Diversity as a product of inter-specific interactions

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Abstract

We demonstrate diversification rather than optimization for highly interacting organisms in a well-mixed biological system by means of a simple model of coevolution. We find the cause to be the complex network of interactions formed, allowing species that are less well adapted to an environment to succeed, instead of the 'best' species. This diversification can be considered as the construction of many coevolutionary niches by the network of interactions between species. The model predictions are discussed in relation to experimental work on dense communities of the bacteria *Escherichia coli*, which may coexist with their own mutants under certain conditions. We find that diversification only occurs above a certain threshold interaction strength, below which competitive exclusion occurs.
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1. Introduction

Understanding how diversity arises through evolution and is sustained in an ecosystem is an important issue. One of the key questions therein is whether interactions between organisms enhance or suppress diversity. If there is no explicit symbiotic interaction, it would be expected that the competition for a given resource leads to exclusion of many types. This results in monodominance, i.e. the survival of the fittest, as determined by Gause's competitive exclusion principle (Gause, 1934). In contrast, in the presence of strong interactions, diversification has been shown to occur both in numerous models and in experiment (Helling et al., 1987; Czárán et al., 2002). We attempt to understand the relationship between interaction and diversity at a general level, and will relate our work to experimental findings on evolution in *Escherichia coli* (Kashiwagi et al., 2001).

We show that the diversification can indeed be facilitated by the interaction, using a range of different fitness concepts. We do this by adopting a slightly modified version of the Tangled Nature (TaNa) model (Christensen et al., 2002; di Collobiano et al., 2003; Hall et al., 2002). In addition to the standard inter-specific interaction in the TaNa model, we allow types to differ in 'intrinsic fitness'—the fitness of a type in the environment, in the absence of other types. A self-supporting, dominant genotype may coexist with, or be displaced by, a number of other genotypes that are less efficient competitors for the resource individually, provided that strong enough interactions are permitted. Diversity is maintained via the complex network of interactions, and we demonstrate a cutoff interaction strength below which monodominance persists. We split the 'intrinsic fitness' of a type into *density dependent* (i.e. the interaction with own type) and *density independent* parts, and study them separately. The conditions on the interaction strength are, respectively: (1) the net positive interaction with *other* types is greater than the *density-dependent* fitness, (2) the net positive interaction with other types is greater than the *density-independent* fitness *difference* between types.

The idea that diverse states can be supported by interaction is not new. Gause's competitive exclusion principle states, in the general case (Dieckmann et al., 2003), that 'the dimension of the environmental interaction variable is an upper bound for the number of species that can generically exist at steady state'. Although

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environmental interactions cannot in general be uniquely identified, and so this dimension is not known, it is still possible to support high diversities robustly (Tokita and Yasutomi, 2003; Meszéna et al., 2006) (i.e. still supported with a small change in the environmental parameters). This diversity remains finite even in the case of an infinite environment interaction variable (Gyllenberg, 2005), as species must be 'different enough' (MacArthur and Levins, 1967) to coexist stably. In addition, a greater number of species than environmental factors may be supported by oscillations or chaos, e.g. Vandermeer et al. (2002), Huisman and Weissing (1999), and Kaneko and Ikegami (1992). The appearance of diversity in a system with strong interaction is therefore not a surprise by itself, as each interaction contributes to the effective dimensionality. Still, it is important to understand how diversity is mediated by the interaction.

We follow May (1973) in using generalized, random interactions. In his book he discusses the ecological implications of such models in detail; we will be looking at the effects of evolution on that stability. Such simple models may most accurately describe molecular replicators (e.g. Eigen et al., 1988), and simple bacterial systems. However, because only the net interaction and reproduction probability is considered, there are other biological cases which can be approximated by this approach.

Our model is individual-based without any individual aging, considering a generalized system of organisms so that interactions are random. Genotype space is pre-defined, so that the interactions between all possible organisms are fixed from the start, and mutations are local. In the spirit of other null models, these interactions are not correlated in this version of the model. We consider one reproduction attempt as the basic unit of time, and we allow mutation to occur during the population dynamics. The total population is a result of the dynamics. We will consider an intrinsic fitness landscape in the presence of strong interactions. For general background reading on individual-based modelling and for discussion on many basic features the reader is referred to Drossel (2001), to Droz and Pękalski (2004) for a population dynamics perspective, and Pigliucci and Schlichting (1997) for a genetics point of view.

The features described above mean that the existence of diversity can be seen to arise in the following way: from an initially monodominant state we find that evolution forces a search of genotype space for the most stable configurations. Often these states are diverse, provided the intra-specific competition exceeds inter-specific competition (or, equivalently, the beneficial inter-specific interaction is greater than the intrinsic fitness). Such diverse states do not exist for low interaction strength, and all states are diverse in the limit of very high interaction strength. Stability is determined by the properties of a given configuration in genotype space, and states are, on average, more stable as time progresses. In addition, we find a sharp

threshold in interaction strength below which diversity does not occur.

