Niche Differentiation and Coexistence in a Multi-Resource Ecosystem with Competition

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Abstract. As a step towards modeling the evolution of food webs from an individual-based perspective, here we study the evolutionary dynamics of a simple multi-resource ecosystem model of the basal level of a food web. We combine two trade-off mechanisms in resource utilization (consumption abilities) and stoichiometric constraints (consumption needs) into a minimal model, and study the evolution of niche differentiation and coexistence through the interaction. Under a broad range of circumstances the model shows the emergence of specialization. By introducing stoichiometric constraints various evolutionary trajectories become possible but in this simple model we found no evidence for the coexistence of specialists and generalists.

1 Introduction

Understanding the emergence, evolution and stability of food webs is one of the most challenging tasks in theoretical and computational ecology today. Although several population-level models exist (see [8]), the systematic study of this problem has not been attempted from an explicit individual-based perspective using ALife techniques. This is what we begin here.

We study the dynamics of a minimal model of a multi-resource ecosystem at the lowest trophic level of a food web. At this basal level, species feed on non-replicating abiotic energy resources and compounds (such as sunshine and the available chemical substances in terms of a real ecosystem). We study the evolution of niche differentiation of species at this level using two contrasting trade-offs:

1. *Abilities trade-off:* Given a limited number of resources, species differ in their utilization of resources. In terms of this factor, species can be classified as either generalists or specialist, depending on their consumption of resources. This rests on the assumption is that a trade-off exist between generalists and specialists: Generalist can consume everything, but with a small efficiency. Specialists, on the other hand, consume only a single resource, but do that with a high efficiency.
2. *Needs trade-off*: Conventional ecological models are often based on the assumption of energy as a 'single currency'. Individual organisms, in contrast,

are composed of many chemical compounds, and need to obtain multiple resources in order to survive and reproduce (stoichiometry). This introduces a second trade-off: Generalists are in the comfortable position of having the ability to uptake multiple types of resource, while specialists that consume only a single resource are limited by the resources they have a limited ability to consume.

This is modeled using an individual-based ecosystem model inhabited by a population of asexually reproducing organisms with genetically determined resource consumption abilities and needs. Using this model, we study the dynamics of emergence and maintenance of populations of specialists and generalists. This fits into the framework of recent ecological and evolutionary studies on specialist/generalist coexistence [1][2], stoichiometric ecology [9] and dynamic energy budgets [7]. The current study emerges from a broader proposal where (in the context of the EvoTech/FATINT project [6]) we attempt to understand the factors that enable multiple species with different ecological tasks to emerge and coexist in a process that also supports the increase of evolutionary complexity of various kinds.

2 The Model

We study the interaction of the trade-offs in resource utilization (abilities) and stoichiometric constraints (needs) in a simple individual-based ecosystem model. We define a minimal non-spatial environment which hosts a number of resource populations and (initially) a single consumer population. The environment is implemented as a vector, where each location can be occupied by either a resource or a consumer. In each step, a consumer randomly selects a location from the vector and, if it encounters a resource there, attempts to consume it.

The resources are modeled as abiotic entities that cannot reproduce (e.g. chemical substances or units of energy). The influx of resources from outside the system is taken to be constant per time step, and equal for all resource types. When adding a resource token, a location is randomly chosen in the environment vector. If the chosen location is empty, the resource is successfully added to the environment. In this way, total resource abundance saturates towards a maximum. Each resource represents a nutritional value transferred to the consumer when the resource token is consumed, whereupon the latter is removed from the environment. Additionally, the resource abundance suffers from a small dilution rate.

Consumers are modeled as replicating individuals. They are specified with a genotype, a 'stomach' (resource storage), and a variable energy value. The energy value regulates the consumer's life history: the consumer can reproduce when its energy exceeds a certain threshold, and dies when the energy value is turning negative. Energy is not directly increased upon the consumption of resources (as in the case of a 'single currency'), but requires a *combination* of resources to be consumed. The specific combination of resources that is required to convert

raw resource to useful energy depends on the genotype of the individual. The ability to consume a given type of resource is encoded on the genotype as well. These two factors (the energy function and the consumption function) stand for trade-off 1 and 2, respectively.

