Low $\theta$ is skewed by its heavily populated two-clusters. The plots for high $\theta$ show the log-normal form observed in many real ecosystems and in other ecological models,
They appear to become more log-normal as time increases with the dip between four and eight individuals falling, even though the diversity is rising. Hence, the SAD is evolving. From this, it seems that the high $\theta$ case structures itself more like a real ecosystem than low $\theta$, whose SAD develops a sharper peak as the two-clusters become densely occupied. The single cluster of highly interdependent genomes produces a reasonable SAD that cannot be formed by patches of isolated clusters.

Thus the abstract parameter $\theta$, which cannot be measured in a simple way in real systems, is directly linked to the easily observed SAD. We recall that low values of $\theta$ correspond to a world in which different species, or types, are able to influence only a small number of other species. High values of $\theta$ correspond to the situation where different types may have an impact on the vitality of a large number of other species.

The initial descent in both curves from the global peak at $\rho = 1$ is due to the large number of sites with only one occupant. In nature, sampling difficulties would mean that these sites would not be detected so this first aspect is not seen in observed SADs. (It is particularly marked for our model since we use each site as one species and do not coarse-grain.) But the second peak does correspond well to results from the field, though it should be pointed out that the proportion of all sites with more than two individuals is only about 30% in each case. However, this is sufficient to detect the evolution of the SAD.

We note that a recent study of a simplified version of the Tangled Nature model by Rikvold and Zia found no temporal evolution of the statistics of the model. The reason for this may be that they use a relatively short genome length $L = 13$ together with a very substantial simulation time of order $10^7$ generations. We have observed previously that the time to reach a stationary state explodes with genome length [Christensen et al., 2002].

Neutral and niche theory

There has recently been much interest in the neutral theory of biodiversity [Hubbell, 2001]. Despite making assumptions that are anathema to traditional niche models (all individuals are the same and adaptations to specific environmental niches are essentially unimportant) it has been successful in making predictions about real world ecology — although its effectiveness in modelling the species abundance has recently been called into question [McGill, 2003].

At $t = 0$, the Tangled Nature model is neutral as all individuals are the same. However, the dynamics immediately breaks this neutrality as configurations are spontaneously generated. Once individuals become differentiated, interactions matter and the evolution is better described by niche-theory — although $\mu$ and $p_{\text{kill}}$ remain neutral. Unlike the models in [Hubbell, 2001], we have no spatial aspect: we deal with only one large metacommunity as opposed to many local communities aggregating to form the metacommunity.

The only measure in our model considered by the neutral theory is the species abundance, which we find takes an approximate log-normal form. The shape predicted by neutrality, the zero-sum multinomial (ZSM) distribution, is quite similar to the log-normal except that the ZSM has a long right tail and is much harder to calculate [McGill, 2003]. To detect whether our distributions are closer to the ZSM or the log-normal would be computationally prohibitive as the genome length $L$ would need to be much larger. Perhaps in the future, models like Tangled Nature could be used to investigate the relative importance of niche and neutral effects.
Discussion

Our most important results are that temporal evolution of the network properties of an ecosystem and a realistic form for the species abundance are only seen if the genotype space is well connected. This is interpreted here as meaning that an occupied genotype is likely to interact with many other (potentially occupied) genotypes. No evolution at the level of ecosystems can occur in a world where most possible genotypes are inert, i.e. whether they are present or not will have very little influence on other organisms. It is easy to overlook the importance of the entire network of interactions when dealing with small communities of organisms on a macroscopic scale, but easier to visualise with colonies of billions of bacteria.

We suggest that this observation can be used to gain insight into the potential underlying connectivity between biota. Imagine two microbial evolution experiments. In one case, the microbial ecosystem evolves towards an interwoven or entangled ecology. In the other, little evolution is observed in the structure of the ecological properties of the microbial community. One might, according to the result from our model, anticipate that the first system consists of microbes from a part of genotype space in which types influence each other, whereas the second system consists of genotypes from a region of space consisting of mainly inert organisms.

From our results, it is tempting to speculate that the observed degree of diversity, complexity and adaptation of living matter may be directly related to a high level of interdependence between organisms. Thus Darwin’s entangled bank may be a useful image to keep in mind when studying the evolution of large collections of individuals.

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References

[Albert and Barabási, 2002] Albert, R. and Barabási, A.-L. (2002). Statistical mechanics of complex networks. Reviews of Modern Physics, 74:47–97.

[Bell, 2001] Bell, G. (2001). Neutral Macroecology. Science, 293:2413–2418.

[Christensen et al., 2002] Christensen, K., di Collobiano, S. A., Hall, M., and Jensen, H. J. (2002). Tangled Nature: A Model of Evolutionary Ecology. J. theor. Biol., 216:73–84.

[di Collobiano et al., 2003] di Collobiano, S. A., Christensen, K., and Jensen, H. J. (2003). The tangled nature model as an evolving quasi-species model. J. Phys. A: Math. Gen., 36:883–891.

[Hall et al., 2002] Hall, M., Christensen, K., di Collobiano, S. A., and Jensen, H. J. (2002). Time-dependent extinction rate and species abundance in a tangled-nature model of biological evolution. Phys. Rev. E, 66(011904):1–10.
[Hubbell, 2001] Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

[Loreau and Hector, 2001] Loreau, M. and Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412:72–76.

[Mallet, 1995] Mallet, J. (1995). A species definition for the Modern Synthesis. *Trends Ecol. Evol.*, 10(7):294–299.

[McGill, 2003] McGill, B. J. (2003). A test of the unified theory of biodiversity. *Nature*, 422:881–885.

[McKane et al., 2000] McKane, A., Alonso, D., and Solé, R. V. (2000). Mean-field stochastic theory for species-rich assembled communities. *Phys. Rev. E*, 62(6):8466–8484.

[Rikvold and Zia, 2003] Rikvold, P. and Zia, R. (2003). Flicker noise in a model of co-evolving biological populations. In Landau, D., Lewis, S., and Schütter, H.-B., editors, *Computer Simulation Studies in Condensed Matter Physics XVI*. Springer-Verlag, Berlin. e-print: arXiv:nlin.AO/0303010.

[Yedid and Bell, 2002] Yedid, G. and Bell, G. (2002). Macroevolution simulated with autonomously replicating computer programs. *Nature*, 420:810–812.
Figure 1: Top: Degree histogram for $\theta = 0.005$. Bottom: $\theta = 0.25$. Solid lines, random; dotted lines, simulation. From the left, the pairs of curves are for $t=500, 5000$ and $500000$. At later times, the number of active links increases for both the simulation and random data.
Figure 2: Top: Distribution of interaction strengths between individuals for $\theta = 0.005$. Bottom: $\theta = 0.25$. Inset: Entire distribution. Solid lines, random; crosses, simulation at $t=500$; dotted lines, simulation at $t=500000$. All plots are normalised so that their area is one. For high $\theta$, a significant increase in positive interactions is seen. For low $\theta$, a change is seen but for trivial reasons.
Figure 3: Maximum cluster size across all realisations for $\theta = 0.005$. Solid line, random; dotted line, simulation. Clusters produced by the simulation are larger than those produced in a history-independent network.
Figure 4: Species abundance functions for the simulations only. Dashed line, $t=500$; dashed-dotted line, $t=5000$; solid line, $t=500000$. Low $\theta$ on the left, high $\theta$ on the right. The ecologically realistic log-normal form is only seen for high $\theta$. 