2. Definition of the model

We now define the TaNa model. Individuals are represented as a vector $\mathbf{S}^{\alpha} = (S_1^{\alpha}, S_2^{\alpha}, \ldots, S_L^{\alpha})$ in genotype space $\mathscr{S}$. The S_i^{α} take the values ± 1, and we use $L = 20$ throughout, giving $2^{20} = 1\,048\,576$ possible types. Each $\mathbf{S}$ string represents an entire type with unique, uncorrelated interactions. The small value of L is necessary for computational reasons as all types exist in potentia and have a designated interaction with all other types.[1] There are therefore $(2^{20})^2$ interactions to be considered in this model. We consider random interactions for simplicity, which would be correlated in reality. Introducing significant correlation whilst maintaining randomness in this relatively small hypercubic genotype space has proved difficult, and so we consider uncorrelated interactions here. Note that controlled correlations have been achieved in another version of the model (Laird and Jensen, 2006).

We refer to individuals by Greek letters $\alpha, \beta, \ldots, = 1, 2, \ldots, N(t)$. Points in genotype space are referred to as $\mathbf{S}^a, \mathbf{S}^b, \ldots$, and any number of individuals may belong to a point in genotype space $\mathbf{S}^a$.

In the original TaNa model, individuals α are chosen randomly and allowed to reproduce with probability p_{off}:

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

They are then killed with probability p_{kill}, which is a constant parameter. The difference between the original model and the one used here is the definition of the weight function $H(\mathbf{S}^{\alpha}, t)$. The original version used

$$H_0(\mathbf{S}^{\alpha}, t) = \frac{k}{N(t)} \sum_{\mathbf{S} \in S} J(\mathbf{S}^{\alpha}, \mathbf{S}) n(\mathbf{S}, t) - \mu N(t). \quad (2)$$

Here k ($\equiv 1/c$ from previous papers) determines the maximum strength of interactions, $N(t)$ is the total number of individuals at time t, and $n(\mathbf{S}, t)$ is the number of individuals with genotype $\mathbf{S}$ at that time. The *interaction matrix* $J(\mathbf{S}^{\alpha}, \mathbf{S})$ represents all possible couplings between all genotypes, with $J_{ii} = 0$ always and $J_{ij} = J_{ji} = 0$ with probability Θ. If the interaction is not zero, then J_{ij} and J_{ji} are both generated randomly in the range $(-1, 1)$, so that mutualism, predator–prey, and competition are all possible, but amensalism and commensalism only occur in

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[1]When discussing the model, we refer to points in genotype space as a type. It is a matter of interpretation whether we consider genotype space to be 'coarse-grained' (resulting in each genotype being a different species—valid when k and ε are 'large' so that genotype differences affect reproduction probability greatly; see Eq. (2) for definitions), or whether we consider genotype space to be a small sample of a much larger space, meaning genotypes are *types* of a base species (which would be valid when k and ε are small, and so all genotypes have similar reproduction probabilities). As we operate in neither extreme and reproduction is asexual, the distinction between species and type is difficult.

the case when one interaction is randomly generated to be very small. Since the functional form of $J(\mathbf{S}^a, \mathbf{S}^b)$ does not affect the dynamics, provided that it is non-symmetric with mean 0, we choose a form of the interaction matrix that speeds computation (Christensen et al., 2002). In the analysis sections, we will use shorthand versions: J_{ab} as the interaction of an individual from type b on an individual from type a, and n_a as the number of individuals with genotype a.

In the extended model we consider here, we also allow an intrinsic fitness term, representing the different ability of types to survive in the environment. There are at least two possible ways of doing this—either as a *density-dependent* fitness term, or a *density-independent* fitness. With these fitness concepts, correlations can be introduced easily so we will look at both the case of uncorrelated and correlated landscapes. The correlation we choose is a type of *Fujiyama* landscape[2] (Drossel, 2001) defined as follows. One type α has a fitness of 1, and with each mutational step away from this type we subtract Δ ($= 0.1$ in simulations), down to a minimum of 0. An uncorrelated landscape is generated with each type having a fitness drawn uniformly from (0, 1). See Section 3.2 for an explanation and Fig. 2 for results. The modified weight functions take the following forms:

1. Density-dependent fitness (or equivalently, the interaction with an individual's own type), defined by

$$H_d(\mathbf{S}^\alpha, t) = H_0(\mathbf{S}^\alpha, t) + \frac{\varepsilon}{N(t)} n(\mathbf{S}^\alpha, t) E(\mathbf{S}^\alpha). \qquad (3)$$

