Ecological dynamics can regulate functional community composition independent of taxonomic composition

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September 27, 2017

Abstract

Next-generation sequencing techniques such as RNA-Seq allow cataloging of functional characteristics of microbial community members as well as their taxonomic identity. Such studies have found that a community’s functional composition can be conserved more strictly across multiple sources of variation than taxonomic composition is. I use a standard ecological resource-consumer model to examine the dynamics of traits relevant to resource consumption, and compare the dynamics of functional composition to the dynamics of taxonomic composition. This model demonstrates that interaction with essential resources can regulate the community-wide abundance of related traits, keeping them at consistent levels despite large changes in the abundances of the species housing those traits in response to changes in the environment. An expanded model accounting for inheritance and selection is included, demonstrating that this configuration in which the community’s functional composition is regulated independent of its taxonomic composition can be evolutionarily stable. This pattern of regulation is then shown to be connected to the functional form of the consumer species’ responses to resource availability, changes in which can blunt and even reverse the contrast between the dynamics of functional and taxonomic composition.

1 Introduction

Community ecology theory often focuses on questions of import primarily to communities of plants and animals, examining models of interactions among a relatively small number of species, whose traits are stably defined, to explain patterns of coexistence and diversity. In microbial ecology, where organisms of different taxa share and exchange genes, and diversity can be very high and hard to quantify, it may be useful to ask different questions.
Taxonomic composition of microbial communities has been found to be more variable than the community-wide distribution of functional traits, both in metagenomic studies, analyzing the collection of DNA sequences found in samples [1–3], and in metatranscriptomic studies, which detect which genes are presently being expressed in a sample [4,5].

Support is increasing for supplementation of the traditional theories of species abundance and interactions by theories based on distributions of traits [6–9] and of genes [8,10,11] in a community or metacommunity.

In microbial ecology and the microbiome in particular, where species compositions observed in microbial communities can vary widely from one host, location within the body, or point in time to another, the distributions of ecologically relevant traits may be more meaningful to explanation of the community’s function and dynamics than its taxonomic composition [12,13].

In this article I rework a classic model of resource-consumer dynamics, shifting the focus away from the common questions of diversity and productivity to the mutual regulation of resources and consumers, and use that model framework to demonstrate how interaction with resources can regulate the community-wide prevalences of ecologically relevant traits, even in circumstances in which the species abundances are variable due to changes in the habitat. I show that ecological regulation of the functional composition of the community is as simple to explain (if not more so) as the well-understood regulation of species abundances and limitation of diversity.

1.1 Regulation in resource-consumer dynamics

The standard model framework for resource-consumer dynamics is well understood, given a finite number of distinct species without spatial patchiness [14] and see Appendix A.1.

When individuals’ reproduction rates depend on the availability of a limiting resource, while mortality rates are determined by other factors, the population size grows until the increasing use of resources lowers their availability to a level at which the reproduction and mortality rates are equal. In this way, the resource abundance is regulated by the population: its abundance at equilibrium is a quantity determined by those organism’s processes of reproduction and mortality.

The population brings its limiting resource to the same equilibrium level, conventionally known as $R^*$, regardless of whether the flow of the resource into the community is small or large. If there is a large inflow, the population size grows until it is consuming the resource at an equally high rate, to bring its abundance down to the required level. In this way the size of the population is determined by the resource supply rate.

When there are multiple populations (typically, multiple species) and multiple resources, each popula-
tion requires a particular relation between the limiting resources to balance its birth and death rates. With \( n \) populations and \( m \) resources, these relations take the form of \( n \) equations, one for each population, each in \( m \) variables. This is why \( m \) resources can support at most \( m \) coexisting populations in these models: because no more than \( m \) equations can generally be solved for \( m \) variables simultaneously \[15, 16\]. The equilibrium resource abundances, taken together, are the solution of that system of equations. Thus the combination of all \( m \) resource abundances at equilibrium is determined by the requirements of all the consumer populations combined.

That balance of resources is enforced by the sizes of consumer populations: the bigger they are, the faster they draw resources, until the resources are drawn down to the required levels and supply rates are matched by the rates of consumption. Thus the consumer population sizes, all taken together, are determined by the supply rates of all the relevant resources taken together, in such a way that the inflow and outflow rates are balanced.

In summary, the resources’ steady-state values are determined by the populations — specifically by balancing their resource consumption against their mortality rates — and the population sizes’s steady-state values are determined by the resources’ supply rates, by balancing that inflow against the outflow due to uptake by consumers.

