

Trait adaptation promotes species coexistence in diverse predator and prey communities

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Abstract

Species can adjust their traits in response to selection which may strongly influence species coexistence. Nevertheless, current theory mainly assumes distinct and time-invariant trait values. We examined the combined effects of the range and the speed of trait adaptation on species coexistence using an innovative multi-species predator-prey model. It allows for temporal trait changes of all predator and prey species and thus simultaneous coadaptation within and among trophic levels.

We show that very small or slow trait adaptation did not facilitate coexistence because the stabilizing niche differences were not sufficient to offset the fitness differences. In contrast, sufficiently large and fast trait adaptation jointly promoted stable or neutrally stable species coexistence. Continuous trait adjustments in response to selection enabled a temporally variable convergence and divergence of species traits. That is, species became temporally more similar (neutral theory) or dissimilar (niche theory) depending on the selection pressure, resulting over time in a balance between niche differences stabilizing coexistence and fitness differences promoting competitive exclusion. Furthermore, coadaptation allowed prey and predator species to cluster into different functional groups. This equalized the fitness of similar species while maintaining sufficient niche differences among functionally different species delaying or preventing competitive exclusion. In contrast to previous studies, the emergent feedback between biomass and trait dynamics enabled supersaturated coexistence for a broad range of potential trait adaptation and parameters.

We conclude that accounting for trait adaptation may explain stable and supersaturated species coexistence for a broad range of environmental conditions in natural systems when the absence of such adaptive changes would preclude it. Small trait changes, coincident with those that may occur within many natural populations, greatly enlarged the number of coexisting species.

Introduction

Hutchinson's famous paradox of the plankton questions how a large number of phytoplankton species can coexist in a rather homogeneous environment while all compete for the same few limiting resources (Hutchinson 1961). Since then, many potential mechanisms have been identified to promote species coexistence in time and space including resource partitioning, endogenous consumer-resource cycles, imperfect prey selectivity of predators and temporal changes in the physical environment (Tilman et al. 1982; Abrams and Holt 2002; Angert et al. 2009; Ryabov et al. 2015).

According to contemporary theory, species coexistence depends on a balance between niche and fitness differences among species (Chesson 2000). Niche differences stabilize coexistence by intensifying intraspecific competition relative to interspecific competition whereas species-level average fitness differences promote competitive exclusion of less favored species (Tilman 1990; Chesson 2000). Stable coexistence requires that stabilizing niche differences are strong enough to offset the effect of fitness differences (HilleRisLambers et al. 2012). This inequality results in negative frequency dependent selection so that each species is released from overall competition when rare (Chesson and Kuang 2008). For example, an inferior and a superior resource competitor (indicating fitness differences) may coexist due to selective predation on the dominant one (imposing niche differences) as this provokes that each species is either limited by resources or predators (Holt 1977; Leibold 1996; Chase et al. 2002). All processes which reduce fitness differences decrease the extent of niche differentiation necessary for coexistence and slow down the rate of competitive exclusion (Hubbell 2005; Holt 2006; Adler et al. 2010).

Current theory of species coexistence mainly assumes species to have distinct and time-invariant trait values (Tilman et al. 1982; Abrams 1998; Adler et al. 2007) thereby ignoring the potential impact of trait adaptation on coexistence in species rich communities. However, individual species are able to adjust their mean trait values in response to selection on time-scales concurrent with changes in their population densities via adaptive evolution or adaptive phenotypic plasticity (Abrams and Matsuda 1997; Hairston et al. 2005; Abrams 2010; Cortez 2011). Such trait adaptation promoted coexistence in consumer-resource models (Abrams 2006a; Lankau and Strauss 2007; Vasseur et al. 2011; Mougi 2013), by enhancing stabilizing niche differences or reducing destabilizing fitness differences among species. For instance, trait adaptation in resource utilization traits reduced the fitness differences between two competitors by allowing for trait convergence (Fox and Vasseur 2008). Furthermore, trait changes within a generalist species stabilized its coexistence with two specialist species in a consumer-resource (Abrams 2006c) and a predator-prey system (Yamamichi et al. 2011) by promoting recurrent cycles in the limiting factors in which either the generalist or the specialists were favored. This strengthened temporal niche differentiation among species. However, these studies make two critically assumptions which are unlikely to be realistic in nature: they restricted trait adaptation

to one trophic level and assumed that species could adapt their trait values along the entire trait axis of the community.