Here, ε is the magnitude of the density-dependent part of the 'intrinsic fitness strength' and $\varepsilon E(\mathbf{S}^\alpha)$ is the intrinsic fitness[3] of individual α. $E(\mathbf{S}^\alpha)$ is determined according to the case studied:
   1(a) Uncorrelated, density-dependent intrinsic fitness landscape.
   1(b) Correlated, density-dependent intrinsic fitness using a 'Fujiyama' landscape.
2. Density-independent fitness, defined by

$$H_i(\mathbf{S}^\alpha, t) = H_0(\mathbf{S}^\alpha, t) + \varepsilon_I E(\mathbf{S}^\alpha). \qquad (4)$$

Here, ε_I is the magnitude of the density-independent part of the intrinsic fitness strength. E_i is again determined by the case studied:
   2(a) Uncorrelated, density-dependent intrinsic fitness landscape.
   2(b) Correlated, density-dependent intrinsic fitness using a 'Fujiyama' landscape.

All individuals of the same type will have the same weight function and therefore the same offspring probability at a given time; i.e. if individual α was from type a then $H(S^a) = H(S^\alpha)$. Reproduction occurs asexually, and

on a successful reproduction attempt two daughter organisms replace the parent, with each $\mathbf{S}_i^\alpha$ mutated (flipped from 1 to -1, or from -1 to 1) with probability p_{mut}. Thus mutations are equivalent to moving to an adjacent corner of the L-dimensional hypercube in genotype space, as discussed in Christensen et al. (2002).

A time step consists of choosing an individual[4] α randomly, and processing according to:

- α is allowed to reproduce with probability p_{off}.
- α is killed with probability p_{kill} (if α reproduced, it is one of the two daughter organisms that is killed).

We define a generation as the amount of time for all individuals to have been killed, on average, once. For a stable population size, this is also the time for all individuals to have reproduced once, on average. The diversity is defined as the number of genotypes with occupancy greater than 20 to eliminate unsuccessful mutants from our count, and is called the wild-type diversity. This definition comes from the observed population structure, as discussed in the next section. The total number of genotype points occupied is approximately L times the wild-type diversity.

Unless otherwise stated, the parameters used will be: $\Theta = 0.2$, $\mu = 0.01$, $p_{mut} = 0.015$, $\varepsilon = 2.0$, and $p_{kill} = 0.1$; see Christensen et al. (2002) for more details. These parameters are selected to allow the population to remain moderately high (to avoid accidental extinction), and to be well away from the mutation threshold present in this system (di Collobiano et al., 2003) (cf. (Eigen et al., 1988): as the mutation probability is increased, the time spent for the system to find a quasi-stable state—described in the next chapter—increases until it becomes infinity, and the quasi-stable structure described below is lost). The results are robust to moderate parameter changes; that is, the same qualitative behaviour can be found for all small parameter changes by making an appropriate small change in the other parameters. In particular, the cutoff for diversity persists over a region of other parameters, although the value of the cutoff might change slightly.

For case 1(a) and case 2(a), the initial conditions are determined by allowing the system to find a monodominant state by running the system for 5000 generations with all interaction disabled ($k = 0$) (starting from a random set of individuals), thus one of the best competitors in the initial set is selected. Then the interaction was enabled by setting k to the desired value. For case 1(b) and 2(b) of the Fujiyama landscape, we simply start the whole population on the fitness peak.

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[2]Named because it has a single, large peak.

[3]We do not merge it with the J term in Eq. (2) in order to allow different values of the strengths.

[4]In previous versions a different individual was chosen for reproduction and killing actions. Here, we select only one individual and process it for reproduction and killing for code efficiency reasons—above the level of fluctuations the two methods are equivalent.

2.1. The reproduction equation

Eq. (2) consists of two terms: the first is an *average interaction* term, and the second a *resource competition* term with all other individuals. Thus, k controls the strength of the average interaction and therefore has relation to a density (as closer individuals will interact more strongly). This makes our model valid for systems in which the population density is roughly constant in time, and individuals compete for a single, fixed quantity of resource (determined by μ). Clearly, this is true of all systems in steady state and will be approximately true of many other systems.

The introduction of Eq. (1) is in order to turn the infinite ranged H into a probability. One could instead treat H as a stochastic growth rate, and use e.g. the Gillespie algorithm (Gillespie, 1976; Bernstein, 2005); this defines the time step as the expected waiting time to the next event instead of using a fixed time step as we do. We do not choose to do it this way for two reasons. Firstly, there is no reason to assume that the rate of increase of a species (given by $p_{off} - p_{kill}$) will be linear in the quantities defined in H. We have exchanged linearity for the logical simplicity of having an explicit p_{off}. Secondly, our method is computationally easier. The form of Eq. (1) was chosen for its simplicity, and the particular form is not essential to the model. Almost any monotonic continuous mapping of H to p_{off} will give equivalent qualitative results (this is tested for a few functions, although no proof can be given due to the complexity of the results).