Below, I will use this standard model in a nonstandard way, by considering usage of a given resource to be a trait, and analyzing the prevalence of that trait in the community. I will show that the community-wide prevalences of those traits are regulated by the need to balance inflow and outflow of resources, with the consequence that when environmental conditions change, trait prevalences can remain constant while species abundances fluctuate. Second, I will show that those trait frequencies necessary to the ecological balance of inflow and outflow can be stable in the presence of natural selection, and third I will examine how the regulation of functional and taxonomic composition is affected by the functional form of populations’ dependence on resources.

## 2 Methods

I illustrate the regulation of community-wide trait abundances using a mathematical model of four resources and four consumers. For each resource there is a trait corresponding to consumption of that resource, which may be present in multiple consumer populations in varying frequencies. The trait of consumption of the fourth resource is assumed to be emergent from a complex but fixed interaction between the other three traits. The first three resources are supplied at a constant rate, while the fourth resource is supplied at a rate that changes from time to time. When the community composition shifts in response to
the changing supply of the fourth resource, we will examine how the abundances of consumer populations change, and how the community-wide abundances of these four traits change.

First I consider a minimal consumer-resource model with fixed trait frequencies in each population. This system is modeled by an ordinary differential equation (Appendix A.2) whose state variables are the abundances of each consumer population, $X_i$ for $i = 1, \ldots, 4$, and of each resource, $R_j$ for $j = 1, \ldots, 4$.

Each population has traits, possibly associated with shared genes, in differing frequencies, that correspond to consumption of each resource. The community-wide abundance of each trait at each moment is found by summing the trait’s frequency in each consumer population multiplied by the population’s abundance.

The above model takes the trait frequencies to be fixed in each species, differing between species but not changing with time within each species. However, because these traits are associated with differences in ability to make use of natural resources, implying differences in fitness, traits associated with higher fitness than others can be expected to become more common in each population as time passes, calling into question the assumption of fixed trait frequencies.

For this reason, I also model a case in which these traits are heritable and their frequencies are subject to change in each population due to differential rates of reproduction. In this case, because selection will modify trait frequencies, the affinity of each species for each resource will change with time, as changing resource availabilities drive change in the community composition (Appendix A.3). Community-wide trait abundances are, as above, the sum of trait abundances in each population, but now have the potential to change separately from consumer abundances as traits’ frequencies within populations may change.

In this model, the first three resource consumption traits are assumed heritable independently, while the fourth trait is determined by a nonlinear but fixed combination of the first three.

The above two studies assume a simple, linear functional relationship between resources’ availability and their uptake by consumers, governed by the frequencies of the relevant traits. Before concluding, I unpack the consequences of this assumption by defining a spectrum of different functional forms in the differential equation model, in which the linear form previously assumed is only one special case, and analyzing the impact of these assumptions on the dynamics of the functional and taxonomic composition of the model community.
3 Results

3.1 Fixed-traits model

The fixed-traits model and parameter values are presented in Appendix A.2. Trait frequencies in each species are fixed in time (Figure 1, for comparison with the corresponding figure in the next section). Three resources are supplied at constant rates, while the supply rate of the fourth resource rises and falls, defining three different time periods (Figure 2). The abundances of the four populations making up the model community come to equilibrium when their habitat is unchanging, but when the supply rate of resource 4 changes, their abundances all shift to different equilibrium levels (Figure 3).

However, despite these complex shifts in all the consumer populations’ abundances, and the differences in trait frequencies within each population, the community-wide abundances of the traits of consumption of the first three resources are conserved at equilibrium across these changes in community structure, aside from brief transient adjustments (Figure 4). Of the four traits modeled, only the fourth changes in equilibrium abundance in response to the changing resource supply (Figure 5).

![Figure 1: Trait frequencies in fixed-traits model are constant in time within each species.](image)

In this model, each population consumes each resource at a rate proportional to the population abundance, the resource abundance, and the frequency of the relevant trait in that population. It can be shown (Appendix A.2.2) that the abundance of each resource at equilibrium is independent of its supply...
Figure 2: **Supply rates of resources** in fixed-traits model are constant for resources 1, 2, and 3. Changing supply rate of resource 4 defines three different environments for the model ecological community.