First, restricting trait adaptation to one trophic level neglects the potential of prey and predator species to mutually adjust their trait values in response to each other (Kishida et al. 2006; McGhee et al. 2013). For instance, prey species may change their size in response to altered predation pressure to reduce their grazing losses (Kuhlmann and Heckmann 1985; Bergkvist et al. 2012; Gilbert and McPeck 2013). To counteract prey defenses and thus to avoid long periods of food shortage grazers may also adjust their size or feeding behavior (Kopp and Tollrian 2003; Kishida et al. 2006; Tirok and Gaedke 2007). This may provoke coadaptation in defensive and offensive strategies of prey and predators that may strongly influence the stability and the shape of their dynamics (Abrams 1986; Dercole et al. 2006; Mougi 2012a; Cortez and Weitz 2014). However, its influence on coexistence of predator species and prey species is still unknown.

Second, assuming that species are able to adapt their trait values along the entire trait axis of the community disregards that species generally differ in their functional traits (McGill et al. 2006) and thus their abilities to cope with different environmental conditions including the relative and absolute abundances of other species. In general, interspecific trait variation strongly exceeds intraspecific trait variation (Albert et al. 2010; Auger and Shipley 2013). The latter is constrained by various factors including a lack of genetic variation, developmental constraints, genetic correlations or costs of plasticity (Smith et al. 1985; Blows and Hoffmann 2005; Kellermann et al. 2009; Murren et al. 2015). Hence, trait changes occurring within ecological time should be restricted to species-specific limits.

In line with classical niche theory, interspecific trait variation and trade-offs between ecologically important traits may result in niche differences that stabilize coexistence as different species are favored at different times and locations (Taper and Case 1985; Tilman 2004; Violle and Jiang 2009; Kraft et al. 2015). For instance, energy and resources can be used either to increase reproduction or resistance leading to a trade-off between strategies maximizing growth and minimizing losses. In this case, coexistence is stabilized by temporal niche differences as the fast-growing prey is favored at low and the defended prey at high predator densities. In contrast, according to neutral theory (Hubbell 2006; Adler et al. 2007) species coexistence may be promoted by the ecological equivalence of species since less stabilizing mechanisms are needed (Fox and Vasseur 2008). Ecological equivalence likely corresponds to a high trait similarity among species (Vergnon et al. 2009; Violle et al. 2012). Therefore, coadaptation may promote coexistence by allowing species of the same trophic level to be more similar (neutral theory) or dissimilar (niche theory). This convergence (increasing equalizing forces) and divergence (increasing stabilizing forces) of traits may strongly depend on the species' ecological feasible ranges of trait adaptation.

In addition, the impact of trait adaptation on species coexistence may strongly depend on its speed (Abrams 2006b; Mougi 2013). Increasing the speed of trait adaptation may reduce

the time-lag in trait adjustments towards the currently favored trait value which generally promotes species coexistence (Vasseur et al. 2011; Abrams 2006c). However, fast trait changes may also promote biomass oscillations and thus stochastic extinction (Schreiber et al. 2011; Tien and Ellner 2012).

Hence, in this study, we investigate the combined influence of the range and the speed of trait adaptation on species coexistence in a multispecies predator-prey system. In accordance with previous work by Tirok and Gaedke (2010) and Bauer et al. (2014) we assumed the prey species to vary in their intrinsic growth rates and vulnerabilities to predation, while predator species differed in respect to their prey selectivity and ability to graze efficiently on low prey densities. We explicitly consider temporal changes in the trait values of all prey and predator species, thereby allowing for coadaptation between species at the same trophic level and for coadaptation between adjacent trophic levels. We also account for niche differences among species by restricting trait adaptation to species-specific ecologically feasible ranges.