Our reproductive form, then, assumes that interactions sum additively only when close to equilibrium, and that the reproductive advantage gained decreases for additional interactions giving a nonlinear form. This can be considered as a rule of diminishing returns—if there is a net benefit for an individual, each additional benefit results in a smaller effect (in p_{off}). The *ordering* of offspring probabilities $p_{off}(\mathbf{S}^\alpha, t)$ is unchanged by this map; only the *differences between* offspring probabilities will change. The effect is therefore limited to fluctuations as all features of $\{H(\mathbf{S}^\alpha, t)\}_\alpha$ will exist in $\{p_{off}(\mathbf{S}^\alpha, t)\}_\alpha$ as well. The form of this equation does not appear in many mean-field equations—see Section 3.2 and Rikvold (2006).

Using a constant killing probability p_{kill} is a simplifying approximation, as selection certainly will act by differential killing as well as differential reproductive success. However, the dynamics in our model are qualitatively the same without this restriction (provided p_{kill} is not close to 1). This symmetry between selection (i.e. killing probability) and reproductive ability exists in our model because we do not include any individual aging. More complex relations are required in models which permit reproduction only for individuals which have reached a certain age (Chowdhury et al., 2003).

To understand the meaning of the additional density-dependent fitness term in case 1 (Eq. (3)), we consider the weight function of a system with only one type a, $H(S^a) =$ $\varepsilon E(S^a) - \mu n(S^a)$ since $N = n(S^a)$. If we assume that the system is in a steady state ($p_{off} = p_{kill}$), then $H(S^a) = H^* = -\ln(1/p_{kill} - 1)$, which is constant. Thus, we find $n(S^a) = (\varepsilon E(S^a) + |H^*|)/\mu$, meaning that $E(S^a)$ determines how numerous type S^a would be if alone in the system. The same result is obtained for case 2—the differences are apparent only when more than one species is introduced; see Section 3.2.

3. Results

3.1. Observed behaviour

As in the basic TaNa model, the system experiences a number of 'quasi-evolutionarily stable strategies' (called q-ESSs[5] for brevity), during which a single genotype or set of genotypes is present with constant average occupancy. These *q*-ESS may end abruptly, leading to a transition phase before a new q-ESS is found. For the parameter ranges we study, the transition phase usually lasts for tens of generations and so is instantaneous on an evolutionary time-scale. This behaviour is shown in Fig. 1, with some major events labelled. The qualitative behaviour described here is observed regardless of the form of the intrinsic fitness.

The q-ESS phases have several species (from one for small k up to about six for large k) with large, stable populations, and we call these species wild types. The wild types are generally separated in genotype space and are surrounded by mutant types with much lower population. These mutants do not have p_{off} large enough to counteract the death rate, and as such are dependent on the mutations from the wild-type species for their existence; therefore their species lifetimes are short. The species abundance distribution is log-normal on average (Christensen et al., 2002) if only wild types are considered. Transitions between q-ESS states last for only tens of generations at these parameter values; however, it is still possible for a species to mutate over large distances in genotype space in this time. When a new type is successful, it increases in number at the expense of the types it interacts with; by this time another type which benefits from the first may be found, and so there is an effective 'selection gradient' against the dominant species until a q-ESS is reached (Christensen et al., 2002).

Fig. 2 shows that fitness of case 2(a) (uncorrelated, density-independent landscape) yields a non-unity diversity at $k = 0$, due to the high level of neutrality in the system. This is because species with similar (high) fitness are plentiful (as ε_I is uniform distributed) and the transition time between them is high, so average diversity measures pick up diverse states often. This would not be the case if density-independent fitness peaks were very sparse and of

