

Trait response in communities to environmental change: effect of interspecific competition and trait covariance structure

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Abstract The response of ecological communities to environmental disturbances depends not just on the number of species they contain but also on the functional diversity of the constituent species; greater variation in the tolerance of species to different environmental disturbances is generally thought to confer greater resistance to the community. Here, I investigate how the functional diversity of communities changes with environmental disturbances. Specifically, I assume that there is variation in traits among species that confer tolerance or sensitivity to environmental disturbances. When a disturbance occurs, variation in species tolerances causes changes in the relative abundances of species, which in turn changes the average tolerance of the community. For example, if tolerance to an environmental disturbance is conferred by large body size, then the environmental disturbance should be expected to increase the average body size of individuals in the community. Despite this expectation, ecological interactions among species can affect the average community response. For example, if larger species are also strong competitors with each other, then this might reduce the increase in average body size in the community, because interspecific competition limits the growth in population density of large bodied species. Similarly, when disturbances affect multiple traits, the covariance in the distribution of trait values among species may restrict the response of any one trait; if two traits provide tolerance to the same disturbance but negatively covary among species, then the response of one trait will limit the response of the other trait

at the community level. Using a Lotka–Volterra model for competitive communities, I derive general formulae that generate explicit predictions about the changes in average trait values in a community subject to environmental disturbances. These formulae demonstrate that competition can impede the change in average community trait values. However, the impediment is not considerable in comparison to the predominant factors of trait variances and species selection effects when species with the most similar trait values also experience the greatest interspecific competition. Similarly, negative covariances among different traits that confer resistance to the same environmental disturbance will impede their responses. I illustrate these results using phytoplankton data from a whole-lake experiment in which manipulation to the zooplankton community created a disturbance to the phytoplankton that changed the selective consumption of large vs. small phytoplankton.

Keywords Functional trait · Interspecific interaction · Phenotypic diversity · Tradeoff · Trait-based approach · Trait dynamics

Introduction

There is a growing consensus that, in general, species diversity enhances ecosystem function (Hooper et al. 2005). To elucidate the causal factors of biodiversity resulting in the above relationship, the trait-based approach, which attempts to summarize properties of communities in terms of the functional traits of composite species, is useful because such approach may find the relationship between contributions of species to ecosystem function and the species' ecological properties, leading to a mechanistic understanding on the diversity-ecosystem function relation-

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ship (Loreau and Hector 2001; Lavorel and Garnier 2002; Eviner and Chapin 2003; Hooper et al. 2005; Mason et al. 2005; McGill et al. 2006; Barnett and Beisner 2007; Savage et al. 2007; Violle et al. 2007; Fox and Harpole 2008).

Great functional diversity in a community promotes total community productivity via the complementarity of resource niches or selection for species with high ecological performance (e.g., Huston 1997; Tilman et al. 1997; Loreau and Hector 2001). In addition, greater diversity of functional traits in a community may give the community greater stability of functional performance under changing environments (Norberg et al. 2001). Greater diversity, or larger between-species variation, of a trait, which determines species-specific tolerance to an environmental change, is expected to increase the likelihood that species tolerant to the environmental change maintain the ecosystem function that would otherwise be reduced by the loss of susceptible species (Klug et al. 2000; Norberg 2000; Fischer et al. 2001; Vinebrooke et al. 2003).

On the other hand, responses of a community to an environmental change may be measured by traits, changes in statistical indices of the trait (e.g., mean, variance, and higher moments) in a community. The mean value of a trait, which is weighted by species' relative abundances, is the simplest and the most important measure. Large responses of the abundance-weighted mean of the trait that determines species' tolerance to an environmental change indicate that the community composition effectively changes in response to the environmental change (tolerant species increase and susceptible ones decrease), and thus maintain community-level functioning more efficiently, compared with cases in which only small changes in the mean trait follow the environmental change as the communities lack tolerant species and the entire set of species decreases at the same rate. In this article I develop a mathematical model which predicts how the mean of species traits in a community responds to environmental drivers, in order to evaluate the importance of functional diversity and to predict the environmental changes of communities in terms of functional traits.

Two complexities should be addressed when developing a general trait dynamics model, multiple traits and interspecific interactions. In real communities, several qualitatively different environmental factors, such as temperature, pH, nutrient level, etc., may act as driving forces of species composition, and multiple traits corresponding to these multiple drivers may result in tradeoffs that determine the relative species composition under a particular set of environmental factors (Frost et al. 1999; Vinebrooke et al. 2004; Litchman et al. 2007; Litchman and Klausmeier 2008). In addition, ecosystem functioning is itself multifactorial, and multiple functions, each defining a separate functional trait, should be incorporated into a functional analysis of communities (Gamfeldt et al. 2008). These

functional traits are likely to be correlated with each other among species in a community, temporarily forming community-specific phenotypic covariance structures. Correlations between traits may complicate the identification of true causal factors because any traits (e.g., body size) correlated with the true target trait (e.g., pH tolerance), that is responsible for the community response to an environmental change (e.g., acidification), may also change as a side effect of the trait correlation, even if the correlated trait (body size correlated with pH tolerance) does not contribute to the community response. Correlation between traits among species can occur as a result of evolutionary divergence of a set of traits that have physiological or genetic tradeoffs, or because of physiological constraints that lead to parallel phenotypic changes in species of a lineage. And they may not be predictable from associations between traits in terms of ecological functions. Responses of the mean trait to environmental changes on the basis of the modeling framework of this study do not depend on the cause of the trait correlation in community.

Previous studies have investigated changes in the distribution of multiple traits (Savage et al. 2007, cf. Norberg et al. 2001), or of a single trait with interspecific competition (Norberg et al. 2001; Tanaka and Yoshino 2009). Very few studies, however, have clearly examined the effects of interspecific interaction on multivariate trait dynamics in a community. Norberg et al. (2001) modeled a change in biomass in relation to a particular trait value based on a growth function of the trait value, the environmental driver, and the total biomass of the community. They derived the dynamics of the mean and variance (or higher moments) of the trait on the basis of the linear relationship between the growth function and the moments of the trait (the moment-enclosure method). Savage et al. (2007) extended the model to include a frequency-dependent response, an interaction function (representing niche complementarity between species) of the trait value, and two distinct correlated traits (e.g., temperature optimum and predator defense).

Here I incorporate in two ways more general regimes of interspecific interaction and trait covariances among arbitrary numbers of traits into a trait dynamics model which predicts changes in abundance-weighted means of traits under an environmental change. Firstly, the model is based on the general Lotka–Volterra equation, and it converts the change in the equilibrium species abundances into the change in the abundance-weighted means of traits in a community. The advantage of the Lotka–Volterra equation is its clear and ecologically relevant definition of interspecific interactions. Secondly, the model adopts the multivariate quantitative genetic model in order to include the indirect effect of an environmental driver directly affecting the mean of a trait to indirectly affect the mean of another trait through the correlation between the traits (Lande 1979, 1982).

To illustrate the use of the trait dynamics model to extract causal factors explaining community responses to environmental changes, I apply the derived model to the response of a phytoplankton community to a whole-lake biomaniipulation experiment, as reported by Jonsson et al. (2005) (cf. Carpenter and Kitchell 1993), and estimate the net selection effect on plankton traits from the observed trait responses to the manipulation and the trait covariances among species. The estimated driving forces of the trait responses in phytoplankton indicate that the existence of top-down cascading effects at the phenotypic level as well as at the biomass level. The discrepancy between the predicted selective forces and the observed trait responses highlights the importance of trait covariances in identification of target trait, through which an environmental driver affects community composition.

Models and analyses

The trait dynamics model

Formulation of trait dynamics with multi-species interaction

The mean functional trait in a community, \bar{Z} , is defined by the abundance-weighted mean trait among the composite species of a community,

$$\bar{Z} = \sum_{i=1}^s p_i Z_i, \tag{1}$$

where p_i is the relative abundance of the i th species, Z_i is the functional trait of the i th species, and s is the number of species in the community. This is the aggregate measure of communities that the present analysis will focus on, and the entire analyses of this article seek the answer to the following questions. How does the mean trait in a community respond to an environmental change? How does the correlation between traits, the interspecific competition or the species richness influence the trait response?

The present analysis depicts the proximate mechanism of the community response to environmental factors as the change in relative species abundances (changes in p), and it does not address local extinction or immigration of species. Thus, the composite species, which is defined as an assemblage of species that compose a community and contribute to community property, remain constant across time. The change in the mean trait per unit time as a result of changes in the relative abundances of the composite species is

$$\frac{d\bar{Z}}{dt} = \sum_{i=1}^s Z_i \frac{dp_i}{dt}. \tag{2}$$

Substituting partial differentials for the total differential of p_i with respect to t , $dp_i/dt = (dn_i/dt)(\partial p_i/\partial n_i) + (dN/dt)(\partial p_i/\partial N)$, where n_i is the abundance of the i th species and N is the total abundance $\sum_i n_i$, into the above equation gives

$$\frac{d\bar{Z}}{dt} = N^{-1} \sum_{i=1}^s (Z_i - \bar{Z}) \frac{dn_i}{dt}, \tag{3}$$

because $\partial p_i/\partial N = -p_i/N$. Thus, the trait change depends on the deviations of species-specific trait values from the community mean values. This quantity, $Z_i - \bar{Z}$, is hereafter denoted by z_i .

The trait response to environmental change can thus be determined from the difference in the mean trait value between the community before and after the environmental change. Note that both before and after the environmental change the population abundances of all composite species are at demographic equilibrium by individual species' reproduction and intra- and interspecific competition. The shift of the mean trait, $\Delta\bar{Z}$, is evaluated by the change in equilibrium abundances, $\Delta\tilde{n}$, as

$$\Delta\bar{Z} = N^{-1} \sum_{i=1}^s z_i \Delta\tilde{n}_i. \tag{4}$$

Without loss of generality, the Lotka–Volterra model describes the rate of change in population abundances of the composite species constituting a competitive community, as follows:

$$\frac{dn_i}{dt} = r_i n_i - \sum_{j=1}^s a_{ij} n_i n_j, \tag{5}$$

where r_i and a_{ij} , respectively, denote the intrinsic growth rate of the i th species and the per capita effect of intra- and interspecific ecological interaction by the j th species on the i th species. In this study, I postulate competition to be the major interspecific interaction, but other categories of interaction, such as predation and cooperation, could be included in the model with minor notational changes.