We show that a sufficiently large and fast potential for trait adaptation as it generally exists in natural communities strongly promoted species coexistence. Coexistence was generally stable when trait adaptation was restricted to a subset of the entire trait space and rather neutrally stable and thus sensitive to stochastic but not to deterministic extinction when all species could attain almost the same trait values.

Methods

Description of the Multispecies Predator-Prey Model

Based on previous studies (Tirok and Gaedke 2010; Tirok et al. 2011; Bauer et al. 2014) we use a modification of the Rosenzweig and MacArthur (1963) model with an extension to multiple prey types (Murdoch 1973). The model contains S predator and S prey species that differ in their selectivity and edibility, respectively (Fig. 1). To investigate the influence of the range and the speed of trait adaptation on species coexistence, we allow the mean trait values of the individual prey and predator species to change in response to selection. The biomass dynamics of the i -th prey (P_i) and the j -th predator (C_j) species are described by the following equations:

$$\frac{dP_i}{dt} = r_i \cdot \left(1 - \left(\sum_{z=1}^S P_z \right) \cdot K^{-1} \right) \cdot P_i - \sum_{j=1}^S g_{i,j} \cdot C_j \quad (1)$$

$$\frac{dC_j}{dt} = \left(e \cdot \sum_{i=1}^S g_{i,j} - d \right) \cdot C_j \quad (2)$$

where r_i is the intrinsic growth rate of the i -th prey species, K is the common carrying capacity of the prey community, e is the conversion efficiency and d is the per capita death rate of the predators. Foraging on prey i by predator j is defined by the per capita grazing rate $g_{i,j}$ for which we assume a type II functional response:

$$g_{i,j} = \frac{g_{\max} \cdot q_{i,j} \cdot P_i}{\sum_{z=1}^S q_{z,j} \cdot P_z + H_j} \quad (3)$$

where g_{\max} is the maximum per capita grazing rate of all predator species and H_j is the half-saturation constant of the j -th predator species. The interaction between the i -th prey and j -th predator is determined by the preference $q_{i,j}$ depending on the species-specific edibility of the prey, φ_i , and on the species-specific selectivity of the predator, ω_j , both ranging between 0 and 1 (Fig. 1; Fig. 2, A, B).

$$q_{i,j} = \left(1 + e^{-b \cdot (\varphi_i - c \cdot \omega_j)}\right)^{-1} \quad (4)$$

The preference $q_{i,j}$ increases with decreasing values of ω_j and increasing values of φ_i (Fig. 2, C). That is, non-selective predators ($\omega_j \approx 0$) have high $q_{i,j}$ values for all prey species whereas more selective ones ($\omega_j \gg 0$) have high $q_{i,j}$ values only for a more restricted prey spectrum ($\varphi_i \gg 0$) which is quantified by c . The value of b determines the sharpness of the transition of the $q_{i,j}$ values from non-preferred to preferred prey species. We set $b=10$ which generates a sharp cutoff at the edge of the preferred edibility range in agreement with the ‘zero-one rule’ established by optimal foraging theory (Krebs 1980).