Given that the resource abundance is fixed, the total rate of its consumption is controlled by the total abundance of the resource-consumption trait across all consumer populations. Because the total consumption of the resource must balance its supply, equilibrium can only be achieved when the total trait abundance is at the level that balances the resource supply rate. This model community achieves equilibrium by returning those trait abundances to the needed levels after each change in community structure, even though the balance of population sizes embodying those trait abundances is markedly different each time. Additionally, the population sizes are different in just the way necessary to adjust the total abundance of the trait of consumption of resource 4 to match the changing supply rate of resource 4.

This conservation of the community’s functional composition — the unchanging abundances of ecologically relevant traits — together with changing taxonomic composition — the shifts in abundances of each population — reproduces the pattern of relative conservation of functional composition through changes in taxonomic conservation reported in next-generation sequencing studies.
Figure 3: Abundances of species in community in fixed-traits model fluctuate in a shifting balance, responding to changes in habitat structure in the form of changing supply rate of resource 4.

Figure 4: Overall abundances of traits for utilization of resources 1, 2, and 3 in fixed-traits model remain constant with only brief fluctuations at moments of environmental change.
Figure 5: Overall abundance of individuals possessing trait for utilization of resource 4 in fixed-trait model rises and falls with supply rate of resource 4.
3.2 Selection model

The selection model and parameter values are presented in Appendix A.3. In this model, the frequencies of traits within each population change in response to the fitness of individuals with a given trait relative to individuals without it. As in the fixed-traits case, we assume the supply rates of resources are constant with the exception of resource 4, which is supplied at three different rates in three successive periods of time, at the rates shown in figure 2.

Trait prevalences stabilize relatively quickly (figure 6) to high and low levels, defining a community composition similar to that of the fixed-traits model, in which each species specializes on a different three of the four resources.

As the inflow of resource 4 changes, the community responds by a rebalancing of its species composition, changing the abundances of species while simultaneously maintaining the community-wide prevalences of the three independent traits at unchanging levels, very much as in the fixed-traits model (figure 7, figure 8, figure 9).

![Figure 6: Prevalences of resource uptake traits in selection model, for each combination of species (each row) and resource (each column). Trait prevalences stabilize at a diverse configuration, with each species specializing on a different combination of resources as in the fixed model.](image)
Figure 7: **Total abundance of each species** in selection model.

Figure 8: **Community-wide gene frequencies** in selection model. These gene frequencies are equal to the community-wide prevalences of the first three resource uptake traits.
The above results are explained by a mathematical derivation (Appendix A.2.2) in which the linear relationship between trait abundances and resource consumption rates allows trait abundances to be maintained constant by conservation of a linear combination of species abundances. It is not obvious whether anything similar should be possible if the consumption of resources is a nonlinear function of their availability, as it often is in nature [14].

To explore this question briefly, I generalize the linear model of Section 3.1 to one that includes a spectrum of nonlinear cases as well as the linear case. Using a family of functional responses (Appendix A.5) parameterized by a real number $\alpha$, a number of common cases are obtained in addition to the linear model.

In the linear case, we have seen that a change in the supply rate of one resource causes a change in all species abundances, but causes change in the abundance of only the trait relevant to that resource and not in the others.

We have seen that in the linear case, only one trait’s total abundance is affected by each resource supply rate, while on the contrary all population abundances are modified by any changing supply rate.

The linear case models species that consume each resource in proportion to its availability and to the prevalence of the trait for consumption of that resource in that species. Consumption of each resource
is independent of those organisms’ consumption of other resources. As $\alpha$ increases from the linear case ($\alpha = 1$) to larger positive values, the model species begin to exhibit a preference for the most available resource. In the limit as $\alpha$ becomes very large, the community shifts to a purely switching consumption pattern. A sort of weighted availability of each resource for a population, combining the resource abundance and the prevalence of the trait for consumption of the resource, is taken into account, and the resource whose weighted availability is the greatest is the only one consumed by that population.

In that pure-switching case, Appendix A.5 shows that the coordination of species and trait abundance in response to resource supply is exactly reversed from the previous case. Because each species is consuming only one resource, a change in one resource supply affects exactly one species abundance, while all trait abundances are modified.

As $\alpha$ varies continuously from 1 to larger values, the impact of supply changes on traits and species changes continuously from one extreme to the other: for small $\alpha > 1$ species abundances are all affected significantly while effects on trait abundances are mostly limited to one trait, while for very large $\alpha$ all trait abundances are strongly affected while changes are mostly limited to one population abundance.

5 Discussion

In these model examples, and in general, the total rate of uptake of a given resource must balance the resource’s net rate of supply, so that if the supply does not change, and the community continues to consume that resource, the uptake rate must return to the same level, after a possible transient fluctuation, after a perturbation in the community.