Equilibrium communities are composed of species whose equilibrium abundances, $\tilde{\mathbf{n}}$, are $\tilde{\mathbf{n}} = \mathbf{A}^{-1} \mathbf{r}$, in which \mathbf{r} is the column vector of r_i and \mathbf{A} is the community matrix whose ij th element is a_{ij} . The effect of the environmental driver affecting the abundance of each species is measured by the rate of change in the intrinsic growth rate due to the environmental change. The species response to environmental change is indicated by the change in the intrinsic growth rate Δr_i . Species with a positive value of Δr_i is more adaptive in the environment after the change than before and would increase its abundance if interspecific interaction is not taken into account. This scheme of environmental effect is identical to the press type of disturbances on

community (Yodzis 1989; Ives 1995). Let $\Delta \mathbf{r}$ denote the vector of Δr_i , the shift in equilibrium abundances is

$$\Delta \tilde{\mathbf{n}} = \mathbf{A}^{-1} \Delta \mathbf{r}. \quad (6)$$

Equations 4 and 6 indicate that the shift of the mean trait due to an environmental change can be evaluated by

$$\Delta \bar{Z} = N^{-1} \mathbf{z}^T \mathbf{A}^{-1} \Delta \mathbf{r}. \quad (7)$$

Thus, the trait response can be evaluated if we know the trait values of the composite species, the community matrix, and the change in the intrinsic growth rate of each species. I checked the numerical precision of Eq. 7 from Eqs. 1 and 5 with various parameter sets (data not shown).

For example, for three species in a community with trait values (e.g., body size) of 1.2, 1.5, and 2.0 (mm), and relative (biomass or numerical) abundances of 0.2, 0.3, and 0.5, the mean trait value is about 1.7, and the \mathbf{z} -vector is $\mathbf{z} = (-0.5 \ -0.2 \ 0.3)^T$ (T : transpose). From Eq. 5, the intraspecific competition coefficient, the diagonal elements of \mathbf{A} , is equivalent to r_i/k_i (where k_i is the carrying capacity of the i th species). The interspecific competition coefficients can be estimated from relative amounts to the intraspecific competition, and for example

$$\text{we may get, } \mathbf{A} = \begin{pmatrix} 0.02 & 0.005 & 0 \\ 0.005 & 0.01 & 0.004 \\ 0 & 0.004 & 0.01 \end{pmatrix}. \text{ Its inverse is}$$

$$\mathbf{A}^{-1} = \begin{pmatrix} 51 & -10 & 1 \\ -10 & 103 & -10 \\ 1 & -10 & 101 \end{pmatrix}. \text{ If the environmental driver}$$

changes the intrinsic growth rate of each species by $\Delta \mathbf{r} = (0.1 \ 0.02 \ -0.15)^T$, and the total abundance of the community before the change is 10, then the change in the mean trait value of the community is estimated as

$$\frac{1}{10} (-0.5 \ -0.2 \ 0.3) \begin{pmatrix} 51 & -10 & 1 \\ -10 & 103 & -10 \\ 1 & -10 & 101 \end{pmatrix} \begin{pmatrix} 0.1 \\ 0.02 \\ -0.15 \end{pmatrix} \text{ or } -0.75.$$

This means that the mean body size of the composite species decreases by 0.75 because small species have become more adaptive than before the environmental change. The effect of interspecific interaction (competition) in this particular example is negligible because the predicted change in the mean trait in the absence of interspecific competition would be nearly the same, -0.74 .

For a community with many more species, full and precise estimation of interspecific interactions (\mathbf{A} matrix) and of changes in intrinsic growth rates of all individual species may not be possible. However, if we make the following three heuristic assumptions, we are able to derive a simplified analytical solution of Eq. 7. The three assumptions are that: (1) the effect of the environmental driver is linearly associated with a functional trait; (2) the community matrix is decomposable into competition matrices, each of which conforms to a limiting similarity

model describing interspecific competition along a particular niche axis; and (3) interspecific competition is sufficiently weak that it has no effect on the whole-community biomass. Incorporation of the last assumption is suspended until presentation of the final, simplest equation.

Linear approximation of a trait-mediated environmental effect

If a trait plays an important role in the species response to an environmental driver, the environmental effect that increased or decreased species abundances must be associated with the trait value of the species. The tolerance of weeds to grazing pressure, for example, may depend on structural strength and repellants' concentration of leaves, and determine how species abundances respond to increased or decreased grazing pressure. One of the simplest and the most general approximations of the relationship between species traits, e.g., the structural strength and the repellants' concentration, and species growth rates in response to environmental change is the linear function of trait (deviations from the mean) $\Delta r(Z) = \frac{\partial \Delta r}{\partial Z} z + c$; the coefficient $\partial \Delta r / \partial Z$ denotes how greatly the species' response to an environmental change in terms of r depends on a species trait. To measure this dependency of the species response on a trait I use the proportional change in r because r values can be considerably different between species due to other environmental factors, and I refer to this measure as the species selection coefficient,

$$I_z = \frac{\partial \Delta r}{r \partial Z}. \quad (8)$$

A positive species selection coefficient ($I_z > 0$) indicates that larger trait values are more advantageous and species having larger values tend to replace species having smaller values after the environmental change, or the reverse if the value of the coefficient is negative. The species selection coefficient is equivalent to the partial regression slope of the rate of change in r against species trait values. Ignoring the intercept c in the above linear function as it does not contribute to the trait dynamics, the change in the population growth is $\Delta r_i = I_z r_i z_i$, and Eq. 7 can be rewritten under assumption (1) as follows,

$$\Delta \bar{Z} = I_z N^{-1} \mathbf{z}^T \mathbf{A}^{-1} \mathbf{z}', \quad (9)$$

where \mathbf{z}' is the vector of $r_i z_i$.

Equations 7 and 9 may include a general implication about how the association between interspecific interaction and species traits affects the trait change in community. The term $\mathbf{z}^T \mathbf{A}^{-1} \mathbf{z}$ in the right side of Eq. 9 measures the distance between \mathbf{A} and the matrix $\mathbf{z} \mathbf{z}^T$ (r_i is assumed the same

among species for simplicity), which is denoted by $\sqrt{\sum_{i,j} |a_{ij} - z_i z_j|^2}$. The distance linearly increases with $\mathbf{z}^T \mathbf{A}^{-1} \mathbf{z}$ and hence with the trait response. This implies that the trait response is reduced if a_{ij} and $z_i z_j$ are positively correlated, or a pair of species which have similar trait values tend to compete more strongly with each other than other combinations of species. In other words, responses to environmental changes by traits that are more strongly connected to interspecific competition than other traits are more constrained by competition than other traits.

Decomposition of the community matrix into multiple niches

The community matrix **A** reflects intra- and interspecific competitions in the total niche space, which is composed of multiple niche axes. In this section, the community matrix **A** is decomposed into niche axes in order to derive an analytical approximation of trait dynamics that is as intuitively interpretable as possible.

The second heuristic assumption allows decomposition of an arbitrary community matrix at a single trophic level as follows. First, **A** is decomposed into the intraspecific competition matrix **B** and the interspecific competition matrix **C**, as $\mathbf{A} = \mathbf{B} + \mathbf{C}$. Matrix **B** includes only the diagonal elements of **A** as non-zero elements. The interspecific competition matrix **C** is further decomposed into niche axis-specific competition matrices **C_k** each representing competition along the (*k*th) niche axis, such that $\mathbf{A} = \mathbf{B} + \sum_{k=1}^{D_N} \mathbf{C}_k$, where D_N is the niche dimension (the number of niche axes). For example, a two-dimensional niche space, where six species compete for two different resources, is illustrated in Fig. 1. If the original community matrix, describing this competition regime, is

$$\mathbf{A} = \begin{pmatrix} 0.8 & 0.5 & 0 & 0.4 & 0 & 0 \\ 0.5 & 0.9 & 0.5 & 0 & 0.3 & 0 \\ 0 & 0.5 & 0.8 & 0.4 & 0.5 & 0.4 \\ 0.4 & 0 & 0.4 & 0.8 & 0.5 & 0.5 \\ 0 & 0.3 & 0.5 & 0.5 & 0.7 & 0.5 \\ 0 & 0 & 0.4 & 0.5 & 0.5 & 0.8 \end{pmatrix}, \text{ then } \mathbf{A} \text{ can be}$$

$$\text{decomposed into } \mathbf{B} = \begin{pmatrix} 0.8 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.9 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.8 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.8 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.7 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.8 \end{pmatrix},$$

$$\mathbf{C}_1 = \begin{pmatrix} 0 & 0.5 & 0 & 0 & 0 & 0 \\ 0.5 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0.4 & 0 & 0 \\ 0 & 0 & 0.4 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0.5 \\ 0 & 0 & 0 & 0 & 0.5 & 0 \end{pmatrix}, \text{ and}$$

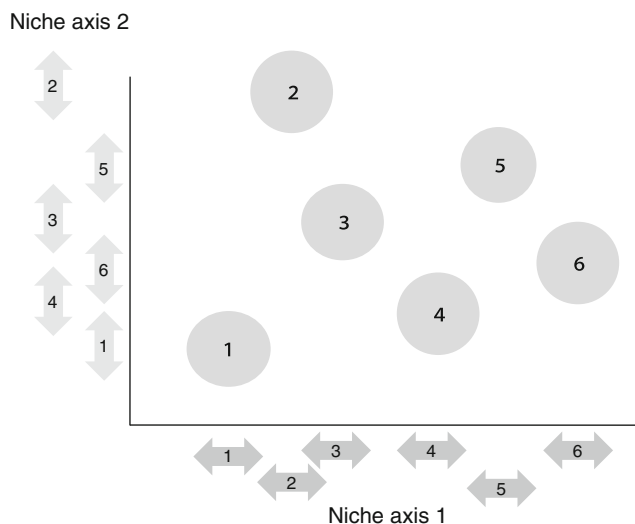


Fig. 1 Schematic drawing of two-dimensional niche space. The numbers indicate species identities, and the shaded rounds represent species niches. The interspecific competition arising from this niche profiles corresponds to the community matrix **A** referred in the text. Competition coefficients along the second niche axis generates the competition matrix **C₂**. Species should be reordered to convert the competition matrix **C₂** into **C₂^{*}** referred in Appendix 1

$$\mathbf{C}_2 = \begin{pmatrix} 0 & 0 & 0 & 0.4 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.3 & 0 \\ 0 & 0 & 0 & 0 & 0.5 & 0.4 \\ 0.4 & 0 & 0 & 0 & 0 & 0.5 \\ 0 & 0.3 & 0.5 & 0 & 0 & 0 \\ 0 & 0 & 0.4 & 0.5 & 0 & 0 \end{pmatrix}, \text{ corresponding}$$

to the two niche axes (see also Appendix 1).