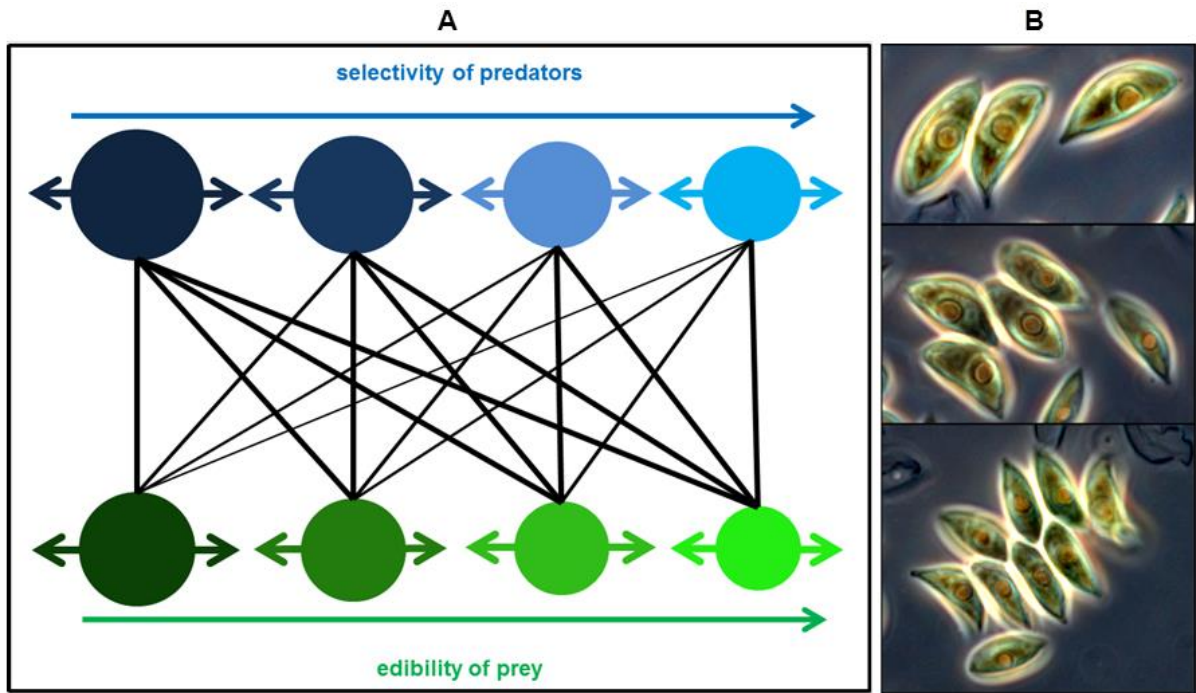


Figure 1. A) Feeding interactions in the predator-prey system: four prey (bottom; green) and four predator (top; blue) species differ in their edibility (φ) and selectivity (ω), respectively, increasing from left to right as also indicated by the size of the circle. The thickness of the lines

corresponds to the degree of the preference $q_{i,j}$. The latter depend on both, φ and ω , and are thus also subject to changes of the mean trait values φ and ω (indicated by horizontal arrows). B) Intraspecific size (trait) variation in phytoplankton species because of colony formation. The species shown is *Acutodesmus obliquus* and forms colonies of 2, 4 and 8 cells which may enable an adaptation to altered grazing pressure by changing its effective cell size.

We assume the intrinsic growth rate of the prey (r_i) to trade off linearly with its edibility (φ_i) (cf. Leibold 1996; Norberg 2004; Fine et al. 2006) and the half-saturation constants (H_j) of the predators to trade off linearly with their selectivity (ω_j) (cf. Tessier et al. 2000; Straub et al. 2011) (Fig. 2, A, B):

$$r_i = (r_{\max} - r_{\min}) \cdot \varphi_i + r_{\min} \quad (5)$$

$$H_j = -(H_{\max} - H_{\min}) \cdot \omega_j + H_{\max} \quad (6)$$

That is, the most edible prey species ($\varphi_i=1$) has an intrinsic growth rate of r_{\max} and the least edible prey species ($\varphi_i=0$) of r_{\min} . Similarly, the maximum (H_{\max}) and minimum (H_{\min}) half-saturation constants correspond to the food demand of the least ($\omega_j=0$) and most ($\omega_j=1$) selective predator species in the model, respectively. Hence, high food selectivity is connected with the ability to maintain positive net-growth at low prey densities.