Consumption abilities The length of the genotype G for a consumer (henceforth: individual) is equal to the number of resources n: $\{G_i, ..., G_n\}$ and determines the individual's abilities and needs. In all presented experiments, we used $n = 3$. Each gene G_i has a real value in the interval $[0, 1]$. The gene values are normalized (indicated by Φ below), such that $\sum_{i=1}^{i=n} G_i = 1$. This normalization expresses that resource consumption is an activity of the organism, where the total time of "feeding" is distributed among the resources in an exclusive-or way. Normalization implies a specialist/generalist trade-off, because an increase in one gene causes a decrease in the others.

Upon encounter between an individual and a resource of type i, the resource is consumed with a probability A_i, which we call an individual's *ability* for i. An individual has abilities for all types of resources that depend on the gene value at the given locus corresponding to the given type of resource. In a system with $n = 3$, individuals have consumption abilities defined as:

$$A = \Phi\{G_1^s, G_2^s, G_3^s\} \tag{1}$$

where Φ denoted normalization and the exponent s is a key parameter that amplifies or suppresses the effect of genetic differences on an individual's abilities. First, consider the case where $s = 1$. Suppose that an individual has genotype $\{0.7, 0.1, 0.2\}$ and encounters a resource of type 2, then it has 10% probability of consumption. At $s = 1$, the genotype directly codes for the consumption abilities ($A = G$). With $s > 1$, the relative differences in G will be increased, and with $s < 1$, the relative differences are decreased. Figure 1 shows the dependence of A_i on G_i for various values of s.

Energy needs Upon consumption, an individual stores the resource of a given type in R_i. The energetic value of resources for an individual is calculated as a function of the stored resources. The resulting energy value then determines the reproduction and the survival/death of the individual.

In models where energy is a dealt with as a single currency that converts resource to offspring, every resource contributes equally to the energy value. In the present model, in contrast, the relative contribution of resources types to energy, i.e. the *need* for resources, differs depending on the individual's genotype.

We take the need N_i for a given type of resource for an individual to be the *inverse* of the corresponding genotype value, such that the resource on which an individual is most specialized contributes the least to its overall energy value. We calculate the contribution of the various resources, and normalize the result to 1:

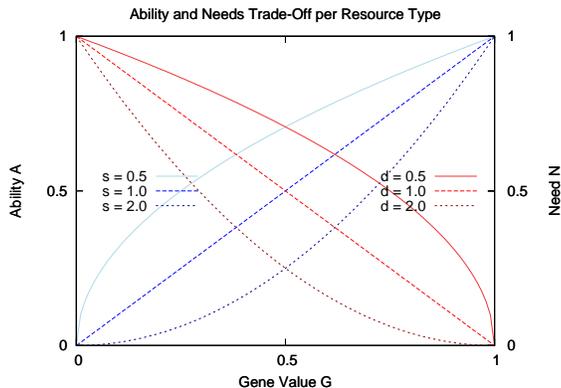$$N = \Phi\{(1 - G_1)^d, (1 - G_2)^d, (1 - G_3)^d\} \tag{2}$$

Fig. 1. Trade-off between ability A_i and need N_i as functions of gene G_i for a resource type i for various values of s and d.

Then, we calculate the overall energy E for the individual by summing over all stored resources R_i multiplied by their relative contribution: $E = \sum_{i=1}^{i=n} N_i R_i$. The exponent d in eq. 2 allows us to increase or decrease the relative differences in G to obtain the energy contribution N in the same way as before when consumption abilities were calculated. At $d = 0$, genetic differences do not affect energy contribution at all, which recovers the 'single currency energy' model. With increasing $d > 1$, genetic differences are amplified, such that the contribution of the resource to which an individual is not specialized becomes increasingly larger. Figure 1 show how the need N_i of a resource type i depends on G_i, for various values of d.

Stored resources are continually discounted by metabolism with a fixed amount per stored resource, and energy declines linearly with time. The individual dies when $E \leq 0$ and reproduces when E exceeds a reproduction threshold.