The change in the mean trait is described by Eq. 10 if the strength of the intraspecific competition does not vary among species (shown in Appendix 2), and the interspecific competition conforms to the ideal limiting similarity model (see Appendix 3) in that interspecific competition coefficients are the same between pairs of competing species along each niche axis (the interspecific competition coefficient, α , is a niche axis-specific value),

$$\Delta \bar{Z} = I_z \text{Var}_p(Z) (2 - \beta \lambda_{\max}^{-1} - L \lambda_{\max}^{-1}), \tag{10}$$

where $\text{Var}_p(Z)$ is the abundance-weighted trait variance, $\sum_i p_i z_i^2$; L denotes the effect of competition, $L \cong 1.8 (1 + \frac{2}{s} - \frac{60}{s^2}) \sum_{k=1}^{D_N} \alpha_k \rho_k^2$, where α_k is the interspecific competition coefficient for the *k*th resource (in the *k*th niche axis), ρ_k is the correlation coefficient between the species trait values and the ordered niche position (natural numbers) of the species (see Fig. 2), β is the intraspecific competition coefficient (which is assumed to be the same among species), and λ_{\max} is the largest eigenvalue of **A**.

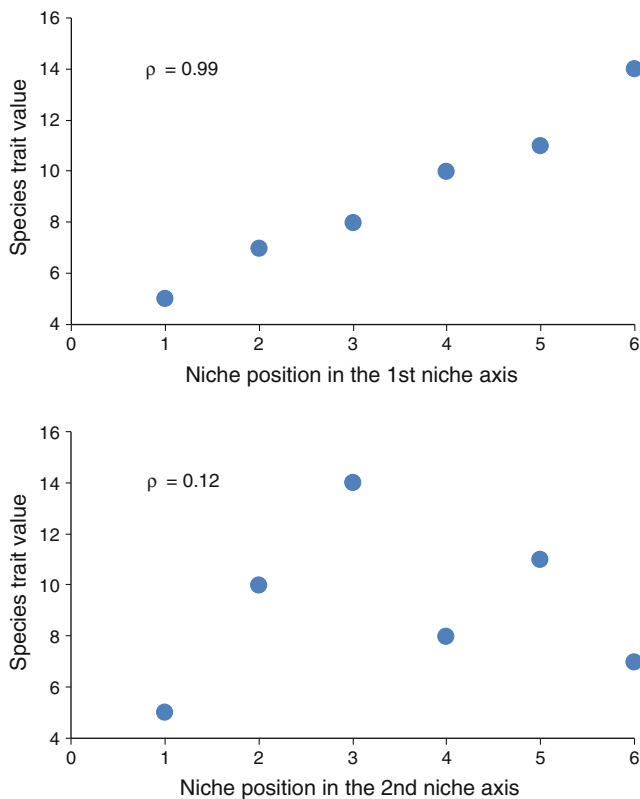


Fig. 2 Two examples of association between species trait values and species niche position. The species traits are $z_1=5$, $z_2=7$, $z_3=8$, $z_4=10$, $z_5=11$, and $z_6=14$ (see Appendix 1). Species niche positions follow the example in the text and Fig. 1. The species traits are highly correlated with the niche positions on the first niche axis, whereas they are poorly correlated with the niche positions on the second niche axis. Consulting with Eq. (11) in the text, the effect of interspecific competition (L/β) is $\frac{2}{0.8} \left(1 + \frac{2}{s}\right) (0.48 + 0.006) = 1.63$ (The competition coefficient for each competition matrix takes the mean value of the coefficients. The interspecific competition coefficients are too large and the number of species is too small for the assumptions for Eq. (11) to be met)

Assumption (3) further simplifies Eq. 10 to

$$\Delta \bar{Z} \cong I_z \text{Var}_p(Z) \left\{ 1 - \frac{1.8}{\beta} \left(1 + \frac{2}{s} - \frac{60}{s^2} \right) \sum_{k=1}^{D_N} \alpha_k \rho_k^2 \right\}, \quad (11)$$

because $\lambda_{\max} \cong \beta$ if the interspecific competition does not influence the total community biomass (see Appendix 4).

Equations 10 and 11 both imply that the trait response is governed by the species selection coefficient and the (abundance-weighted) trait variance, and that it is partly constrained by interspecific competition. Traits that are more closely related to species niche position (ρ is close to unity) have more constrained responses than other traits that are weakly related to species niche position (see Fig. 2). However, the strength of interspecific competition, α , affects the rate of trait response differently depending on whether the total community abundance is affected by

interspecific competition, as implicitly assumed by the Lotka–Volterra equation (whether or not assumption 3 is met).

The influence by interspecific competition to the trait response through the change in the total abundance of community by competition can be inferred from the extreme case in which the trait completely determines the species niche position ($\rho=1$). If the resource partitioning is complete, then the composite species are dynamically independent to each other, and the equilibrium population abundance of individual species is r/β , and the total community abundance is $\beta^{-1}s\bar{r}$. On the other hand, the Lotka–Volterra model (Eq. 5) postulates that interspecific competition due to incomplete resource partitioning results in a total community abundance of $\lambda_{\max}^{-1}s\bar{r}$, where λ_{\max} is the maximum eigenvalue of the community matrix (Appendix 4). Thus, interspecific competition decreases the total community abundance at the rate of β/λ_{\max} . Because the species trait values weighted by the changes in species abundances are normalized by the total community abundance to derive the change in mean trait (Eq. 4), the reduced total abundance by interspecific competition would reinforce the change in mean trait if other factors are kept constant.

Let us consider the special case of a single niche dimension with ideal limiting similarity (all diagonal elements of \mathbf{A} are β , and all sub- and super-diagonal elements are α); thus $\lambda_{\max} = \beta + 2\alpha$. Then, Eq. 10 becomes $\Delta \bar{Z} \cong I_z \text{Var}_p(Z)$ if the number of species is large. Thus, interspecific competition does not affect the trait response because the effect of competition to constrain the trait response and the effect of competition to enhance the trait response by decreasing the total abundance (see Eq. 9) cancel to each other. This is the special case investigated by Tanaka and Yoshino (2009) with more explicit and specific assumptions about competition.

On the other hand, the trait response is slightly influenced by the strength of the competition if the interspecific competition is assumed to have no effect on the total abundance of the community: $\Delta \bar{Z} \cong I_z \text{Var}_p(Z)(1 - 2\alpha/\beta)$. The weak interspecific competition assumption, which enables the above approximation, requires the interspecific competition coefficient, scaled by the intraspecific competition coefficient, to be much smaller than 0.5, reflecting the limited effect of competition on the trait response.

Multiple traits

Consider two traits, Z_1 and Z_2 , which are correlated among species in a community. The response of trait Z_1 consists of the direct effect of species selection, I_1 , which denotes the environmental driving force that affects species relative abundances according to the trait value Z_1 possessed by the

species, and an indirect effect, which is induced by the correlation with the other trait Z_2 but is not attributable to species selection on the focal trait Z_1 itself. Let us consider a hypothetical example in which the body size (Z_1) of zooplankton is negatively correlated with their tolerance (Z_2) to chemical pollutants. Because zooplankton with larger body sizes are more easily captured by planktivorous fish, the fish predation pressure functions as a driving force that reduces the mean body size, $I_1 < 0$. On the other hand, chemical pollution, although it is not a direct driving force on body size, also reduces the mean body size because zooplankton with smaller body sizes are more tolerant to pollutants (the covariance between the traits, $C_{1,2}$, is negative). The species selection coefficient on tolerance to pollutants is positive, $I_2 > 0$, and thus, the total response of body size to pollution and predation at a contaminated site with increased fish density is negative, $I_1 V_1 + I_2 C_{1,2} < 0$, where V_1 is the variance of Z_1 .

In general, the slope of the regression of Z_1 on Z_2 is $C_{1,2}/V_2$, in which V_i is the abundance-weighted variance of the i th trait, and $C_{1,2}$ is the abundance-weighted covariance between traits, and thus the total response of a trait in this two-trait system is

$$\Delta \bar{Z}_1 = I_1 \gamma_1 V_1 + I_2 \gamma_2 C_{1,2}, \tag{12}$$

where $\gamma_i = 1 - \frac{2}{\beta} \left(1 + \frac{2}{s}\right) \sum_{k=1}^{D_N} \alpha_k \rho_{k,i}^2$, and $\rho_{k,i}$ is the correlation coefficient between values of the i th trait and the species niche position in the k th niche axis.

Equation 12 can be extended to an arbitrary number of traits,

$$\Delta \bar{\mathbf{Z}} = \mathbf{D} \mathbf{I}_\gamma, \tag{13}$$

where \mathbf{D} is a variance–covariance matrix that contains $D_{ij} = \text{COV}_p(Z_i, Z_j)$ as the ij th elements, and \mathbf{I}_γ is a column vector of $I_i \gamma_i$; species selection coefficients that are adjusted by the effect of competition.

If there is no correlation between traits among species (all trait pairs are independently distributed among species) and the interspecific interaction is negligible, then the trait responses of all traits are proportional to the species selection coefficients and the trait variances; $\Delta \bar{\mathbf{Z}} = I_z V_z$. This simple relationship does not hold when there are trait covariances or interspecific interactions. The tradeoff between traits may inhibit the trait responses to environmental changes. Equation 12 suggests that the response of trait Z_1 does not occur if $I_1/I_2 = -\gamma_2 C_{1,2}/\gamma_1 V_1$ ($I_2 \neq 0$). Thus, if the covariance with another trait has an opposite sign to that of I_1/I_2 and is of sufficient magnitude, it can inhibit the trait response if there is an advantage for the trait. Interspecific competition can facilitate or mitigate the effect of the tradeoff depending on how closely the related traits are associated with the species’ niche position.

Numerical simulation

The analytical solutions for the trait response (Eq. 10) were compared with numerical simulations, which were based only on the Lotka–Volterra equation (Eq. 5), $\tilde{\mathbf{n}} = \mathbf{A}^{-1} \mathbf{r}$, to examine precision of the analytical approximations.