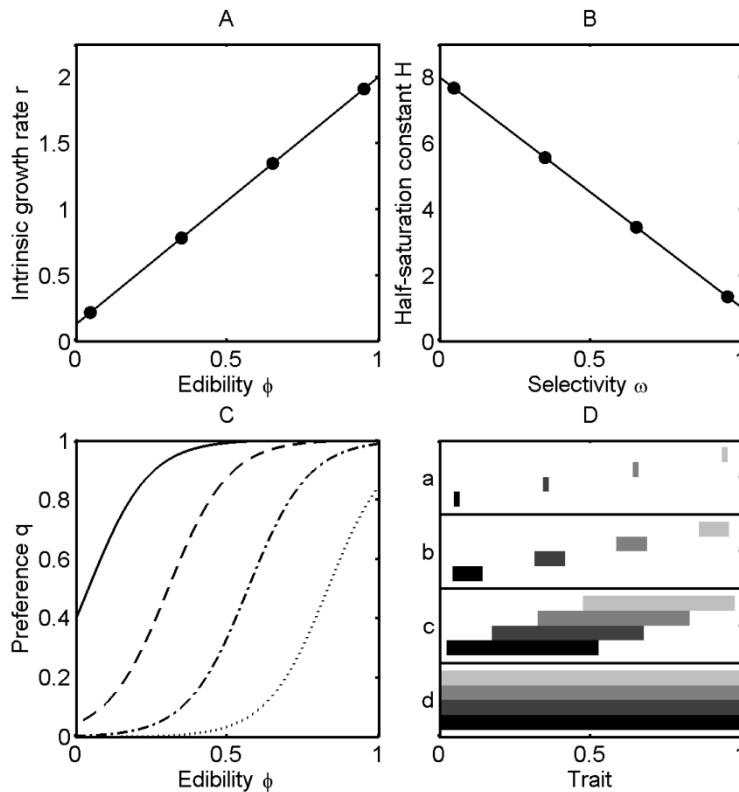


Figure 2. A) Trade-off between the intrinsic growth rate r and edibility φ of the prey species. B) Trade-off between the half saturation constant H and selectivity ω of the predator species. The dots mark the center of the four prey and four predator niches along their trait axes. C) Preference q in dependence of φ for $\omega=0.05$ (solid), $\omega=0.35$ (dashed), $\omega=0.65$ (dashed-dotted)

and $\omega=0.95$ (dotted). D) Width of the ranges of trait adaptation of the 4 species (represented by different shades of grey) that increase from low [a) 0.02, b) 0.1] to high [c) 0.5, d) 1] values of w (cf. methods).

The individual prey and predator species are able to change their edibility (φ_i) and selectivity (ω_j) within species-specific limits in response to altered environmental conditions to increase their per-capita net-growth rates. These changes were modeled using a general description for selection on a quantitative trait (Lande 1976; Abrams et al. 1993; Abrams 2010):

$$\frac{d\varphi_i}{dt} = v \cdot \left(\frac{\partial R_{P_i}}{\partial \varphi_i} + B(\varphi_i, \Phi_i) \right) \quad (7)$$

$$\frac{d\omega_j}{dt} = v \cdot \left(\frac{\partial R_{C_j}}{\partial \omega_j} + B(\omega_j, \Omega_j) \right) \quad (8)$$

where $R_{P_i}=(1/P_i) \cdot dP_i/dt$ and $R_{C_j}=(1/C_j) \cdot dC_j/dt$ are the per-capita net-growth rates of the i -th prey and j -th predator species. We extended the Geber-Price method (Hairston et al. 2005) to multispecies communities to show that the parameter v scales the speed of trait adaptation relative to the species' biomass dynamics (Appendix A). Although the approach of quantitative genetics has been used primarily for traits with a genetic basis (Lande 1982) it may also be used to account for changes in the mean trait value via adaptive phenotypic plasticity (Abrams 2010). In this case v may not only depend on the heritable additive genetic variance or mutation rate within a species' population (Lande 1982; Dieckmann and Law 1996), but also on the speed of an individual's plastic response to selection (Abrams and Matsuda 2004; Mougi and Iwasa 2011). Hence, v expresses the potential for a response to a selective pressure leading to an adaptive or plastic response. In our model, values of $v>0.25$ can only arise in the presence of adaptive phenotypic plasticity since the additive genetic variance cannot exceed this value under our model constraints ($0<\varphi<1$ and $0<\omega<1$). For the sake of brevity, we herein refer to v as the speed of trait adaptation (cf. Mougi 2012b). The boundary function B restricts trait adaptation to the species' ecological feasible range (i.e. its niche) by ensuring that $d\varphi_i/dt$ and $d\omega_j/dt$ strongly increase or decrease when φ_i and ω_j approach their lower ($\varphi_{i,min}=(1-w) \cdot \Phi_i$) or upper ($\varphi_{i,max}=(1-w) \cdot \Phi_i+w$) limits, respectively (cf. Abrams and Matsuda 2004; Abrams 2010):