Evolution Offspring inherit their parent's genotype. The genotype is mutated with a small probability per gene. A gene G_i is mutated by the addition of a small uniform random distribution. The genotype is re-normalized after mutation.

3   Experiments and Results

We performed a series of evolutionary experiments in the above model, using the parameter settings as in Table 1. First, a baseline experiment is shown in which the energy is treated as a 'single currency'. Then we observe the behavior of a model with stoichiometric constraints (needs trade-off) under different settings. We conclude our experiments with an overview of the evolutionary consequences of varying the strengths of both trade-offs.

Parameter	Value
Environment size	2,500 locations
Number of resources	3
Resource influx	100 per resource type
Resource value	15.0
Dilution rate	0.001
Reproduction threshold	10.0
Metabolism	1.0 per resource type
Mutation rate	0.05
Mutation range	0.05

Table 1. Model parameters

3.1 Trade-off in Abilities

Pre-experiment. If the normalizations of genotype G (and abilities A) are canceled, there is no generalist/specialist trade-off, and hence no limitation on generalization or specialization. In this case we find that the consumer population rapidly evolves towards the point where consumption is maximal for all resource types ($A = \{1.0, 1.0, 1.0\}$), and there are no generalists or specialists. All following experiments therefore involve the generalist/specialist trade-off through normalization.

Base-line experiment. In our base-line experiment consumption abilities evolve in the absence of gene-dependent resource needs. The individuals' needs are fixed at $N = \{\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\}$ by putting $d = 0$, by which energy is treated as a single currency. We also put $s = 1$ such that the genotype directly encodes the consumption abilities, $A = G$. Note that normalization implies that the overall consumption probability is kept constant. The left panel in Figure 2 shows that, although specialization does not offer increased overall consumption probability here, the initial generalist population nevertheless evolves into specialists on each of the three resources. In a series of tests we have observed that typically, the population immediately speciates into a specialist on one resource, and a remaining pseudo-generalist population. The specialist then evolves towards the point where consumption of the given resource is maximal (corners in genotype space). The other population first evolves towards a point 'halfway' between the remaining resources, i.e. they become generalists on two of the three. From there, pseudo-generalists tend to speciate further (at approx. 20,000 time steps) towards higher specialization, thus creating three specialist populations that occupy the three available pure niches.

This outcome cannot be explained in terms of the consumption probabilities, because the sum of the probabilities is equal to 1. The effect is the result of positive feedback from relative resource densities, shown in the right panel of the Figure 2. Every mutation from the initial generalist population causes a slight specialization, and therefore a difference in resource abundance. This breaks down the initial symmetry of the latter. If, by chance, there are more mutants with some preference for one resource, this results in a disruptive se-
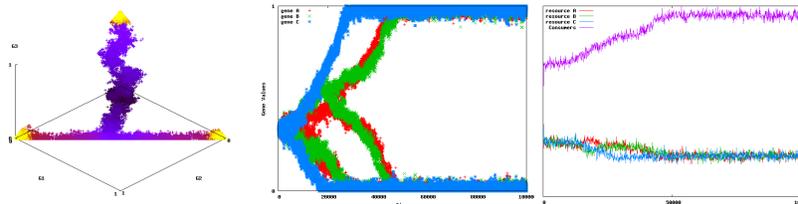
Fig. 2. Evolution of specialists with $s = 1$ and $d = 0$. Left panel shows evolutionary dynamics in genotype space. Genotypes in left panel are on a triangular plane with corners representing specialist genotypes $\{1.0, 0.0, 0.0\}$, $\{0.0, 1.0, 0.0\}$ and $\{0.0, 0.0, 1.0\}$. Colors indicate time: blue indicates begin, yellow indicates end of a run. The middle panel shows gene values over time, where colors represent different genes. The right panel shows population abundances for resource populations and the total consumer population (upper line).

lection pressure via resource abundance. This effect causes the emergence of a specialist to one resource, and pseudo-generalists to the other two resources; the rest also follows.