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[5]Named after Maynard Smith's 'evolutionarily stable strategies'. 'Quasi' refers to the (in)stability of the strategy to collective stochastic fluctuations. See Lawson and Jensen (2006) for a more detailed discussion.
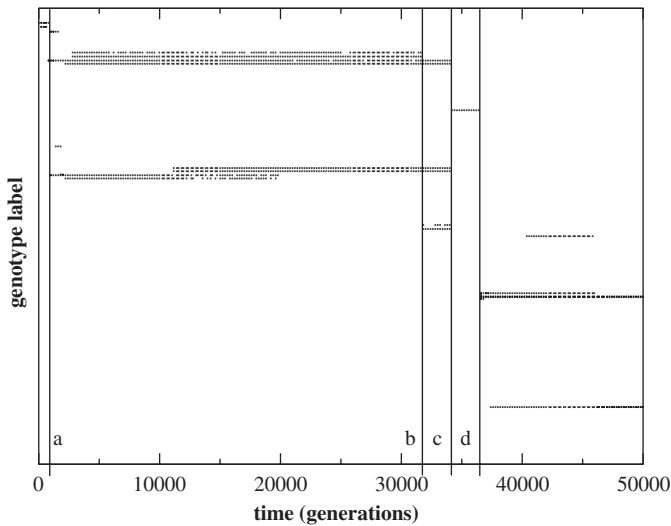
Fig. 1. A sample run ($k = 10$, density-dependent fitness) showing all genotypes with occupations greater than 20 as an unordered genotype label. Times shown correspond to different cross-over situations. (a) is from the original monodominance to a diverse state, which 100 generations later becomes more diverse again. (b) shows a cross-over from one diverse state to another, which at (c) becomes a new monodominant state. Then at (d) the system returns to a new diverse state.
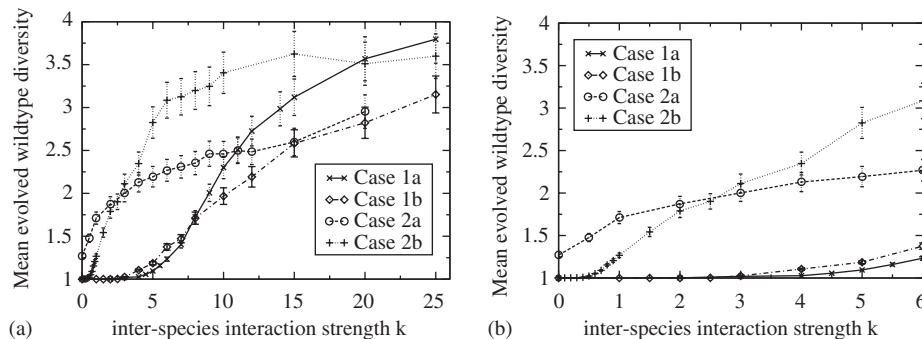
different heights, in which case Gause's Competitive Exclusion Principle would act.

In contrast, the appearance of diversity in cases 1(a), 1(b), and 2(b) follow another pattern. In these cases, at low k there is monodominance, and at high k there is high diversity. Also in all cases, the cross-over region behaves in the same way, with a rapid increase from zero at some characteristic k_{min}, and then a steady increase towards a saturation diversity. Diverse states occur for lower k values for case 2(b) than case 1, and the existence and approximate value of a cross-over in these cases can be shown by a mean-field argument (see Section 3.2).

For case (b), we consider the proportion of time that the most efficient type is observed in the system for varying k values in Fig. 3. We see that the most efficient type is always in existence for small k, and there is a threshold at around $k = 0.8$ (case 2(b)) or $k = 1.8$ (case 1(b)) above which the most efficient type is no longer always present— it may be entirely replaced or drop in numbers to the point at which it is not observed during every generation. This means that in case 1 the most efficient type can be replaced, but not coexist, for a range of k; for case 2, the most efficient type can coexist without possibility of

Fig. 2. Left: k dependence of the average diversity of an evolved system, taken for 40 000–50 000 generations and 500 runs per data point for the case 1, density-dependent ($\varepsilon = 2$, $\varepsilon_I = 0$) fitness, and case 2, density-independent fitness ($\varepsilon = 0$, $\varepsilon_I = 2$). Case (a) has rugged random fitness landscape and case (b) has a Fujiyama landscape. Right: a closer look at the low-k region. Note that cases 1(a), 1(b), and 2(b) display the same qualitative behaviour which can be understood at the mean-field level, see Section 3.2.
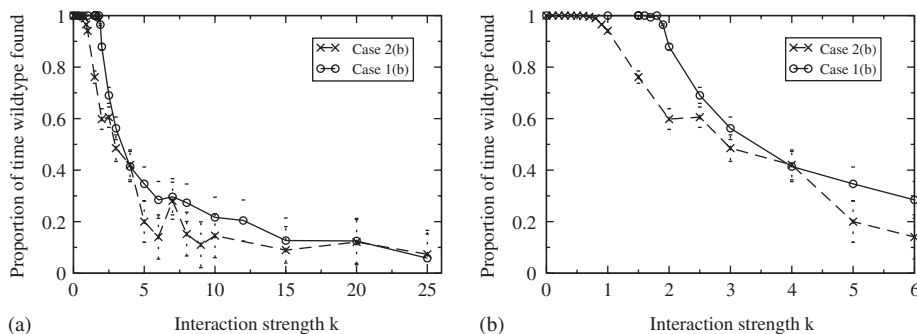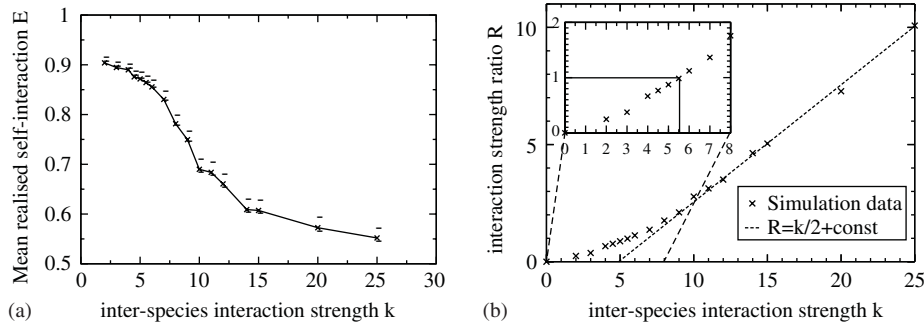