In the fixed-traits and selection models presented above, this matching of outflow to inflow can cause the abundance of resource-consumption traits to be conserved. Conceptually, it is like this: A resource’s inflow rate is determined by its supply rate and its equilibrium abundance, while its outflow rate is determined by its equilibrium abundance and the relevant trait abundance. The resource abundances are determined, as in the standard resource-consumer framework, by the intersection of the consumer species’ ZNGIs (zero net growth isoclines) [14], which reflect only the intrinsic characteristics of the species. Thus a change in one supply rate has to lead to a change in the corresponding trait abundance, while the others do not change, because the other resources’ supply rates and equilibrium abundances are unchanged.

When traits are heterogeneously distributed across multiple species of consumers, and overall trait abundances are regulated in this way, the balance of species can be complexly determined by the necessary abundances of the multiple relevant traits. A single change, such as the fluctuation in one resource supply rate demonstrated here, can induce a complex shift in species abundances (Appendix A.2.2), though its
effect on the trait abundances is restricted to the one trait.

5.1 Conservation of community-wide gene frequencies

In the selection model I proposed that three of the four model traits, corresponding to use of each of three resources, are directly heritable, while the fourth trait is the product of a nonlinear interaction between the first three. For example, these three traits might be in direct correspondence to three genes, while the fourth reflects an epistatic interaction between those three genes. In this scenario, under the modeling assumptions outlined here it follows that the ecological balancing process emerging from this community’s dynamics has the ability to maintain the community-wide frequencies of all three genes at constant levels, while the abundances of the four populations making up the community all change in just such a way as to rebalance the uptake of the fourth resource to match its changing supply rate.

This demonstrates the curious possibility that an ecological community may have very simple and orderly dynamics of shared genes or classes of genes, while the community’s composition of species and possibly larger taxonomic units is more variable.

5.2 Functional responses and open questions

It appears that the kind of perturbation studied here (changes in resource supply rate) tends to reorganize the community’s taxonomic composition while conserving its functional composition when the consumers’ functional response curves are roughly linear, while the opposite result holds — reorganizing the functional composition while leaving the taxonomic composition largely unchanged — when the functional response curves are roughly switching.

This result suggests a number of further questions to be investigated, such as the effects of other functional forms, impacts of mixing functional forms, and responses of the community to other perturbations. The dynamics of functional composition of communities encompassing interactions other than resource consumption is left to be studied, as are the impact of horizontal transfer on the dynamics of functional composition and other evolutionary considerations such as linkage and epistasis. It may be productive to investigate whether a community’s need to regulate its functional composition in certain ways can lead to selection for certain kinds of genetic robustness, dispersal, horizontal transfer, or other characteristics. The present study is offered as an initial investigation, presenting an existence proof of the ability of a community to regulate its functional composition independent of its taxonomic makeup, in hope it will open doors to further work.
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A Appendix

A.1 Resource-consumer dynamics

A standard model framework for modeling resource competition in a community of finitely many populations, with no spatial heterogeneity, is known:

\[
\frac{1}{X_i} \frac{dX_i}{dt} = \sum_j w_{ij} f_{ij}(R_j) - m_i, \quad i = 1, \ldots, n
\]

\[
\frac{dR_j}{dt} = t_j(R_j) - \sum_i f_{ij}(R_j) X_i, \quad j = 1, \ldots, m,
\]

where each function \( f_{ij}(R_j) \) is an increasing function of the resource abundance \( R_j \) describing the rate of consumption of resource \( j \) by population \( i \), and the functions \( t_j(R_j) \) describe the rate of supply of each resource from the outside world.
Analysis of the equilibrium conditions of this system of differential equations — the consistency requirements found by equating the above equations’ right hand sides to zero — yields a well-studied description of the behavior of the model community in terms of equilibrium resource abundances \[14\]. The equilibrium condition derived from each \(dX_i/dt\) equation is an equation in the \(R_j\) variables, whose solution is a locus of points in the space of values of \((R_1, R_2, \ldots, R_n)\) at which the net growth of species \(i\) is zero. Those are combinations of resource abundances at which that population’s birth rate, a function of resource availability, balances its mortality rate, which is assumed independent of the resources. That set of points is the zero net growth isocline (ZNGI) of species \(i\), and for a set of species to coexist at equilibrium, the resource abundances must be at a point where all those species’ ZNGIs intersect.