3.2 Trade-offs in both Abilities and Needs

In addition to the abilities trade-off as above, we now turn on the resource needs trade-off by setting $d = 1$ whereby the energy contribution of a given resource becomes inversely proportional to its consumption ability. The results in Figure 3 show that different evolutionary trajectories are possible, with specialization being the rule. First, notice that the resulting specialist populations are not located in the extreme corners, as with $d = 0$ (see Fig. 2). The gene plots (middle panels) now show that populations never achieve perfect specialization (i.e. $A_i = 1$), since this would imply that the resource i does not contributes to energy at all. Specialists may have a large ability for one resource type, but with $d = 1$ they also need other resources in order to gain energy. We also see that the evolution of specialization does not occur in a linear fashion. Instead, evolution slows down as the level of specialization increases (compare this with Fig. 2).

Figure 3 shows two different evolutionary trajectories obtained from the same model setting. In case 1, the initial generalist population immediately speciates into three populations that evolve specialists. In the second case, initially a two-specialist situation evolves. Here, after a long transient, one of the specialist populations suddenly speciates further (after 300,000 time steps!) and a third specialist population occupies the empty niche. After this event, a similar situation to case 1 is retrieved with all niches occupied.

Fate of an initial specialist population. The above experiments were initialized using a generalist population. Now (using the same parameters) we start from a single specialist population occupying one of the three corners, leaving the
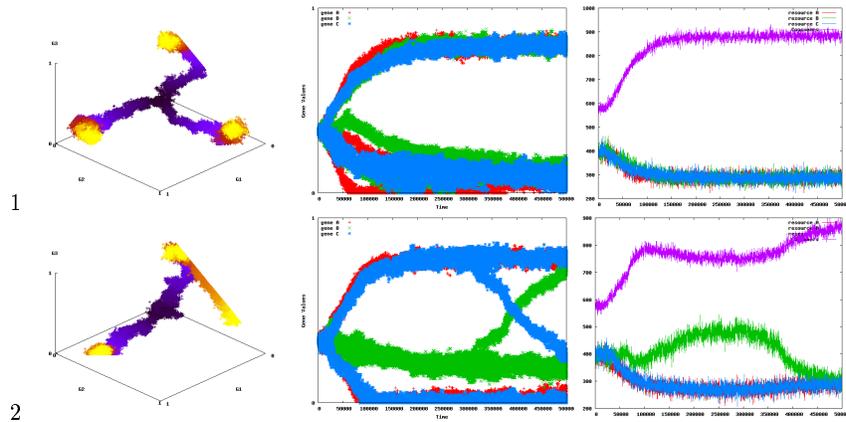
Fig. 3. Two evolutionary runs with $s = 1$ and $d = 1$. Multiple runs using several random seeds for this as well as other figures are available at http://www.evotech.hu/ecal2007-figures.pdf

others empty. The results, depicted in Figure 4, again show qualitatively different evolutionary outcomes with a common tendency. We initialize the experiment with $G = A = \{0.8, 0.1, 0.1\}$. In case 1, the initial population first evolves into a generalist population consuming all resources. Then, the population speciates into three, one of which directly evolves towards specialization. The other two populations first evolve to become pseudo-generalists as above (consuming two of the three resources), just to become specialists after-wards. This results in an evolutionary cycle in the sense that the niche of the initial population is first abandoned, but after a long evolutionary trajectory that leads through generalist and pseudo-generalist stages, later re-occupied. Such a cycle does not always occur, as shown in case 2 (bottom row of Figure 4). Here, the initial population rapidly speciates into two populations that continue to specialize further on the two resources that were initially empty. This results in a stable two-specialist situation, and the niche from which both populations evolved, is finally left empty.

3.3 Varying Trade-offs Strengths

The experiments in the last section were conducted with $s = 1$ and $d = 1$, such that the abilities A_i and needs N_i were (inversely) proportional to gene values G_i in a linear fashion. By changing these key parameters, we can alter the strengths of the ability trade-off and the needs trade-off respectively, and also alter their relative strengths. We study the evolutionary consequences of the relative trade-offs strengths by running a series of experiment with varying s and d.