The first set of simulations was conducted to check the precision with a wide range of responses of a trait that is perfectly linked to species niche position ($\rho = 1$). The symmetrical community matrix was generated by assigning a random number from a uniform distribution between 0 and 0.02 for each pair of sub- and super-diagonal elements (thus the mean competition coefficient $\bar{\alpha}$ is about 0.01). The intraspecific competition coefficient is set $\beta = 0.1$. The intrinsic population growth rate for each species was randomly sampled from a normal distribution with mean 0.5 and standard deviation 0.05. The species trait values were determined from a stochastic linear function: $Z_i = 10 + b(i - 1) + \varepsilon_{i \in N(0,4)}$, where Z_i is the trait value of the i th species (ordered as the niche position), b is the regression slope of trait values to niche positions, and $\varepsilon_{i \in N(0,4)}$ is a random normal variable with mean 0 and standard deviation 4. In this set of runs, I assumed $s = 20$ and $b = 1$, resulting in $\rho \cong 1$. The species selection coefficient I_z was set 0.01 and 0.02, respectively, for two subsets of simulation each consisting of 60 runs, in order to realize a wide range of trait responses. The intrinsic population growth rate of species after the environmental change r' was determined from the change of r expected from the trait value to the species selection coefficient: $r' = r(1 + I_z z)$. The equilibrium community composition before and after the environmental change was respectively determined as $\tilde{\mathbf{n}} = \mathbf{A}^{-1} \mathbf{r}$ and $\tilde{\mathbf{n}}' = \mathbf{A}^{-1} \mathbf{r}'$. The trait responses were calculated as the difference between the abundance-weighted trait means after and before the environmental change.

The trait responses predicted by Eq. 10 accorded well with the simulated trait responses (Fig. 3). The prediction of the simplest equation, $\Delta \bar{\mathbf{Z}} = I_z \text{Var}_p(\mathbf{Z})$, which disregarded interspecific interaction, tended to give underestimates, whereas the differences from the results of simulation were less than 20% in most cases, implying that the trait variance between species and the species selection coefficient are the dominant factors in determining trait responses of community.

The second set of simulations examined the cases where the correlation between species traits and niche positions was less than unity. To generate various values of ρ , I set various b values, 0.1, 0.2, 0.4, 0.6, 0.8, and 1. And thus I repeated ten runs of simulation for each b value (60 runs in the total; Fig. 4). The other parameter values were set the same as in the previous simulation except for $s = 30$, $I_z = 0.01$, and α was constantly 0.02.

The results of simulation did not greatly deviate from those of the theoretical prediction for a wide range of

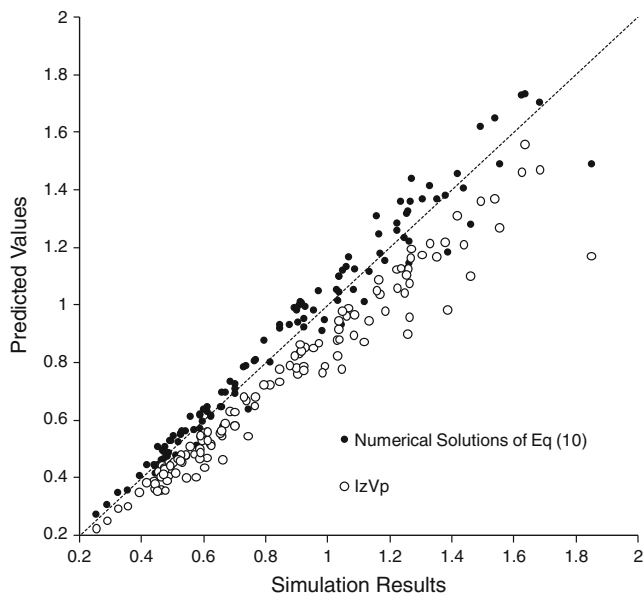


Fig. 3 Trait responses to environmental change predicted from the analytical approximation (Eq. 10; vertical axis) and simulations on the basis of the Lotka–Volterra equation (Eq. 5; horizontal axis). The broken line represents the cases where analytical approximations and simulations are the same. The open circles denote I_2V_p as the predicted values. See text for explanation

correlations between trait and niche (Fig. 4a). The reason why the trait response increased as the correlation increased was that the trait variance increased with b , which decides the amount of the variance component due to regression. The deviation of the predicted responses from the simulation in term of proportion is depicted in Fig. 4b. Predictions of the simplest equation were also presented for comparison. The both predictions were underestimated with ρ less than unity. Equation 10 gave better estimates than the simplest equation, but could not completely adjust the effect of untangling the association between traits and interspecific competition.

As for the second set of simulation, parallel simulations were conducted for the case where interspecific competition did not influence the total abundance in community. To meet this assumption I adjusted the equilibrium species abundance in the simulation \tilde{n}^* by giving each species an uniform apportionment of decrement in the total community abundance that would have resulted from interspecific competition, $\tilde{n}^* = \tilde{n} + s^{-1}(K_T - \sum \tilde{n})$, where K_T was the total abundance in community if interspecific competition were absent, $\sum_i r_i/\beta$. Other procedures of numerical calculations were the same as above except that Eq. 11 was used in the place of Eq. 10.

Similar results as before were derived with the assumption that the total abundance of community was constant, in that results of the simulation did not greatly deviate from theoretical predictions for a wide range of ρ (Fig. 5a). In

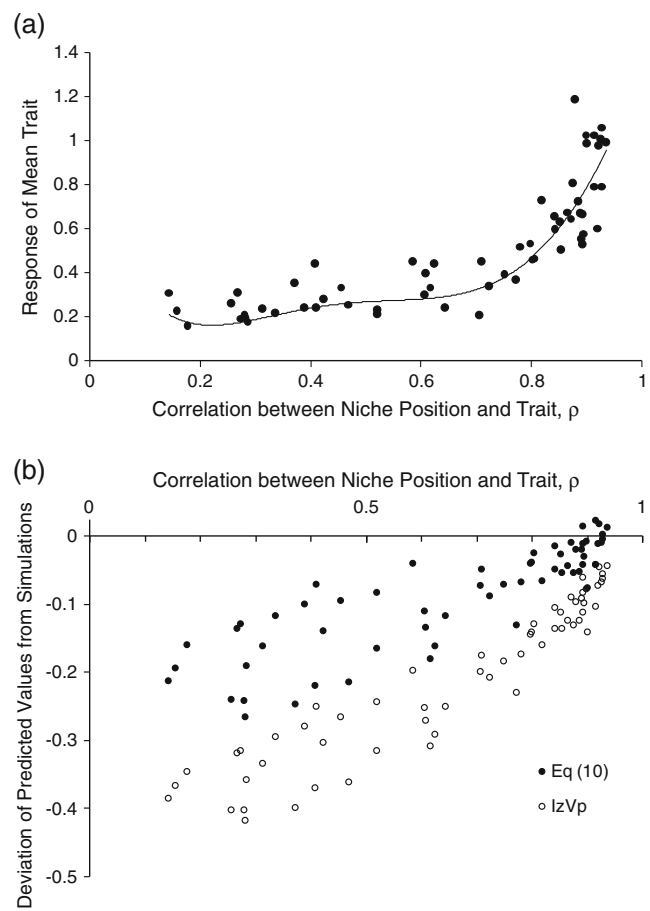


Fig. 4 Trait responses with various strengths of association between species traits and interspecific competition in the case where interspecific competition influences total community abundances; **a** Response of mean trait plotted against correlation ρ between trait values and species niche positions, and **b** association between ρ and deviations in trait responses of predicted values from observed values by simulation. The dark dots in the upper figure **a** denote results of simulation on the basis of Lotka–Volterra equation, and the solid curve is the fifth-order spline curve of the trait responses predicted by Eq. (10). The dark dots in the lower figure **b** denote deviations of the analytical approximations on the basis of Eq. (10) from results of simulation; whereas, the open circles denote parallel values on the basis of I_2V_p . See text for explanation

contrast to the previous case, however, deviations of predicted responses from simulations did not change with values of ρ (Fig. 5b).

Application

Trait responses to biomanipulation in a lake plankton community

To illustrate the application of the present model to real community data, I performed a trait-based analysis (the details of calculation is described in Appendix 5) in an attempt to interpret a published data set of phytoplankton

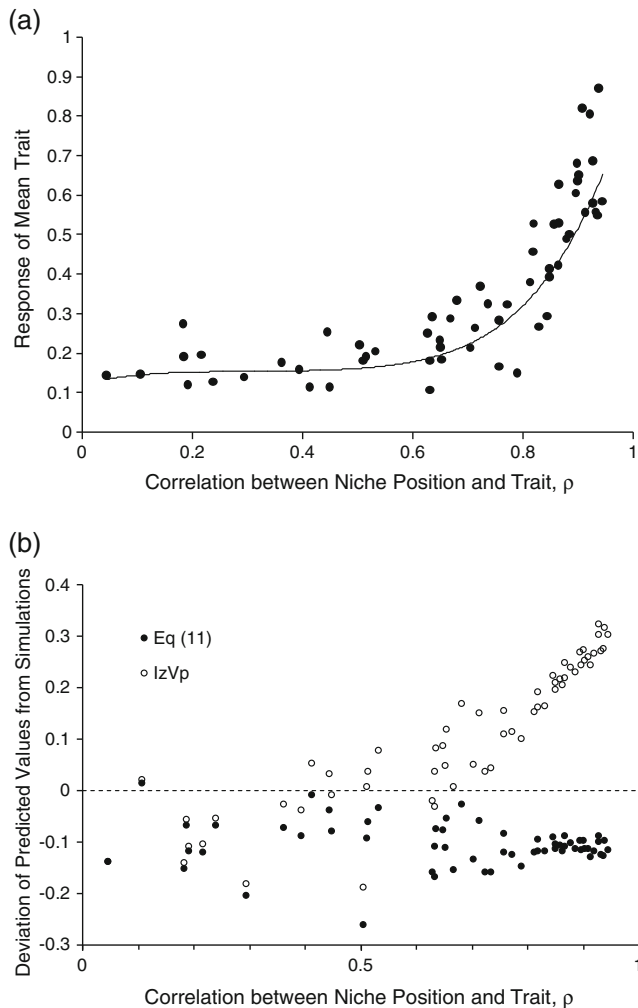


Fig. 5 Trait responses with various strengths of association between species traits and interspecific competition in the case where interspecific competition does not influence total community abundances; **a** Response of mean trait plotted against correlation ρ between trait values and species niche positions, and **b** association between ρ and deviations in trait responses of predicted values from observed values by simulation. The *dark dots* in the upper figure **a** denote results of simulation on the basis of Lotka–Volterra equation, and the *solid curve* is the fifth-order spline curve of the trait responses predicted by Eq. (11). The *dark dots* in the lower figure **b** denote deviations of the analytical approximations on the basis of Eq. (11) from results of simulation; whereas, the *open circles* denote parallel values on the basis of $IzVp$. See text for explanation

community changes in response to a biomanipulation experiment, namely, the exclusion of planktivorous fish and the addition of piscivorous fish to Tuesday Lake, Michigan, USA (Pace et al. 1998; Cohen et al. 2003; Jonsson et al. 2005, cf. Carpenter and Kitchell 1993). The major changes in species diversity after the biomanipulation were a loss of two planktivorous fish and the addition of four phytoplankton species; no change in zooplankton species richness was observed. There were cascading biomass changes between trophic levels (Carpenter and

Kitchell 1993); whereas, relationships between body mass and trophic status or numerical abundances within each trophic level did not noticeably change (Cohen et al. 2003).