$$B(\varphi_i, \Phi_i) = -\tan \left(\frac{\pi}{2} \cdot \left(\frac{2}{w} \cdot (\varphi_i - (\Phi_i - w \cdot (\Phi_i - 0.5))) \right)^{(2 \cdot s + 1)} \right) \quad (9)$$

$$B(\omega_j, \Omega_j) = -\tan \left(\frac{\pi}{2} \cdot \left(\frac{2}{w} \cdot (\omega_j - (\Omega_j - w \cdot (\Omega_j - 0.5))) \right)^{(2 \cdot s + 1)} \right) \quad (10)$$

The parameters Φ_i and Ω_j determine the locations of the prey and predator niches along their trait axes and thus refer to general niche differences among species (Fig. 2). The width of the species' niches and thus their accessible ranges of trait adaptation are determined by the parameter w (Fig. 2, D). For $w=0$ species are not able to change their trait values in response to selection whereas for $w=1$ all species share the same range of trait adaptation. The parameter s determines the steepness of B at the edges of the species' trait range. A more detailed discussion of eq. 7 and eq. 8 is given in Appendix B and in Abrams (2010).

Numerical simulations

We conducted numerical simulations of our model for different values of w and v in which we allowed (extinction study) or prevented species extinction (invasion study). The first approach enables the investigation of the extent and stability of species coexistence by recording the final richness, i.e., the number of species surviving until the end of the simulation, the presence of long-term trends in the species biomass dynamics and their sensitivity to environmental noise. Coexistence is expected to be stable if the biomass dynamics exhibit no long-term trends and rather low sensitivities to environmental noise. The second approach reveals the stabilizing and equalizing mechanisms crucial for species coexistence.

Extinction Study

We simulated a full-factorial combination of 31 values of the speed v ($[10^{-3}, 10^{-2.9}, \dots, 10^0]$) and 21 values of the range w ($[10^{-2}, 10^{-1.9}, \dots, 10^0]$) of trait adaptation for a system with initially 4 prey and 4 predator species (cf. Fig. 1, A). We assumed a regular spacing of the values of Φ_i and Ω_j along the respective trait axes with Φ_1 and Ω_1 equal to 0.05 and Φ_4 and Ω_4 equal to 0.95 representing a high niche differentiation among species in the absence of trait adaptation. Initial trait values φ_i and ω_j were set equal to the species-specific constants Φ_i and Ω_j . To generalize the results we also simulated systems with 16 prey and 16 predator species for $w=0.2$ and for three different values of v ($10^{-1.5}$, 10^{-1} , $10^{-0.5}$).

We parameterized our model in accordance with previous studies (Table 1; Tirok and Gaedke 2010; Tirok et al. 2011; Bauer et al. 2014) for planktonic systems consisting of phytoplankton and their ciliate predators (Hansen et al. 1997; Tirok and Gaedke 2007). We kept the initial total biomass of prey and predators constant at $K/2$ and $K/6$, respectively, but varied the initial distributions of species' biomasses in 5 ways: even across species, decreasing and increasing linearly along the trait axes, and negative and positive parabolic distributions. The resulting 25 different initial conditions (5 for the prey, 5 for the predator) allowed us to capture potential variation in the final species composition. Each simulation lasted for 10^5 time units. We assumed species as extinct and set their biomasses to zero if their biomasses dropped below 10^{-9} of the carrying capacity K .

To distinguish between stable coexistence and prolonged co-occurrence we evaluated the presence of long-term trends in the species biomass dynamics which indicate prolonged

transients and ongoing competitive exclusion (Chesson 2000). We estimated the long-term trends for systems showing at least some biomass variation in time ($CV > 10^{-3}$) by calculating the Pearson correlation between \log_{10} biomass and time, using the last 10^4 time steps. We evaluated the significance of the correlation coefficients by comparing their values against a null distribution of 100 correlation coefficients that were obtained from randomized time series of biomasses ($p < 0.05$).