The results of these evolutionary simulations are depicted in the upper panels of Table 2. In general it appears that (1) the stronger the abilities trade-off, the
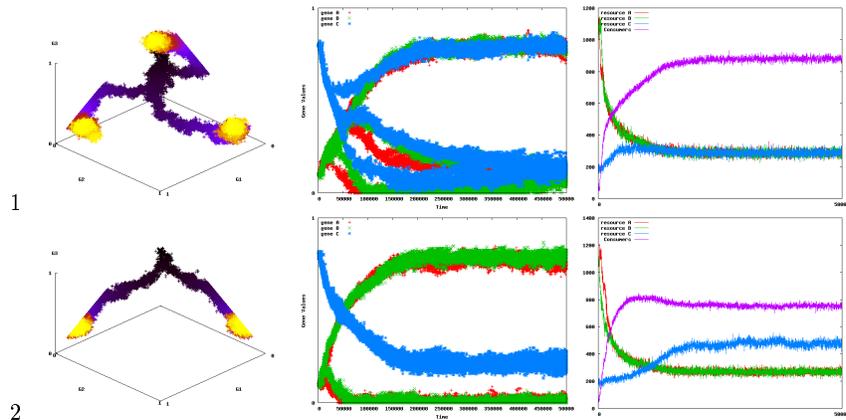
Fig. 4. Sample runs with initial specialist population on one resource (top corner) with $s = 1$ and $d = 1$.

stronger the selection pressure towards specialists, and (2) the stronger the needs trade-off, the stronger the selection towards generalists, as may be expected.

Table 2 shows that specialists do not evolve when the generalist/specialist trade-off is weak ($s < 0.1$), or when the needs trade-off is strong ($d > 1.0$). When both trade-offs are strong, however, the population does speciate into specialists ($s = 10.0$ and $d = 10.0$).

By combining equations 1 and 2, we can derive the energy that an individual with a given genotype is expected to receive disregarding resource availability. Given a genotype G, the expected energy $E_e = \sum_{i=1}^{i=n} A_i N_i$, which combines both trade-offs and thus depends on values for s and d. The lower panels in Table 2 show the expected energy for the entire genotype space and varying trade-off strengths.

This shows that generalists can actually result from very different situations, e.g. where selection for the specialists is weak (see $s = 0.1, d = 0.1$), but also where the selection for generalists is strong (see $s = 1.0, d = 10.0$). Moreover, we can predict that under strong trade-off in resource needs, the evolution of pseudo-generalists is much less likely than when there is a strong ability in trade-off needs (compare $s = 1.0$, $d = 10.0$ with $s = 10.0$, $d = 1.0$).