The reported data on species composition, numerical abundance, body mass, and predation matrices were based on multiple samplings from May to September in both 1984 and 1986, that is, before and after the biomanipulation (Carpenter and Kitchell 1993). The body mass data, which were originally measured as volumes (m^3), were transformed into the logarithmic scale. These data are available for determining biomass abundance (body mass produced by numerical abundances) and abundance (biomass)-weighted mean trait values. Three phytoplankton traits were analyzed: body mass (BM), mean body mass of the consumers exploiting the focal species (mean consumer size, MC), and the consumer body mass range (consumer size range, RC). Note that MC and RC as well as BM were individually determined for each phytoplankton species as species-specific trait values; MC and RC were defined as the unweighted mean and the range of body mass of zooplankton species (specified from the predation matrix) which consume a particular phytoplankton species. The mean consumer size and the consumer size range represent the edibility of the focal phytoplankton species by their grazers. Completely tolerant phytoplankton species that were not exploited by any zooplankton species were not included in the analysis. And I assumed that the effect of interspecific competition on the trait response in the community was negligible ($\gamma=1$; note, I did not assume there was no competition), because the analyzed traits are unlikely to be highly correlated with the competition ability of phytoplankton for important resources such as light and nutrients (Litchman et al. 2007; Litchman and Klausmeier 2008).

Because the trait values, except body mass, of a particular phytoplankton species depended on the transient species composition of another trophic level (e.g., RC changes with the species composition of the grazer zooplankton), trait changes in the community were decomposed (Table 1) into change due to the context-dependent effect, $\Delta_c Z$, that is attributed to change in the trait values of particular species, and change due to the selection effect, $\Delta_s Z$, that is attributed to changes in species' relative abundances (Fox 2006; Fox and Harpole 2008). Because the present trait-based model deals with the driving force that results in the selection effect, the total trait change in the community must be discounted by the context-dependent effect. The context-dependent change was calculated from the abundance-weighted means of changes in the trait values of particular species before and after the manipulation (Appendix 5). The trait variances and covariances were calculated from species trait values and relative biomass abundances in 1984 because the variance–covariance structure at the earlier time step is

Table 1 Changes in mean functional traits in a phytoplankton community by biomanipulation whole-lake experiment in Tuesday Lake on 1986

Trait	$\Delta_T Z$	$\Delta_C Z$	$\Delta_S Z$
BM	0.040	0	0.040
MC	0.123	0.005	0.118
RC	-0.960	-0.027	-0.933

The total change $\Delta_T Z$ is decomposed into the changes by the condition-dependence effect $\Delta_C Z$ and the selection effect $\Delta_S Z$ (see text for explanation)

BM body mass, MC mean size of consumers, RC range of consumer sizes

expected to influence the trait dynamics caused by environmental changes more than the structure at the later time step.

The expected trait change in response to the biomanipulation was increases in mean body mass of zooplankton, owing to diminished predation pressure from large predators (fish). The observed trait change in the zooplankton agreed with the expected changes (data not shown). However, the observed trait changes in the phytoplankton did not agree with those expected. In phytoplankton, the values of traits BM and MC were expected to decrease under the increased top-down effect of larger zooplankton, whereas the observed changes of BM and MC in the phytoplankton due to the selection effect were positive; that is, both BM and MC increased (Table 1). On the other hand, a large, negative change in RC was observed.

This discrepancy can be explained by trait covariances in the phytoplankton. Body mass (BM) was highly positively correlated with MC and highly negatively correlated with RC, and MC and RC were also highly negatively correlated with each other (Table 2). Large phytoplankton species were grazed only by large zooplankton, whereas small phytoplankton species could be consumed by zooplankton with a wide range of sizes. In addition, the variance of phytoplankton trait MC was very small in comparison with that of the other two traits. Negative species selection on

Table 2 Trait variances/covariances (the upper triangular cells) and correlations (the gothic letters in the lower triangular cells) in the phytoplankton community of Tuesday Lake on 1984

	BM	MC	RC
BM	0.798	0.258	-1.23
MC	0.85	0.115	-0.433
RC	-0.91	-0.84	2.30

BM body mass, MC mean size of consumers, RC range of consumer sizes

MC induced by the increased body size of zooplankton would result in a decrease of MC if the correlation with RC were disregarded. Our result implies that strongly negative selection on RC, which had a large trait variance, canceled the negative (direct) response of MC to the increased zooplankton body size.

The species selection coefficient estimated from the variance–covariance matrix and Eq. 13, $I_z = \mathbf{D}^{-1} \Delta \mathbf{Z}$, reveals the net selection effect on each trait. I disregarded BM from the analysis for the species selection from \mathbf{D} -matrix because BM had very high correlations with the other two traits and might confound the result. In agreement with the qualitative interpretation developed in the previous paragraph, the species selection coefficients for phytoplankton traits were all negative: $I_z = -1.72$ for MC and -0.730 for RC, and the selection pressure was stronger on MC.

In summary, the trait responses are consistent with a top-down cascade effect of the biomanipulation. The reduction of predation pressure on zooplankton generated strong species selection for larger body size in the zooplankton community. The induced change in zooplankton size generated negative selection pressure on both the mean and the range of consumer size for the phytoplankton. This top-down effect was indicated by the species selection coefficients, although the observed trait changes did not necessarily indicate the true driving force of community change because of the confounding effect of trait correlation.

Discussion

In this analysis, I showed that the trait covariance structure and competition regime affect trait shifts due to environmental changes. In general, phenotypic diversity (trait variance) in a community facilitates the rate of change in trait dynamics (Norberg et al. 2001; Savage et al. 2007; Tanaka and Yoshino 2009). However, covariances between traits may either retard or enhance responses of a particular trait to selective forces at the species level, depending on the sign and magnitude of the covariance (Savage et al. 2007), by analogy with the phenotypic evolution of multiple correlated characters (Lande 1979, 1982). A large covariance between traits may even reverse the direction of the observed response to the net force of species selection.

In addition, the competition regime influences the trait dynamics. For the special case of symmetric or quasi-symmetric competition, in which ecological succession does not proceed and multiple species can coexist at equilibrium owing to the lack of strong asymmetry of competition, the trait responses to environmental changes, deduced from Eqs. 11 and 13, can be summarized as follows.

Firstly, the correlation between species traits and environmental effects, that is, the species selection coeffi-

cient, is one of the major determinants of multiple trait dynamics if the covariance between traits is disregarded. However, covariance between traits among species can affect the rate, or even reverse the direction, of trait responses to environmental changes. Tradeoffs between traits, if present, should be taken into account in order to identify the true target trait of species selection that brings about community compositional changes. Secondly, traits that function in resource partitioning are likely to exhibit less responses to the environmental driver than traits, subject to the same environmental driver, that do not function in resource partitioning.

If interspecific interaction greatly affects the magnitude of the trait response at the community level, the trait-based approach may be seriously limited as a tool to identify the drivers of community changes, because in that case full and precise descriptions of ecological interactions among all composite species in a community are needed. The present results indicate that the effect of interspecific interaction does not noticeably alter the rate of a trait response to environmental change when the trait is not correlated with the species niche position ($\rho=0$ in Eq. 10), or when the resource partitioning is equal between competitors (the competition coefficients are symmetric between competitors) and the interspecific competition is considerably weaker than the intraspecific competition.

Thus, a trait-based approach can identify and evaluate environmental drivers without considering interspecific competition if the analysis is limited to traits responsible for community responses to environmental changes or gradients but not directly associated with interspecific competition. For example, phytoplankton body size under changes in zooplankton size or abundance may be one such trait, whereas the ability of phytoplankton to uptake nutrients is likely to be associated with resource competition between species (Cottingham 1999; Litchman and Klausmeier 2008).

On the other hand, the asymmetry of competition may greatly facilitate responses of traits that are associated with competing ability to environmental changes. Some plant traits, such as grazer selectivity (liability to grazing), gap-colonizing ability, and the ability to compete for light (plant height), show long-term responses to changes in grazing pressure (Bullock et al. 2001). Among these traits, grazer selectivity may not be associated with interspecific competition, whereas gap-colonizing ability and the ability to compete for light may influence interspecific competition. The grazer selectivity responded to grazing pressure in winter and spring much more than the other traits, whereas in summer the opposite trend was observed (Bullock et al. 2001). The observation that traits determining species' competitive ability respond to environmental changes more than the trait neutral to competition does not agree with the

present theoretical result. Nonetheless, the competition for vacant gaps and for light with which these traits are associated is likely to be largely asymmetric between species, and the environmental change (increased grazing pressure) may facilitate the competition, which is a situation not considered by the present model.

Asymmetry of competition is caused by resource exploitation or differential minimum resource requirements among species (cf. Tilman 1982), and by vertical ecological interactions in a food web, neither of which is addressed by this paper. Traits that determine a species' ability to dominate other species in asymmetric competition may exhibit more rapid responses to environmental changes than traits neutral to competition when environmental drivers change the strength of competition and thus the relative abundances of species with different competitive abilities. The extraordinarily asymmetric community matrix generated by prey–predator interaction may lead to trait dynamics that are unpredictable within the present modeling framework. Further theoretical studies are necessary to elucidate the effect of asymmetric species interaction on trait dynamics in communities.