Fig. 3. Left: The proportion of generations that the most efficient type is observed in for cases 1(b) (density-dependent fitness) and 2(b) (density-independent fitness), as a function of interaction strength k, averaged over 100 runs per k value. Right: a closer look at the low-k region.

Fig. 4. Analysis of case 1(a). Left: $\langle E_\alpha \rangle$ as a function of interaction strength k, which decreases towards the mean value of $\frac{1}{2}$ for large diversities, demonstrating the decline of importance of individual efficiency as a selection factor. Right: average value of the ratio of the relative interaction strengths R as a function of k, approximately a straight line for $k \gtrsim 10$.

replacement for a range of k. These results are understood in Section 3.2.

We now analyse case 1(a) (uncorrelated density-dependent fitness) in more detail. Fig. 4(a) shows the selective drop of E_i with increasing k. The appearance of diversity is clear when considering the ratio of total interactions to intrinsic fitness, $R = \langle k \sum J_{ij} n_j / \varepsilon E_i n_i \rangle$ shown in Fig. 4(b). At $k \approx 5.55$, $R = 1$, so the average interaction is greater than the average intrinsic fitness for $k > 5.55$. For $k \gtrsim 10$, $R \sim k$ as interaction becomes the dominant driving force and selection acts to maintain positive interactions. For large k, each term in $\sum J_{ij} n_j$ is already maximized by selection, and is therefore independent of k (again ignoring fluctuations).

For $k \leqslant 5.55$, interactions do not contribute to fitness of the wild type. For $k \in (5.55, 10)$, the relative importance of the two selection forces changes. Below $k = 5.55$ diverse q-ESS states are not found[6] as interaction is always weaker than intrinsic fitness leading to monodominance. Manual examination of the runs confirms that the diverse states found for $k < 5.55$ never have temporal stability, and that diverse, temporally stable states exist for $k = 5.55$ which correspond to q-ESS.

The number of q-ESS switches is higher in high-k systems than in low k. At low interaction strengths, monodominant q-ESSs tend to remain for the entire run, with a small possibility of a switch to another mono-dominant q-ESS with higher intrinsic fitness. As interaction strength increases, the number of q-ESS switches also increases leading to a greater rate of exploration in genotype space. It was shown in Christensen et al. (2002) that the length of q-ESS epochs increases logarithmically with time, as does the average population size. It would appear that the additional stability of large populations to fluctuations plays a role in determining the stability of the q-ESS. In addition, the properties of the genotype space

near extant types plays a large role in determining the stability of a state.

3.2. Mean-field predictions

For cases 1 and 2(b), we can show the existence of a cross-over from monodominance to diverse states in k by a simple argument from the definition of H, although the nature of the cross-over is not determined by this argument. This mean-field result ignores any fluctuations in the system; however, the result provides a surprising match with observation. We can also simply show that random, density-independent fitness will not allow mono-dominance.

We consider the weight function H for the case where species a dominates, and a new species b is added to the system ($n_a \gg n_b$), and require $n_a + n_b = N \approx n_a$. The requirement for invasion is that $H_b > H_a$ so that $p_{off}^b > p_{off}^a$. However, when $n_b \gg n_a$ a diverse state must exist if $H_a > H_b$, and competitive exclusion will occur if $H_a < H_b$ in this case.