Each ZNGI divides the space of possible resource abundances into two regions, one where the population’s birth rate exceeds its mortality, and the other where mortality dominates. When resources’ availability exceeds the zero-net-growth condition, the consumer population grows and increases resource uptake, drawing them down, and when they are below the ZNGI, the population declines and allows resources to accumulate. In this way the populations regulate the resource availability in their environment, delivering them to the fixed point determined by the intersection of consumers’ ZNGIs.

Given those resource abundances, the equilibrium abundances of the consumer populations are implied by the resource dynamics equations. Setting their right hand sides to zero constructs a system of equations that can be solved for the equilibrium population sizes \(X_i\). At most \(m\) populations can in general coexist on \(m\) limiting resources at equilibrium \[16\], because the \(m\) resource equations can not be solved for more than \(m\) unknowns simultaneously. The rate of consumption of resources is proportional to the number of creatures consuming them, and solving those equations for the population sizes amounts to finding a combination of population sizes that exactly balances out all the resources’ supply rates.

### A.2 Fixed-traits model

Let the total rate of consumption of any resource \(R_i\) be written as a quantity \(T_i\) that is a function \(t_i(X_1, \ldots, X_m)\) of the abundances of all the populations, taking into account their affinity for resource \(i\).

We assume the resource dynamics is responsive to the current resource abundances and to the rate of consumption:

\[
\frac{dR_i}{dt} = f_i (R_1, \ldots, R_m, T_i, t).
\]

Here we have included a dependency on time \((t)\), as we will include a time-varying supply rate of one resource while holding the other parameters constant, below. We assume the population dynamics to be expressed as a per capita rate determined by resource abundances (assumed to take into account the
population’s affinities for each resource):

\[
\frac{dX_j}{dt} = g_j(R_1, \ldots, R_m) X_j.
\]

Let \( A_{ji} \) be the frequency of the trait of consuming resource \( i \) in population \( j \). It follows that the community-wide abundance of the trait of consuming resource \( i \) is

\[
T_i = \sum_j A_{ji} X_j.
\]

**A.2.1 Example model: four-resource, four-species community**

We implement this model in a four-resource, four-population setting, using the functional forms

\[
f_i(R_1, \ldots, R_4, T_i, t) = \left( \hat{R}_i - R_i \right) s_i(t) - T_i R_i,
\]

where \( \hat{R}_i \) is a capacity level of \( R_i \) below which the resources is supplied, and \( s_i(t) \) is the rate of supply of \( R_i \), and

\[
g_j(R_1, \ldots, R_4) = \sum_i A_{ji} R_i - m_j
\]

where \( m_j \) is the per capita mortality rate of population \( j \). We will assume the supply rate \( s_4 \) of resource 4 fluctuates in time while the supply rates of resources 1, 2, and 3 remain fixed.

**A.2.2 Analysis of fixed traits model**

The equilibrium analysis of the model behavior is straightforward. The equilibrium resource abundances \( R_i^* \) are determined by the population dynamics equations at equilibrium:

\[
g_j(R_1^*, \ldots, R_m^*) = 0, \quad \text{for each } j,
\]

under the assumption that all population abundances \( X_j \) are nonzero at equilibrium. This system of \( n \) equations in \( m \) variables generically has a nonempty finite set of solutions when \( m = n \), a continuum of solutions when \( m > n \), and no solutions when \( m < n \). These cases have been treated extensively elsewhere. Here we restrict ourself to the most straightforward case in which \( m = n \) and there is a stable equilibrium at positive population sizes and resource abundances. In that case, the form of this system of equations implies that the resource abundances \( R_i^* \) that solve it are constant in time, independent of the population sizes \( X_j \) and of the resource supply rates \( s_i \) or other parameters that affect the resource dynamics.
| Parameter | Value |
|-----------|-------|
| $\dot{R}_1$ | $\frac{11}{10}$ |
| $\dot{R}_2$ | $\frac{11}{10}$ |
| $\dot{R}_3$ | $\frac{11}{10}$ |
| $\dot{R}_4$ | $\frac{11}{10}$ |
| $s_1$ | $\frac{13}{12}$ |
| $s_2$ | 1 |
| $s_3$ | $\frac{6}{5}$ |
| $s_4$ | $\frac{1}{8}u(t - 600) - \frac{1}{4}u(t - 1200) + \frac{9}{10}$ |
| $m_1$ | 1 |
| $m_2$ | 1 |
| $m_3$ | 1 |
| $m_4$ | 1 |

Table 1: **Numerical values of parameters** used in the fixed-traits model example. $u()$ stands for the unit step function, i.e. $u(t - x) = 1$ for $t \geq x$, 0 for $t < x$.