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Appendix 1

Decomposition of community matrix The original community matrix **A** is decomposed into an intraspecific competition matrix **B** and interspecific matrices **C** as described in the text. The next step of simplification needed to derive the approximate solution is reordering of the niche-specific interspecific competition matrices. The interspecific competition matrix is reordered (the species order in a **C** matrix is exchanged between species) to produce a matrix **C*** such that neighboring species are the most competitive for any particular species and the approximate limiting similarity model is applicable. For example, Fig. 1 illustrates a two-dimensional-niche space for six species. The reordered competition matrix for C_2 is

$$C_2^* = \begin{pmatrix} 0 & 0.4 & 0 & 0 & 0 & 0 \\ 0.4 & 0 & 0.5 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & 0.4 & 0 & 0 \\ 0 & 0 & 0.4 & 0 & 0.5 & 0 \\ 0 & 0 & 0 & 0.5 & 0 & 0.3 \\ 0 & 0 & 0 & 0 & 0.3 & 0 \end{pmatrix}.$$

The reordering is 1–4–6–3–5–2 from 1–2–3–4–5–6 as the species number (see Fig. 1). The matrix element of C_2^* is $a_{i^*j^*}$, where i^* and j^* is the element number after reordering. There is no change for C_1 ($C_1^* = C_1$), because this is already a competition matrix with limiting similarity.

Before calculating $\mathbf{z}^T C_k \mathbf{z}'$, the elements of the column vector of species traits must be rearranged in the same way as the competition matrix to derive the mean trait change in community. I denote the x th eigenvalues of the k th rearranged niche-specific interspecific competition matrix C_k^* as $\lambda_{(k)x}$, and denote the rearranged trait vector as $\mathbf{z}_{(k)}$. For example, if the species traits of the six species in the above example are $z_1=5, z_2=7, z_3=8, z_4=10, z_5=11$, and $z_6=14$, the reordered trait vector for the second niche axis is $\mathbf{z}_{(2)} = (5 \ 10 \ 14 \ 8 \ 11 \ 7)^T$.

Appendix 2

Expression of the community trait change by eigenvalues of the community matrix Transforming the community matrix or its inverse into appropriate orthogonal axes may lead to some simplifications. The community matrix \mathbf{A} can be diagonalized by the \mathbf{V} matrix (if \mathbf{A} has an inverse matrix), which is composed of right eigenvectors \mathbf{v} as columns: $\mathbf{V} = [\mathbf{v}_1 \ \mathbf{v}_2 \ \dots \ \mathbf{v}_s]$, as $\mathbf{A} = \mathbf{V} \mathbf{D} \mathbf{V}^{-1}$. The diagonal matrix \mathbf{D} includes the eigenvalue λ_i of \mathbf{A} as the i th element. The inverse of \mathbf{A} is similarly transformed as $\mathbf{A}^{-1} = \mathbf{V} \mathbf{D}^{-1} \mathbf{V}^{-1}$. The arrays of row vectors composing \mathbf{V}^{-1} constitute the corresponding left eigenvectors, \mathbf{v}^* . For a special case of symmetric competition, in which the i th element and the j th element of \mathbf{A} is the same, the right and the left eigenvectors are identical, $\mathbf{v} = \mathbf{v}^*$. I will restrict the following analyses for this special case. Thus, $\mathbf{z}^T \mathbf{A}^{-1} \mathbf{z}'$ is equivalent to $\sum_x \lambda_x^{-1} (\mathbf{z} \cdot \mathbf{v}_x) (\mathbf{z}' \cdot \mathbf{v}_x)$, and Eq. 9 is transformed as

$$\Delta \bar{Z} = I_z N^{-1} \sum_{x=1}^s \lambda_x^{-1} (\mathbf{z} \cdot \mathbf{v}_x) (\mathbf{z}' \cdot \mathbf{v}_x). \tag{14}$$

If the number of species is large enough so that deviation of several largest eigenvalues from the maximum eigenvalue are small ($\Delta \lambda_x = \lambda_x - \lambda_{\max} \ll \lambda_{\max}$), the inverse of eigenvalue is approximated by $\lambda_x^{-1} = \lambda_{\max}^{-1} - \lambda_{\max}^{-2} \Delta \lambda_x + \dots \cong \lambda_{\max}^{-1} (2 - \lambda_{\max}^{-1} \lambda_x)$. Equation 14 is rewritten as

$$\Delta \bar{Z} \cong I_z \left\{ 2(N \lambda_{\max})^{-1} \sum_{x=1}^s (\mathbf{z} \cdot \mathbf{v}_x) (\mathbf{z}' \cdot \mathbf{v}_x) - N^{-1} \lambda_{\max}^{-2} \sum_{x=1}^s \lambda_x (\mathbf{z} \cdot \mathbf{v}_x) (\mathbf{z}' \cdot \mathbf{v}_x) \right\} \cong I_z \{ 2 \text{Var}_p(Z) - N^{-1} \lambda_{\max}^{-2} \mathbf{z}^T \mathbf{A} \mathbf{z}' \} \tag{15}$$

since $\text{Var}_p(Z) = (N \lambda_{\max})^{-1} \sum_{x=1}^s (\mathbf{z} \cdot \mathbf{v}_x) (\mathbf{z}' \cdot \mathbf{v}_x)$, where $\text{Var}_p(Z)$ is the frequency-weighted variance of species trait values, $\text{Var}_p(Z) = \sum_i p_i z_i^2$, where p_i is the relative species abundance. Note that $\sum_{x=1}^s (\mathbf{z} \cdot \mathbf{v}_x) (\mathbf{z}' \cdot \mathbf{v}_x)$ is equivalent to

$\mathbf{z} \cdot \mathbf{z}' (\sum_i r_i z_i^2)$, and the relative species abundance is $p_i = r_i / (\lambda_{\max} N)$. because the equilibrium species abundance is approximately $n_i \cong r_i / \lambda_{\max}$ if interspecific competition is weak.

Applying the decomposition of the community matrix, $\mathbf{A} = \mathbf{B} + \sum_{k=1}^{D_N} C_k$, to Eq. 15, it is rewritten as

$$\Delta \bar{Z} \cong I_z \left\{ 2 \text{Var}_p(Z) - N^{-1} \lambda_{\max}^{-2} \mathbf{z}^T (\mathbf{B} + \sum_{k=1}^{D_N} C_k) \mathbf{z}' \right\} \cong I_z \left\{ 2 \text{Var}_p(Z) - N^{-1} \lambda_{\max}^{-2} \mathbf{z}^T \mathbf{B} \mathbf{z}' - N^{-1} \lambda_{\max}^{-2} \sum_{k=1}^{D_N} \mathbf{z}^T C_k \mathbf{z}' \right\} \tag{16}$$

It is apparent that $(\lambda_{\max} N)^{-1} \mathbf{z}^T \mathbf{B} \mathbf{z}' = \bar{a}_{ii} \text{Var}_p(Z) + \text{COV}_p(a_{ii}, z^2)$, where a_{ii} is the intraspecific competition coefficient of the i th species (diagonal elements of \mathbf{A}), and \bar{a}_{ii} is its mean. If the focal trait is not associated with intraspecific competing ability, the covariance between a_{ii} and z^2 is likely to be 0. Thus, $(\lambda_{\max} N)^{-1} \mathbf{z}^T \mathbf{B} \mathbf{z}' = \beta \text{Var}_p(Z)$, where β is the mean intraspecific competition coefficient, $\beta = \bar{a}_{ii}$.

Using the reordering of \mathbf{C} (Appendix 1), we can transform the expression $\mathbf{z}^T C_k \mathbf{z}'$ into $\mathbf{z}_{(k)}^T C_k^* \mathbf{z}'_{(k)}$, in which $\mathbf{z}_{(k)}$ and $\mathbf{z}'_{(k)}$ are the reordered vectors of \mathbf{z} and \mathbf{z}' . It is followed by

$$\begin{aligned} (\lambda_{\max} N)^{-1} \mathbf{z}^T C_k \mathbf{z}' &= (\lambda_{\max} N)^{-1} \sum_{x=1}^s \lambda_{(k)x}^* (\mathbf{z}_{(k)} \cdot \mathbf{v}_{(k)x}) (\mathbf{z}'_{(k)} \cdot \mathbf{v}_{(k)x}) \\ &= \text{Var}_p(Z) \sum_{x=1}^s \lambda_{(k)x}^* \frac{(\mathbf{z}_{(k)} \cdot \mathbf{v}_{(k)x}) (\mathbf{z}'_{(k)} \cdot \mathbf{v}_{(k)x})}{\|\mathbf{z}_{(k)}\| \|\mathbf{z}'_{(k)}\|} \end{aligned} \tag{17}$$

where $\lambda_{(k)}^*$ and $\mathbf{v}_{(k)}$ denote the eigenvalues and the corresponding eigenvectors of the k th reordered competition matrix C_k^* . The numerical value of $\sum_{x=1}^s \lambda_{(k)x}^* \frac{(\mathbf{z}_{(k)} \cdot \mathbf{v}_{(k)x}) (\mathbf{z}'_{(k)} \cdot \mathbf{v}_{(k)x})}{\|\mathbf{z}_{(k)}\| \|\mathbf{z}'_{(k)}\|}$ is not largely affected by replacing $\mathbf{z}'_{(k)}$ by $\mathbf{z}_{(k)}$ if the trait values are not correlated with r among species (numerical examples not shown). Hence, $(\lambda_{\max} N)^{-1} \mathbf{z}^T C_k \mathbf{z}' \cong \text{Var}_p(Z) \sum_{x=1}^s \lambda_{(k)x}^* \frac{(\mathbf{z}_{(k)} \cdot \mathbf{v}_{(k)x})^2}{\|\mathbf{z}_{(k)}\|^2}$, where $\|\mathbf{x}\|$ is the norm of \mathbf{x} , $\sqrt{\sum x^2}$.