3.2.1. Case 1: density-dependent fitness
For type a, Eq. (3) becomes

$$H_a = \frac{kn_b J_{ab}}{(n_a + n_b)} + \varepsilon_I E_a \frac{n_a}{(n_a + n_b)} - \mu(n_a + n_b) \tag{5}$$

$$\approx \varepsilon_I E_a - \mu n_a. \tag{6}$$

Similarly for type b,

$$H_b = \frac{kn_a J_{ba}}{(n_a + n_b)} + \varepsilon_I E_b \frac{n_b}{(n_a + n_b)} - \mu(n_a + n_b) \tag{7}$$

$$\approx kJ_{ba} - \mu n_a. \tag{8}$$

From above, we require $H_b > H_a$ for invasion; therefore $k > \varepsilon E_a / J_{ba}$. For a diverse state, the converse must be true: $k > \varepsilon E_b / J_{ab}$.

For case 1(a), E_a has been selected to be high initially, as a was successful on its own; similarly J_{ba} will be selected to be high to ensure b can proliferate. Thus, we can take $E_a = 1$ and $J_{ba} \approx 1$ for both cases 1(a) and (b). Thus, there is a

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[6]The apparent non-unity diversity below the threshold value appears to be due to occasional mutant fluctuations above the wild-type threshold chosen.

positive threshold at around $k_{min} \approx \varepsilon = 2$. It should be a little less for case 1(a) as there is a small variation in E_a below unity.

The inverse relation provides a different value, as neither E_b nor J_{ab} have been selected—we take mean values to get an estimate. E_b is uniform distributed on $(0, 1)$ and thus has mean 0.5, and we take the mean[7] $J_{ab} \approx 0.2$. We therefore find that the minimum value of k for a diverse state to exist is around $k_{min} = 2.5\varepsilon = 5$. For $k \in (2, 5)$ invasion is possible, coexistence is highly unlikely. Fig. 3 shows that replacement of the wild type occurs at just below $k = 2$ and Fig. 2 shows that diverse states exist for $k > 5.55$.

In this case, all interactions should be mutualistic; the ratio $n_a/n_b = (kJ_{ab} - \varepsilon E_b)/(kJ_{ba} - \varepsilon E_a)$ should be positive and of order 1 for stability; this requires both J_{ab} and J_{ba} are positive.

3.2.2. Case 2: density-independent fitness

For type a, Eq. (4) becomes

$$H_a = \frac{kn_b J_{ab}}{(n_a + n_b)} + \varepsilon_I E_a - \mu(n_a + n_b) \quad (9)$$

$$\approx \varepsilon_I E_a - \mu n_a. \quad (10)$$

Similarly for type b,

$$H_b = \frac{kn_a J_{ba}}{(n_a + n_b)} + \varepsilon_I E_b - \mu(n_a + n_b) \quad (11)$$

$$\approx kJ_{ba} - \mu n_a + \varepsilon_I E_b. \quad (12)$$

Using $H_b > H_a$ we find $k > (\varepsilon_I/J_{ba})(E_a - E_b)$ for invasion. For diversity the converse must also be true: $k > (\varepsilon_I/J_{ab})(E_b - E_a)$. For $k \neq 0$ and case 2(a) of a random fitness landscape, the difference $E_b - E_a$ can be arbitrarily small and so can always be satisfied for some J_{ab} and J_{ba}. Therefore, diverse states always exist (for large enough genotype spaces). However, diverse states are not always realized depending on whether such a configuration exists in the local genotype space.

For case 2(b) with a Fujiyama fitness landscape, $E_a - E_b = \Delta = 0.1$. Therefore, invasion will occur for $k > \varepsilon_I \Delta/J_{ba} \approx 0.2$ (as J_{ba} can be selected to be high). The converse equation requires $k > -\varepsilon_I \Delta/J_{ba}$ which can always be satisfied; therefore, diversification can always follow invasion. Only for both $k \gtrsim 1$ and negative J_{ba} will exclusion of the fittest type occur. Fig. 3 shows that replacement of the wild type occurs at just below $k = 1$ and Fig. 2 shows that diverse states exist for $k > 0.5$.

Note that in case 2, diverse states may be parasitic/predatory or mutualistic, depending on the difference in fitness between types. Simple rearrangement of the above weight function yields

$$n_a/n_b = (J_{ab} + (\varepsilon/k)(E_a - E_b))/(J_{ba} - (\varepsilon/k)(E_a - E_b)).$$

This ratio must be positive for a diverse state to exist, and of order 1 for stability. Unless $(\varepsilon/k)(E_a - E_j)$ is small, this

implies J_{ba} and J_{ab} are of opposite signs. Thus, both mutualism and predator–prey interactions are possible.