Table 1. State variables and parameters used in the model following Tirok and Gaedke (2010). The parameters are inspired by considering the biomasses in units of carbon in the upper most 20m of the water column of Lake Constance corresponding approximately to the euphotic zone and the epilimnion (Tirok and Gaedke 2007). Hence, the units g/m^2 of biomasses refer to the biomass in the water column of the upper meters ($\text{m} \cdot \text{g/m}^3 = \text{g/m}^2$).

Variables	Description	Unit	Values
<i>Biomasses</i>			
P	Prey biomasses	g C m^{-2}	-
C	Predator biomasses	g C m^{-2}	-
<i>Traits</i>			
Φ	mean edibility of prey	-	-
Ω	mean selectivity of predators	-	-
Parameters	Description	Unit	Value
<i>Biomasses</i>			
K	common carrying capacity	g C m^{-2}	10
H_{\max}	maximum half saturation constant	g C m^{-2}	8
H_{\min}	minimum half saturation constant	g C m^{-2}	1
E_t	Extinction threshold = minimum biomass	g C m^{-2}	10^{-8}
<i>Rates</i>			
D	death rate of predators	day^{-1}	0.15
g_{\max}	maximum grazing rate of predators	day^{-1}	2
r_{\max}	maximum growth rate of prey	day^{-1}	2
r_{\min}	minimum growth rate of prey	day^{-1}	0.25
<i>Traits</i>			
W	Width of species' potential trait range	-	0.01 – 1
V	Trait responsiveness	-	0.001 – 1
<i>Scaling</i>			
E	conversion efficiency of predators	-	0.3
S	steepness of the boundary function	-	10
C	scaling of the preference function	-	7/8
B	steepness of the preference function	-	10

To further distinguish between stable and neutrally stable coexistence we tested for the sensitivity of the species biomass dynamics to environmental noise by continuing the simulations for 6 parameter combinations of w ($[0.1, 1]$) and v ($[10^{-1.5}, 10^{-1}, 10^{-0.5}]$) with and without noise. In both cases, we started the simulations with the final state of the previous model runs. In the second case we additionally added multiplicative white noise to the biomass dynamics to mimic environmental stochasticity (cf. eqns. 1 and 2 and Braumann 2008):

$$\frac{dP_i}{dt} = r_i \cdot \left[1 - \left(\sum_{z=1}^S P_z \right) \cdot K^{-1} \right] \cdot P_i - \sum_{j=1}^S g_{i,j} \cdot C_j + n(0, \varepsilon) \cdot P_i \quad (11)$$

$$\frac{dC_j}{dt} = \left(e \cdot \sum_{i=1}^S g_{i,j} - d \right) \cdot C_j + n(0, \varepsilon) \cdot C_j \quad (12)$$

The random numbers were drawn independently from a normal distribution with mean and standard deviation equal to 0 and ε for each time step and differential equation prior to the numerical integration. We run 25 replicates of stochastic simulations for 10^5 time steps using two different values of ε (0.05 and 0.005) and compared their average final richness to the final richness obtained without disturbance. Environmental stochasticity is expected to promote stochastic extinctions in case of neutrally stable coexistence but not in case of stable coexistence.

Finally, we evaluated a potential clustering of species in the trait space by discretizing the trait axis into functional groups, each of which had a width equal to 0.01.

Invasion Study

To reveal the causes underlying the pattern in final richness we assessed the effects of w and v on stabilizing and equalizing mechanisms acting within the prey community. First, we estimated time-averaged niche differences (ND) and fitness differences (FD) among prey species by employing two indices given in Carroll et al. (2011):

$$ND = 1 - \prod_{k=1}^S \sqrt{s_k} \quad (13a)$$

$$FD = \exp \left[\left(\frac{1}{S} \sum_{k=1}^S (\ln s_k)^2 - \left(\frac{1}{S} \sum_{k=1}^S \ln s_k \right)^2 \right)^{\frac{1}{2}} \right] - 1 \quad (13b)$$