We can clearly see that populations do not evolve towards the optimal expected energy, but tend to evolve towards the regions where the expected energy is intermediate (red areas). Differences between the upper and lower panels arise because the expected energy calculation disregards resource abundances. Although individuals would evolve towards the point in which expected fitness is optimal in absence of resource competition, this is constrained by differences in resource availability that arises through interaction.
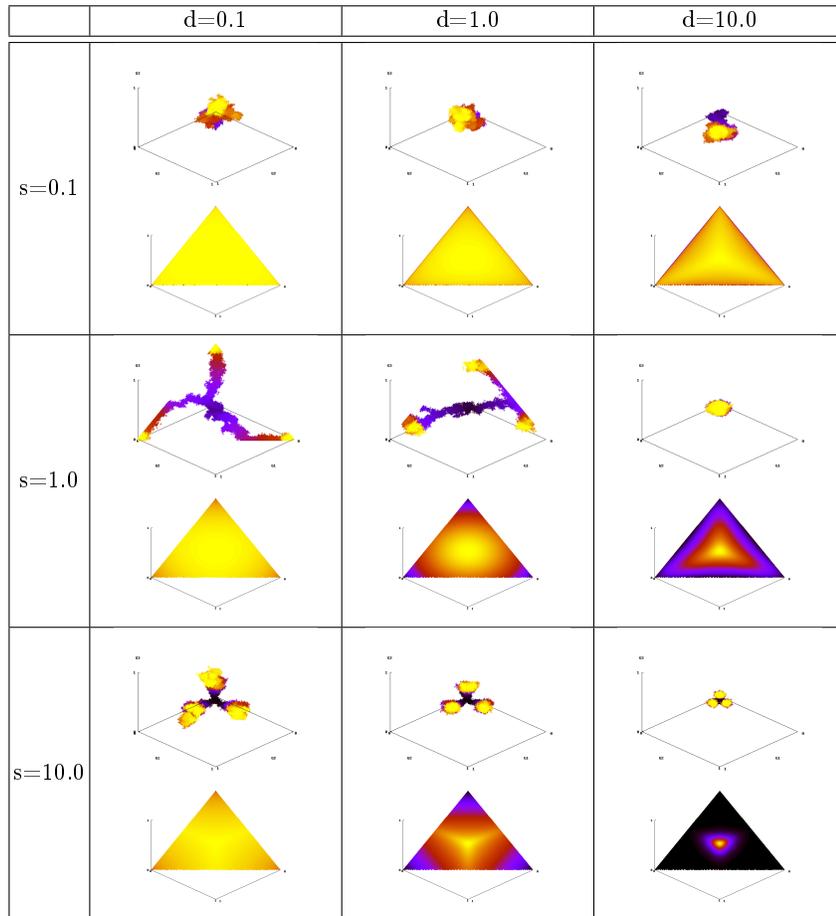
Table 2. Varying trade-offs strengths. Upper panels show evolutionary trajectory in genotype space, initialized with a generalist population. Colors indicates time from blue to yellow. Lower panels show expected energy. Color indicate expected energy from black, low, to yellow, high.

4 Conclusion

Using a minimal individual-based ecosystem with three abiotic resources, we have studied the trade-offs in resource utilization (consumption abilities) combined with stoichiometric constraints (consumption needs). We have shown that in a broad range of conditions specialists emerge and examined some factors that can modify this tendency. The introduction of consumption needs leads to different evolutionary trajectories, which include evolutionary cycling (evolving from specialization to generalists and back to specialization). Variations in trade-off strengths shows that no specialists evolve when either the generalist/specialist trade-off is weak, or the stoichiometric constraints are strong. Under none of the studied situations, however, did the coexistence of specialists and generalists arise in this model.

Since we observed the number of evolved consumer populations to be equal or smaller than the number of resources, these results are in line with the competitive exclusion principle [3][4]. The present model will serve as a baseline model for further investigations to overcome this limitation on the emergence of basal species in an attempt to resolve the paradox of the plankton [5], by relaxing some of its simplifying assumptions (e.g. the symmetry of the gene effects) in a step-by-step manner.

References

1. P. A. Abrams. The prerequisites for and likelihood of generalist-specialist coexistence. *Am Nat*, 167(3):329–342, Mar 2006.
2. M. Egas, U. Dieckmann, M. W. Sabelis. Evolution restricts the coexistence of specialists and generalists: the role of trade-off structure. *Am Nat*, 163(4):518–531, Apr 2004.
3. G. Gause. *The struggle for existence*. Hafner, 1934.
4. G. Hardin. The competitive exclusion principle. *Science*, 131:1292–1297, April 1960.
5. G. E. Hutchinson. The paradox of the plankton. *The American Naturalist*, 95(882):137–145, 1961.
6. G. Kampis, L. Gulyás. Sustained evolution from changing interaction. *Alife IX*, strony 328–333, Boston, 2004. MIT Press.
7. S. A. L. M. Kooijman, T. Andersen, B. W. Kooi. Dynamics energy budget representation of stoichiometric constraints on population dynamics. *Ecology*, 85(5):1230–1243, 2004.

8. A. J. McKane, B. Drossel. *Models of food web evolution*, strony 223–243. Santa Fe Institute Studies on the Sciences of Complexity. Oxford University Press, 2006.

9. S. J. Moe, R. S. Stelzer, M. R. Forman, W. S. Harpole, T. Daufresne, T. Yoshida. Recent advances in ecological stoichiometry: Insights for population and community ecology. *OIKOS*, 109(1):29–39, 2005.