This very simplistic analysis shows that typical species should not be able to coexist below the value of k_{min}. It is surprising that the system explores many exceptional species and even these cannot remain in *stable* coexistence below the mean-field threshold value (approximately, at least). A diverse state at low k is not stable to invasion from mutations; i.e. neighbouring types in genotype space that satisfy the above condition that J_{ba} and J_{ab} both large are not stable to fluctuations. Therefore, these states are not realized for long periods of time (when compared to q-ESS), and appear infrequently in time average measures. On a mean-field level, a cutoff at some value is inevitable as coexistence is impossible for $k \leqslant \varepsilon$ (case 1) or $k \leqslant \varepsilon\Delta$ (case 2(b)). The analysis required to show the true nature of the cross-over is too complex for inclusion here and will be studied in future work.

4. Discussion

In our model, we have found that there will be a cross-over from monodominance to a diverse state as the interaction increases. There appears to be a critical value of interaction strength beyond which the monodominance is broken down. For rugged fitness landscapes, it is vital that the fitness of individuals is (to some degree) *density dependent* for a cutoff in diversity to exist. The cutoff appears in the density-dependent part of fitness for very rough fitness landscapes, and also appears in the density-independent part for highly peaked fitness landscapes. The relative importance of each will depend on the specifics of the system studied. In future work, it will be important to understand the nature of the cross-over theoretically, beyond the naive estimate of the mean-field type calculation given in Section 3.2.

Using density-dependent intrinsic fitness predicts that replacement of a 'fitter' type can occur at lower interaction strength than coexistence. Using density-independent intrinsic fitness predicts that coexistence should occur at lower interaction strength than replacement of a 'fitter' type. This is certainly a feature of working in a fixed genotype space; it will be important to establish whether this is still true in models with correlated interaction matrices.

Each evolutionary course can be different in the simulation. If the initial type has neighbours in genotype space that interact favourably with each other and negatively against the wild type, then it will quickly go extinct and (possibly several) q-ESS switches are observed. Other initial conditions allow the interactions of local mutants to favour the wild type, and monodominance continues for a longer time, possibly beyond the time-scale of the simulation. On a transition from one q-ESS state to another, our model predicts that at low interaction strengths only monodominant states can occur. However, if the interaction strength $k \gtrsim k_{min}$ then all initial wild types

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[7]J has a mean of zero, but here we are taking the mean of the positive part of the distribution, which has non-zero mean.

should be able to diversify eventually via an adaptive walk. If $k \gg k_{min}$ ($> \varepsilon$), the contribution to the weight function from the intrinsic fitness becomes negligible and the system reduces to the original TaNa model with the weight function H_0, meaning all states are diverse.

A similar cutoff was observed for diversification of several types of *E. coli* by Kashiwagi et al. (2001). In this experiment the culture was well mixed and fed with glutamate, the sole nutrition source (of nitrogen). Through mutagenesis, evolution of a single gene was studied—the gene for glutamine synthetase production, which synthesizes glutamine from glutamate. Since the glutamine synthesis is necessary for the growth of the bacteria in this experiment, those with the higher activity of glutamine synthetase will result in faster growth of the bacteria. Indeed, in a low population density condition, only the fittest type (i.e. that with highest enzyme activity) survives. However, in a dense condition, multiple types including those with much lower enzyme activity coexist. Interaction is (amongst other things) via leakage of glutamine, and removal of glutamine from the environment confirms survival of the fittest.

We can identify our interaction strength k as a surrogate to bacterial density in the experimental set-up, as the strength of interaction felt between cells will increase when they are packed together more closely.[8] The comparison is valid for approximately constant population size, which is approximately the case in both experiment and model. Increased density will increase inter-specific interactions more than intra-specific interactions, as the addition of a new substance to the cell will be more significant than the addition of the same amount of an already present substance. Our predictions appear to be consistent with the experiment, and with the subsequent observation that cutting off the interaction prevents the diversification (Kashiwagi et al., 2005).

Our theoretical results enable us to probe the underlying factor allowing diversification that is unobservable in real systems. Essentially we require both:

1. The mean realized interactions for all types are equal to or greater than their own intrinsic fitness. 'Intrinsic fitness' is an absolute measure if fitness is density dependent, but a relative measure if fitness is density independent. The greater the ratio of the interaction strength to the intrinsic fitness strength, the less selection pressure acts via the type's efficiency in the environment. Thus, all types gain more from each other than they do from the environment.
2. The possible mutations from the wild type reinforce themselves, or other types, more than the wild type. This is a constraint of the local genotype space, and means

that the mutant does not interact more positively with the wild type than with itself.

Our model is quite general and so can be considered of relevance to many evolutionary systems. The only fitness concept that fails to give a reasonable interaction vs. diversity graph is uncorrelated density-independent fitness; this would not be considered realistic. We conclude that there should be an interaction cutoff below which no diverse states are found, above which diversity can arise in the absence of space with a single resource.

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[8]Note that this is an additional density dependence to the one explicitly included in the first term in Eq. (2), which represents the likelihood of and individual α meeting an individual of type **S**.

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