The equilibrium rates of resource consumption are determined by the resource dynamics equations at equilibrium:

$$f_i (R_1^*, \ldots, R_m^*, T_i^*, t) = 0, \text{ for each } i.$$  

Because the resource abundances are constant independent of environmental conditions, the equilibrium consumption rates $T^*_i$ will also be constant if the resource dynamics function $f_i$ is time-invariant. Note that if $f_i$ depends on $t$, as it does in our example when $i = 4$, then the consumption rate $T^*_i$ can also vary with time.

From the equilibrium consumption rates we can find the equilibrium population abundances $X^*_j$, by solving the equations for consumption rates,

$$t_i (X_1^*, \ldots, X_n^*) = T^*_i, \text{ for all } i.$$  

This does not make it immediately apparent what the values of $X^*_i$ are, but it demonstrates that each $X^*_i$ is a function of all of the consumption rates $T^*_i$, not just one of them. Consequently, a single changing $T^*_i$ generally implies that all the $X^*_i$ values change.
In our example the population dynamics equilibrium equation involving $g_i$ is

$$\sum_i A_{ji} R_i^* = m_j.$$ 

Since the $A_{ij}$ matrix and $m_j$ vector are fixed, provided the matrix is invertible (which is generically true), the equilibrium resource concentrations are fixed at

$$R^* = A^{-1} m$$

independent of their supply rates.

The $f_i$ equation is

$$\left( \hat{R}_i - R_i^* \right) s_i(t) - T_i R_i^* = 0.$$ 

This affords a solution for the community-wide resource uptakes, $T_i$:

$$T_i(t) = \left( \frac{\hat{R}_i}{R_i^*} - 1 \right) s_i(t).$$

The supply rates $s_i$ are constant except for the last one, $s_4(t)$, and so we will write the other three cases without dependence on $t$, and arrive at three constant and one time-varying community-wide uptakes:

$$T^*_1 = \left( \frac{\hat{R}_1}{R_1^*} - 1 \right) s_1$$

$$T^*_2 = \left( \frac{\hat{R}_2}{R_2^*} - 1 \right) s_2$$

$$T^*_3 = \left( \frac{\hat{R}_3}{R_3^*} - 1 \right) s_3$$

$$T_4(t) = \left( \frac{\hat{R}_4}{R_4^*} - 1 \right) s_4(t).$$

Equilibrium population sizes come from the relation between the $T$ and $X$ variables:

$$T_i = \sum_j A_{ji} X_j$$

$$X(t) = A^{-T} T(t).$$

Because the entire vector $X$ may be affected by the time-varying value of $T_4(t)$, in the general case we expect all population sizes $X_j$ to change when the supply of resource 4 changes, although the above solution for the $T$ variables shows that the $X$ values must change in such a way as to leave the first three $T$ values unchanged.
A.3 Selection model

To model the role of potential changes in trait frequencies, I expand the model to make the inheritance and fitness impact of the traits explicit. Traits are assumed heritable at a fixed rate, with a standard diploid population genetics structure. Assume a number of loci $\ell_i$, each of which can bear either allele $a_i$ or allele $\bar{a}_i$. For each species $j$, let $m_j(t)$ be the total number of instances of a given locus in population $j$ (i.e. twice the population size, and equivalent to the count of gametes giving rise to the present population), let $\mathcal{R}$ be the set of resources, and for any set $K \subseteq \mathcal{R}$ let $m_{jK}(t)$ be the number of gametes bearing alleles $a_i$ for each $i$ in $K$ and $\bar{a}_i$ for each $i$ not in $K$. An individual is characterized by its genome, equivalent to two such sets $K$ and $L$, and mating is random, so that the number of individuals bearing that genome is $X_{jKL} = m_{jK}(t)m_{jL}(t)/m_j(t)$.