Putting $(\lambda_{\max} N)^{-1} \mathbf{z}^T \mathbf{B} \mathbf{z}' = \beta \text{Var}_p(Z)$ and the above expressions for all niche axes into Eq. 16, we get Eq. 10 in the text but with the general and unspecified notation of L .

$$\Delta \bar{Z} = I_z \text{Var}_p(Z) (2 - \beta \lambda_{\max}^{-1} - L \lambda_{\max}^{-1}), \tag{18}$$

where $L = \sum_{k=1}^{D_N} \sum_{x=1}^s \lambda_{(k)x}^* (\mathbf{z}_{(k)} \cdot \mathbf{v}_{(k)x})^2 / \|\mathbf{z}_{(k)}\|^2$.

Appendix 3

Approximate derivation of an analytical L value with the ideal limiting similarity assumption In this appendix, I derive the analytical approximation of $L = \sum_{k=1}^{D_N} \sum_{x=1}^s \lambda_{(k)x}^* (\mathbf{z}_{(k)} \cdot \mathbf{v}_{(k)x})^2 / \|\mathbf{z}_{(k)}\|^2$ to derive Eqs. 10 and 11 for the special case where

the interspecific competition matrix is decomposable into ideal limiting similarity models, in which C_k^* takes the form as

$$\begin{pmatrix} 0 & \alpha_k & 0 & \cdots & 0 \\ \alpha_k & 0 & \alpha_k & & 0 \\ 0 & \alpha_k & 0 & & \vdots \\ \vdots & & & \ddots & \alpha_k \\ 0 & 0 & \cdots & \alpha_k & 0 \end{pmatrix}.$$

The following calculation will focus on the effect of competition concerning the k th niche axis, and the subscript which identifies niche will be disregarded.

Assume that the focal trait is linearly associated with the relative niche position of species, which are sorted in the niche axis such that they compete with adjacent species and are subject to the above ideal limiting similarity model. Thus, the trait value z (deviations from the mean) is expressed in terms of the order of the species possessing the trait in the niche space as follows,

$$z(i) = b(i - s/2) + e, \tag{19}$$

where b is the regression slope of trait values to orders of species, $s/2$ is the mean order, and e is the random deviations of the trait values from the linear regression. As shown below, the slope b does not affect L values and the effect of interspecific interaction. Therefore, the variance of the random deviations e measures the strength of association between trait values and niche positions. Until the last paragraph of this appendix, the deviation is disregarded ($e=0$) to get a simple approximation of L , whereas it will be incorporated in the last paragraph to see the effect of the association between trait values and species niche positions affecting the final approximation. Note that $\|z\|^2 = b^2 \sum_i (i - \frac{s}{2})^2 \simeq b^2 \frac{1}{12} s^3$, and $(z \cdot v_x)^2 = b^2 \sum_i \{(i - s/2)v_{i,x}\}^2$. Putting these expressions into the expression for L (in Eq. 18) for a particular niche axis (subscript k identifying the niche axis is disregarded here), we get

$$L = \frac{12}{s^3} \sum_x \lambda_x^* \sum_i \{(i - s/2)v_{i,x}\}^2. \tag{20}$$

Hence, the regression slope b does not influence L .

The eigenvalues and the corresponding eigenvectors of C^* is $\lambda_x^* = 2\alpha \cos(\frac{x\pi}{s+1})$, and $v_{i,x} = \sqrt{\frac{2}{s+1}} \sin(\frac{ix\pi}{s+1})$ (the i th element of the x th eigenvector). The eigenvectors follow sine functions with different periodicities. And the eigenvectors with the order of odd numbers, v_1, v_3, v_5, \dots , are symmetric at the center of the niche space $s/2$, and does not contribute to L because inner products between these vectors and linear functions are approximately 0.

When x is a natural odd number, it is proven from sums of trigonometric series that $\sum_i \{(i - s/2)v_{i,x}\}^2$

$= \frac{1}{2}(s + 1) \frac{1 + \cos(\theta_x)}{1 - \cos(\theta_x)}$, where $\theta_x = \frac{x\pi}{s+1}$. Then, the product between the above expression and the eigenvalue is

$$\lambda_x^* \sum_i \{(i - s/2)v_{i,x}\}^2 = \alpha(s + 1) \cos \theta_x \frac{1 + \cos \theta_x}{1 - \cos \theta_x}. \tag{21}$$

Numerical check of the above equation was practiced with a mathematical software (MathCad 2000). Because $\cos(\theta_x) \cong 1 - \frac{\theta_x^2}{2}$ when $0 < \theta_x \ll \pi$, the above equation is approximated by

$$\lambda_x^* \sum_i \{(i - s/2)v_{i,x}\}^2 \cong \alpha(s + 1) \left(\frac{4}{\theta_x^2} - 3 \right). \tag{22}$$

Further simplifications may help conceptual understanding on how competition affects the trait dynamics in the sake of numerical precision. If $1 \ll x \ll s$ (the number of species is large and L is explained by several of the most important eigenvectors of C^*) and $\pi \cong 3$, we derive

$$\lambda_x^* \sum_i \{(i - s/2)v_{i,x}\}^2 \cong \alpha(s + 1) \left(\frac{4}{9} (s + 1)^2 x^{-2} - 3 \right). \tag{23}$$

For the approximate evaluation of L , I take the largest three (the second, the fourth, and the sixth) eigenvalues and the corresponding eigenvectors, $L \cong \frac{12}{s^3} \sum_{y=1}^3 \lambda_{2y}^* \sum_i \{(i - s/2)v_{i,2y}\}^2$. Then, we get

$$\begin{aligned} L &\cong \frac{12\alpha(s+1)}{s^3} \sum_{y=1}^3 \left(\frac{1}{9} (s + 1)^2 y^{-2} - 3 \right) \\ &\cong 1.8\alpha \left(1 + \frac{2}{s} - \frac{60}{s^2} \right). \end{aligned} \tag{24}$$

The last expression is a good approximation for $L = \sum_{x=1}^s \lambda_x^* (z \cdot v_x)^2 \|z\|^{-2}$.

Therefore, if a trait determines the niche position of the species such that the trait is linearly associated with the niche position (or, the correlation between the trait and the niche position is 1), the trait response is approximated by $\Delta Z \cong I_z \text{Var}_p(z) \left\{ 1 - \frac{1.8\alpha}{\beta} \left(1 + \frac{2}{s} - \frac{60}{s^2} \right) \right\}$.

However, traits that are incompletely or weakly correlated with the niche position of species are less constrained by competition than the traits that completely determine species' niche position. Such weaker correlation between trait values and niche positions is explained by larger random deviations (e in Eq. 19) from the regression of trait values z to the niche position i . Let $b(i - s/2)$ be written as z_b . It is shown easily that $(z \cdot v_x)^2 = (z_b \cdot v_x)^2 + (e \cdot v_x)^2 + 2(z_b \cdot v_x)(e \cdot v_x)$, where z_b and e are the vectors

of z_b and e . If e is a random variable around 0, it has negligible projection to any eigenvector, $\mathbf{e} \cdot \mathbf{v}_x \simeq 0$. Then, $(\mathbf{z} \cdot \mathbf{v}_x)^2 \simeq (z_b \cdot \mathbf{v}_x)^2$. And, the trait variance is decomposed into the component along the regression line V_b and the variance component around the regression V_e , $s^{-1}\|\mathbf{z}\|^2 = V_b + V_e$. Putting these into the right side of $L = \sum_{x=1}^s \lambda_x^* (\mathbf{z} \cdot \mathbf{v}_x)^2 \|\mathbf{z}\|^{-2}$ gives $L = \sum_{x=1}^s \lambda_x^* (\mathbf{z} \cdot \mathbf{v}_x)^2 \|z_b\|^{-2} \rho^2$, where ρ^2 is the squared correlation coefficient (the coefficient of determination) between trait values and the niche positions, equivalent to $V_b/(V_b+V_e)$. Therefore, L value is approximately equivalent to $2\alpha\rho^2(1 + \frac{2}{s})$ when only a single niche is considered. If the trait is associated with competition on multiple niches, the total L value is summed over all sorts of niche; $L \simeq 2(1 + \frac{2}{s}) \sum_{k=1}^{D_N} \alpha_k \rho_k^2$, where α_k is the competition coefficient on the k th niche axis, and ρ_k is the correlation coefficient between trait values and the niche positions of species on the k th niche axis.

Appendix 4

The “theoretical” change in the total community biomass by interspecific competition The response of mean trait value to environmental change is affected by the total community abundance, N (Eqs. 4, 7, and 9). This implies that the change in mean trait is influenced by whether or not interspecific interaction considerably affect the equilibrium community abundance. This appendix makes the mathematical relationship between the equilibrium community abundance and the interspecific competition explicit.

From $\hat{\mathbf{n}} = \mathbf{A}^{-1}\mathbf{r}$ and $N = \sum_i \hat{n}_i$, the total community abundance is rewritten using the same transformation utilized in Eq. 14 as

$$N = \sum_{x=1}^s \lambda_x^{-1} (\mathbf{r} \cdot \mathbf{v}_x) (\mathbf{u}_s \cdot \mathbf{v}_x) = (\mathbf{r} \cdot \mathbf{u}_s) \sum_{x=1}^s \lambda_x^{-1} \frac{(\mathbf{r} \cdot \mathbf{v}_x)(\mathbf{u}_s \cdot \mathbf{v}_x)}{(\mathbf{r} \cdot \mathbf{u}_x)} \tag{25}$$

where \mathbf{u}_s is the s -dimensional column vector of unity; $\mathbf{u}_s^T = \overbrace{(1 \ 1 \ \dots \ 1)}$. Because \mathbf{v}_x are orthogonal to each other, the summation of $(\mathbf{r} \cdot \mathbf{v}_x)(\mathbf{u}_s \cdot \mathbf{v}_x)$ is equivalent to $\mathbf{r} \cdot \mathbf{u}_s$. Thus the summation in Eq. 25 is the weighted-average of the inverse eigenvalue by $(\mathbf{r} \cdot \mathbf{v}_x)(\mathbf{u}_s \cdot \mathbf{v}_x)$. The maximum eigenvalue of the community matrix, in which the diagonal elements are the dominant elements (interspecific competition is weak in comparison to intraspecific competition), has the corresponding eigenvector whose elements are all positive or negative. The other eigenvectors have much smaller element summations than

the eigenvector of the maximum eigenvalue, $\sum \mathbf{v}_{\max} \gg \sum \mathbf{v}_k$ meanwhile \mathbf{v}_k is not \mathbf{v}_{\max} . Therefore, the total community abundance is about $N \simeq \lambda_{\max}^{-1} (\mathbf{r} \cdot \mathbf{u}_s) \simeq \lambda_{\max}^{-1} s\bar{r}$, where \bar{r} is the unweighted average of r among species. Because $N = \sum_i r_i / \alpha_{ii} = \beta^{-1} s\bar{r}$ if there is no interspecific interaction and the intraspecific competition is constant ($\beta \equiv \alpha_{ii}$), $\lambda_{\max} > \beta$ implies that intraspecific competition decreases the total community abundance than that predicted only by intraspecific density effect in the Lotka–Volterra system.

Appendix 5

The numerical calculation of the species selection coefficient from real community data Relative numerical abundances for all phytoplankton species before and after the biomanipulation was conducted were available from Jonsson et al. (2005) (rearranged in Table 3 in this article), who also supplied data of the body mass in m^3 (BM) and the predation matrix, which specified all trophic relationships, for all phyto- and zooplankton species (data not shown in this article). From the predation matrix, we obtained distribution of BM among zooplankton species which grazed a particular phytoplankton species. The mean and the range of BM of the zooplankton were regarded as phytoplankton traits which represent edibility of the phytoplankton species and were referred to as MC and RC. These traits of particular phytoplankton species could change between the 2 years (1984 and 1986) partly because the species composition of the grazer zooplankton changed between years. These changes were listed as ΔMC and ΔRC (Table 3). The mean values of ΔMC and ΔRC across species weighted by relative biomass abundance (normalized values of $BM \times NA_{84}$) of the phytoplankton are equivalent to $\Delta_C Z$ for MC and RC listed in Table 1. The differences between the 2 years in the mean trait values weighted by relative biomass abundance for each year are equivalent to $\Delta_T Z$ listed in Table 1. The variance-covariance matrix of the three traits were obtained as variances and covariances of species traits, which were weighted by the relative biomass abundances, in the basis of data collected in 1984. For example, the covariance between MC and RC was derived as $\frac{\sum_i BM_i \cdot NA_{84_i} \cdot MC_i \cdot RC_i}{\sum_i BM_i \cdot NA_{84_i}} - \overline{MC} \cdot \overline{RC}$, where \overline{MC} and \overline{RC} are the abundance-weighted means of MC and RC, and the subscripts denote species identities. The \mathbf{D} -matrix was determined as $\mathbf{D} = \begin{pmatrix} 0.115 & -0.433 \\ -0.433 & 2.30 \end{pmatrix}$, and the observed trait responses were transformed by \mathbf{D}^{-1} into the species selection intensities as $\mathbf{I}_z = \mathbf{D}^{-1} \begin{pmatrix} 0.118 \\ -0.933 \end{pmatrix} = \begin{pmatrix} -1.72 \\ 0.730 \end{pmatrix}$.

Table 3 List of phytoplankton species, their abundances and functional traits used for the trait-based analysis of the phytoplankton community in Tuesday Lake (data source: Jonsson et al. 2005)

Species name	BM	NA84	NA86	MC84	RC84	MC86	RC86	ΔMC	ΔRC
<i>Nostoc</i> sp.	$7.97 \cdot 10^{-13}$	$2.0 \cdot 10^6$	0	-7.49	1.79				
<i>Ankyra judayi</i>	$1.53 \cdot 10^{-13}$	0	$1.3 \cdot 10^7$			-8.16	2.36		
<i>Arthrodesmus</i> sp.	$1.52 \cdot 10^{-12}$	$4.9 \cdot 10^7$	0	-7.37	1.19				
<i>Cryptomonas</i> sp1.	$2.44 \cdot 10^{-13}$	$6.4 \cdot 10^7$	$3.3 \cdot 10^7$	-8.13	4.14	-8.01	4.14	0.112	0.00
<i>Cryptomonas</i> sp2.	$1.51 \cdot 10^{-12}$	$2.8 \cdot 10^7$	0	-7.58	1.94				
<i>Cryptomonas</i> sp3.	$6.72 \cdot 10^{-13}$	0	$1.8 \cdot 10^7$			-7.43	1.00		
<i>Cryptomonas</i> sp4.	$1.64 \cdot 10^{-12}$	0	$2.8 \cdot 10^7$			-7.43	1.00		
<i>Chroococcus dispersus</i>	$2.39 \cdot 10^{-13}$	$2.0 \cdot 10^7$	$5.0 \cdot 10^6$	-8.13	4.14	-8.01	4.14	0.112	0.00
<i>Chroococcus limneticus</i>	$1.31 \cdot 10^{-12}$	0	$1.6 \cdot 10^7$			-8.01	4.14		
<i>Closteriopsis longissimus</i>	$2.18 \cdot 10^{-13}$	$1.0 \cdot 10^8$	$1.0 \cdot 10^6$	-7.76	3.47	-7.65	2.81	0.107	-0.660
<i>Cosmarium</i> sp.	$3.71 \cdot 10^{-12}$	0	$1.0 \cdot 10^6$			-7.43	1.00		
<i>Dinobryon bavaricum</i>	$3.90 \cdot 10^{-12}$	$3.0 \cdot 10^7$	$8.0 \cdot 10^6$	-7.29	0.301	-7.29	0.301	0.00	0.00
<i>Dinobryon cylindricum</i>	$3.03 \cdot 10^{-12}$	$3.0 \cdot 10^6$	$6.7 \cdot 10^7$	-7.49	1.79	-7.29	0.301	0.199	-1.48
<i>Dactylococcopsis fascicularis</i>	$1.32 \cdot 10^{-13}$	$4.6 \cdot 10^7$	$1.0 \cdot 10^6$	-7.49	1.79	-7.43	1.00	0.053	-0.783
<i>Dictyosphaerium pulchellum</i>	$4.57 \cdot 10^{-13}$	$1.3 \cdot 10^7$	$1.0 \cdot 10^6$	-7.58	1.94	-7.43	1.00	0.145	-0.943
<i>Dinobryon sertularia</i>	$1.08 \cdot 10^{-12}$	$2.0 \cdot 10^6$	$2.0 \cdot 10^6$	-7.22	0.42	-7.43	1.00	-0.210	0.581
<i>Dinobryon sociale</i>	$6.41 \cdot 10^{-13}$	$2.8 \cdot 10^7$	0	-7.58	1.94				
<i>Glenodinium quadridens</i>	$7.54 \cdot 10^{-12}$	$6.7 \cdot 10^7$	0	-7.19	2.52				
<i>Glenodinium pulvisculus</i>	$5.20 \cdot 10^{-12}$	0	$8.0 \cdot 10^6$			-7.43	1.00		
<i>Gloeocystis</i> sp.	$9.46 \cdot 10^{-11}$	0	$5.0 \cdot 10^6$			-7.29	0.301		
<i>Microcystis aeruginosa</i>	$1.62 \cdot 10^{-11}$	$1.3 \cdot 10^7$	$2.0 \cdot 10^6$	-7.29	0.301	-7.29	0.301	0.00	0.00
<i>Mallomonas</i> sp1.	$1.03 \cdot 10^{-12}$	$1.9 \cdot 10^7$	0	-7.22	0.420				
<i>Mallomonas</i> sp2.	$1.41 \cdot 10^{-12}$	$2.3 \cdot 10^7$	0	-7.37	1.19				
Unclassified flagellates	$3.46 \cdot 10^{-13}$	$1.9 \cdot 10^9$	0	-8.13	4.14				
Unclassified microflagellates	$1.02 \cdot 10^{-13}$	0	$1.3 \cdot 10^8$			-8.01	4.14		
<i>Oocystis</i> sp1.	$3.86 \cdot 10^{-12}$	0	$2.4 \cdot 10^7$			-7.43	1.00		
<i>Oocystis</i> sp2.	$6.32 \cdot 10^{-12}$	0	$3.0 \cdot 10^6$			-7.43	1.00		
<i>Oscillatoria</i> sp.	$1.61 \cdot 10^{-12}$	0	$6.0 \cdot 10^6$			-7.49	0.882		
<i>Peridinium limbatum</i>	$6.46 \cdot 10^{-11}$	$1.7 \cdot 10^7$	$1.0 \cdot 10^6$	-7.29	0.301	-7.29	0.301	0.00	0.00
<i>Peridinium cinctum</i>	$4.06 \cdot 10^{-11}$	$8.0 \cdot 10^6$	0	-7.22	0.420				
<i>Peridinium pulsillum</i>	$1.58 \cdot 10^{-12}$	$1.2 \cdot 10^8$	$1.0 \cdot 10^6$	-7.58	1.94	-7.43	1.00	0.145	-0.943
<i>Peridinium wisconsinense</i>	$3.56 \cdot 10^{-11}$	$1.4 \cdot 10^7$	0	-7.29	0.301				
<i>Quadrigula lacustris</i>	$7.13 \cdot 10^{-12}$	0	$1.0 \cdot 10^8$			-7.29	0.301		
<i>Quadrigula</i> sp2.	$9.48 \cdot 10^{-13}$	0	$1.1 \cdot 10^7$			-7.29	0.301		
<i>Chromulina</i> sp.	$3.03 \cdot 10^{-14}$	$1.5 \cdot 10^8$	$2.1 \cdot 10^8$	-8.13	4.14	-8.01	4.14	0.112	0.00
<i>Schroederia setigera</i>	$6.37 \cdot 10^{-13}$	0	$8.9 \cdot 10^7$			-7.43	1.00		
<i>Selenastrum minutum</i>	$2.72 \cdot 10^{-13}$	$2.0 \cdot 10^8$	$1.1 \cdot 10^7$	-8.13	4.14	-8.01	4.14	0.112	0.00
<i>Sphaerocystis schroeteri</i>	$1.08 \cdot 10^{-11}$	0	$2.0 \cdot 10^6$			-7.43	1.00		
<i>Synedra</i> sp.	$4.61 \cdot 10^{-11}$	$1.0 \cdot 10^6$	$2.0 \cdot 10^6$	-7.29	0.301	-7.29	0.301	0.00	0.00
<i>Trachelomonas</i> sp.	$1.75 \cdot 10^{-13}$	$2.2 \cdot 10^8$	0	-8.13	4.14				

BM body mass, NA84 and NA 86 numerical abundance in 1984 and 1986, MC84 mean consumer size in 1984, MC86 mean consumer size in 1986, RC84 consumer size range in 1984, RC86 consumer size range in 1986, ΔMC species-specific change in MC, ΔRC species-specific change in RC

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