Let $h_j(K, P, Q)$ be the number of gametes of type $K$ produced by an individual of type $PQ$. We can assume that

$$h_j(K, P, Q) = M_{PQ}(K)w_j(P, Q)$$

where $M_{PQ}(K)$ is the probability that a gamete produced by genotype $PQ$ is of type $K$ and $w_j(P, Q)$ is the reproduction rate of an individual of type $j$ with genotype $PQ$. To make $M_{PQ}$ concrete we assume independent assortment, so that

$$M_{PQ}(K) = \prod_i \pi(I_i(K), I_i(P), I_i(Q))$$

where $I_i(X)$ is an indicator function for $i$, 1 if $i \in X$ and 0 otherwise, and $\pi(a, b, c)$ is the frequency of allele $a$ arising in a gamete when the parent has alleles $b$ and $c$ at the same position: with mutation at rate $\delta$,

$$\pi(a, b, c) = \begin{cases} 
1 - \delta & \text{if } a = b = c \\
\frac{1}{2} & \text{if } b \neq c \\
\delta & \text{if } a \neq b = c.
\end{cases}$$

The reproductive fitness function embodies an increase in fitness conferred by consumption of each resource to which the parent is adapted:

$$w_j(P, Q) = r_j \left(1 + \sum_i s(A_{Pi} + A_{Qi})R_i\right),$$

where $r_j > 0$ is a baseline reproductive rate, $s > 0$ is the increase in reproduction conferred by resource usage, and $A_{Ki}$ is the rate of consumption of resource $i$ per unit by an individual of type $K$. The
consumption rate $A_{Ki}$ is generally taken to be 1 if type $K$ includes trait $i$ and 0 otherwise, though the derived trait for resource 4 in the example model is handled differently: see below for details.

This suffices to define the function $h_j$. The rate of production of gametes of type $K$ is then

$$r_{jK}(t) = \sum_p \sum_q h_j(K,P,Q) \frac{m_{jP}(t)m_{jQ}(t)}{m_j(t)},$$

and the rate of production of genotype $KL$ is

$$r_{jKL}(t) = \frac{r_{jK}(t)r_{jL}(t)}{\sum_{K'} r_{jK'}(t)}.$$ We take mortality to be independent of resource usage, at constant per-capita rate $\mu_j$.

The dynamics of genotype $KL$ in species $j$ is then

$$\dot{X}_{jKL}(t) = r_{jKL}(t) - \mu_j X_{jKL}(t).$$

Because the traits act and are inherited independently, the dynamics can be expressed in terms of single types $K$ rather than the paired genotypes $KL$:

$$\dot{m}_{jK}(t) = \sum_L \dot{X}_{jKL}(t)$$
$$= r_{jK}(t) - \mu_j \sum_L X_{jKL}(t)$$
$$= r_{jK}(t)$$
$$= \mu_j \sum_L m_{jK}(t)m_{jL}(t) / \sum_Q m_{jQ}(t)$$
$$= r_{jK}(t) - \mu_j m_{jK}(t).$$

The dynamics of the resources is similar to the previous model:

$$\dot{R}_i(t) = \left(\dot{R}_i - R_i\right) s_i(t) - T_i(t)R_i,$$

where

$$T_i(t) = \sum_{j,K,L} \left(A_{Ki} + A_{Li}\right) X_{jKL}(t)$$

is the total rate of consumption of resource $i$ by all species:

$$T_i(t) = \sum_{j,K,L} \left(A_{Ki} + A_{Li}\right) m_{jK}(t)m_{jL}(t) / \sum_Q m_{jQ}(t)$$
$$= 2 \sum_{j,K} A_{Ki} m_{jK}(t).$$
| Parameter | Value |
|-----------|-------|
| \( R_1 \) | 11/10 |
| \( R_2 \) | 11/10 |
| \( R_3 \) | 11/10 |
| \( R_4 \) | 11/10 |
| \( s_1 \) | 13/12 |
| \( s_2 \) | 1 |
| \( s_3 \) | 6/5 |
| \( s_4 \) | \( \frac{1}{8} u(t - 300) - \frac{1}{4} u(t - 600) + \frac{9}{10} \) |
| \( r_1 \) | 3/4 |
| \( r_2 \) | 3/4 |
| \( r_3 \) | 3/4 |
| \( r_4 \) | 3/4 |
| \( \mu_1 \) | 225/289 |
| \( \mu_2 \) | 225/289 |
| \( \mu_3 \) | 225/289 |
| \( \mu_4 \) | 225/289 |
| \( \tau \) | 1/10 |
| \( \delta \) | 1/50 |

Table 2: Numerical values of parameters used in the selection model example.

### A.4 Example community of genes model

For the illustration discussed in this paper, we instantiate this model with three genes indexed 1, 2, and 3, and correlated exactly with uptake of resources 1, 2, and 3 respectively. Thus the uptake rates of those resources are

\[
A_{P_i} = \begin{cases} 
1 & \text{if } i \in P \\
0 & \text{if } i \notin P
\end{cases}, \quad i = 1, 2, 3.
\]

We assume the trait of uptake of resource 4 to arise in an epistatic interaction between the above three genes:

\[
A_{P_4} = \max_{i=1,2,3} (1 - A_{P_i}).
\]

Using this mapping we are able to create a community with roughly the same pattern of uptake per species as the fixed-trait model, as can be seen in the initial values of the frequencies shown in Figure 6. The other numerical values used are listed in Table 2.
A.5 Varying functional response relationships

The model of (Appendix A.2), in which the response of each species to resource abundances is a linear function weighted by the traits $A_{ij}$, can be redefined as one of a family of models, mostly nonlinear, parametrized by a real value $\alpha$:

$$
\phi_i = \left( \sum_j (A_{ij} R_j)^\alpha \right)^{1/\alpha}
$$

$$
f_{ij} = (A_{ij} R_j)^\alpha \left( \sum_k (A_{ik} R_k)^\alpha \right)^{1/\alpha - 1}
$$

$$
\frac{dX_i}{dt} = (w_i \phi_i - m_i) X_i
$$

$$
\frac{dR_j}{dt} = t_j - \sum_i f_{ij} X_i.
$$

The linear case is recovered when $\alpha = 1$. In all cases, the total consumption $\phi_i$ by species $i$ is equal to the sum $\sum_j f_{ij}$.

The equilibrium conditions of these dynamics equations, assuming nonzero population sizes, can be written in matrix form:

$$
w \otimes f 1 = m
$$

$$
t = f^T X,
$$

where $\otimes$ stands for pointwise multiplication of vectors.

The vector of trait abundances $M_j = \sum_i A_{ij} X_i$ is $M = A^T X$ in matrix notation. In the following I will assume that matrices $A$ and $f$ are nonsingular.

The dependence of species abundances $X_i$ on resource supply rates $t_j$ is described by the Jacobian matrix $\partial X/\partial t$, whose entries are the partial derivatives $\partial X_i/\partial t_j$. From the above we can see that at equilibrium

$$
\frac{\partial t_i}{\partial X_i} = f_{ij},
$$

or

$$
\frac{\partial t}{\partial X} = f^T.
$$

The opposite Jacobian is the inverse of the above one:

$$
\frac{\partial X}{\partial t} = f^{-T}.
$$

In the $\alpha = 1$ case, we have

$$
f_{ij} = A_{ij} R_j,
$$

which can be written in matrix notation

$$
f = A \text{ diag}(R)
$$

$$
f^{-1} = \text{diag}(R)^{-1} A^{-1}.
$$
In general these matrices are not diagonal. However, the Jacobian matrix for the dependence of trait abundances on resource supplies is
\[
\frac{\partial M}{\partial t} = A^T \frac{\partial X}{\partial t} = A^T f^{-T},
\]
and in the linear case this becomes
\[
\frac{\partial M}{\partial t} = A^T A^{-T} \text{diag}(R)^{-1} = \text{diag}(R)^{-1}.
\]
This matrix is diagonal, confirming the result of Appendix A.2.2 that a change in resource \(j\)'s supply rate affects the abundance of trait \(i\) only and leaves the other traits unchanged.

In the \(\alpha \to \infty\) case, we will see that this dichotomy — community-wide trait abundances are held constant despite changes in species abundances — is perfectly reversed.

The \(\alpha \to \infty\) limit of \(\phi_i\) is a form in which each species identifies the resource it most prefers, as a result of its preference \(A_{ij}\) and the availability \(R_j\), and consumes only that resource:
\[
\phi_i = \max_j (A_{ij} R_j)
\]
\[
f_{ij} = \begin{cases} A_{ij} R_j & \text{if } j = \arg \max_k (A_{ik} R_k) \\ 0 & \text{otherwise} \end{cases}
\]
in the generic case where only one such optimum resource exists for each species. Let us assume without loss of generality that indexes are ordered so that species \(i\) consumes resource \(i\) at equilibrium. Then clearly the matrix \(f\) is diagonal, and it follows that \(f^{-1} = f^{-T}\) is diagonal as well.

That matrix is the Jacobian \(\partial X/\partial t\), implying the result that a change in one resource’s supply rate alters the abundance of the one species that is consuming that resource and leaves the other species unchanged.

However, the Jacobian for community-wide trait abundances,
\[
\frac{\partial M}{\partial t} = A^T f^{-1}
\]
is not diagonal in general, so these trait abundances will in general all be affected by a single resource supply rate, reversing the \(\alpha = 1\) result.