with

$$s_k := \frac{I_{k,a} - I_{k,p}}{I_{k,a}} \quad (13c)$$

The index s_k describes the standardized difference between the invasion growth rates (I) of the k -th prey species in the absence ($I_{k,a}$) and presence ($I_{k,p}$) of its resident community. This index thus represents the species' sensitivity to interspecific competition such as direct resource or predator-mediated, apparent competition (Carroll et al. 2011). An invader with substantial niche differences to the resident community experiences weak negative effects from interspecific competition, keeping I_p close to I_a and s_k small. In contrast, small niche differences yield strong competition among species which reduces I_p and increases s_k . Large fitness differences (FD) imply that the effect of interspecific competition on the fitness of a focal species varies greatly

among species whereas small fitness differences (FD) arise when all species experience a similar intensity of interspecific competition. In contrast to Carroll et al. (2011), we subtract 1 from the main expression in eq. 13b so that FD is zero when all species have equal fitness.

We calculated I_a for the prey analytically using their intrinsic growth rates in monoculture at their maximum edibility. To determine I_p we set the biomass of the invading prey species to zero which prevents actual growth in its biomass but we still allowed its trait value to change in response to selection. To prevent the exclusion of the resident species we added a small immigration rate ($I=10^{-8}$) to equations 1 and 2 describing the prey and predator biomasses dynamics. We conducted these simulations by following a bifurcation approach which allows us to stick to a certain attractor of the species composition. Hence, we initially ran the model for 10^5 time steps with low values of w (0.01) and v ($10^{-1.5}$) and then used the final values to initialize runs at slightly higher parameter values, iterating this process across a range of w ($[10^{-2}, 10^{-1.97}, \dots, 10^0]$). We estimated I_p from the last 10^4 time steps.

This approach is based on the invasibility criterion, stating that prey species stably coexist if all are able to increase from low densities in the presence of their competitors, i.e. if intraspecific competition is larger than interspecific competition at low density (Chesson 2000). Furthermore, when applied to non-equilibrium dynamics, the invasibility criterion relies on temporal averaging and therefore ignores niche differences that may arise only during critical temporary periods. Hence, we also assessed temporal niche differences among prey species based on pairwise temporal correlations between their mean trait values using the last 10^4 time steps of simulations where all species were kept in the system by adding a small immigration rate to equations 1 and 2. Positive correlations between trait dynamics indicate that species respond very similar to environmental changes whereas negative correlations indicate differences in response.

Simulations and analyses were performed in MATLAB, version 7.13, using solver ode23 for ODEs (The MathWorks Inc., Natick, MA, 2011). We increased the precision of the solver by reducing the absolute and relative tolerance to 10^{-10} and 10^{-8} and the maximum step size to 0.001.

Results

The range (w) and speed (v) of trait adaptation strongly influenced species coexistence. For brevity, we block the presentation of the results into 4 regions of the parameter space that exhibit common patterns and discuss their dynamics and underlying mechanisms. In general, small ($w < 0.04$) and slow ($v < 0.03$) trait adaptation did not promote species coexistence (Fig. 3 A, regions E1, E2). A simultaneous increase in w and v resulted in considerable adjustments of the species' mean trait values that enabled both stable (Fig. 3 A, region C1) and rather neutrally stable coexistence (partly very slow exclusion; Fig. 3 A, region C2). These general findings are independent of the exact parameter values chosen (see Appendix C). Since final prey and predator richness were highly correlated ($R^2=0.89$) we jointly consider them.

Small trait adaptation did not promote species coexistence - Region E1

Small ranges of trait adaptation ($w < 0.04$) prevented distinct changes in the trait values over time whereas the biomasses showed large amplitude oscillations at the beginning of the simulation leading to rapid exclusion of numerous species and low final richness, irrespective of v (Fig. 3, A; Fig. 4). After 10^5 time units typically one predator-prey pair survived showing either oscillatory or stable dynamics depending on the remaining trait values (Fig. 3, D; Fig. 4). The initial prey and predator species exhibited considerable trait and niche differences as indicated by high values of the related index, ND , where each species occupied its own niche with little overlap to others, stabilizing coexistence (Fig. 3, E). However, the species also exhibited large fitness differences as indicated by high values of the index, FD , promoting competitive exclusion (Fig. 3, E). According to the difference between ND and FD the niche differences among species did not stabilize coexistence sufficiently to compensate for their fitness differences giving rise to species extinction (Fig. 3, F).

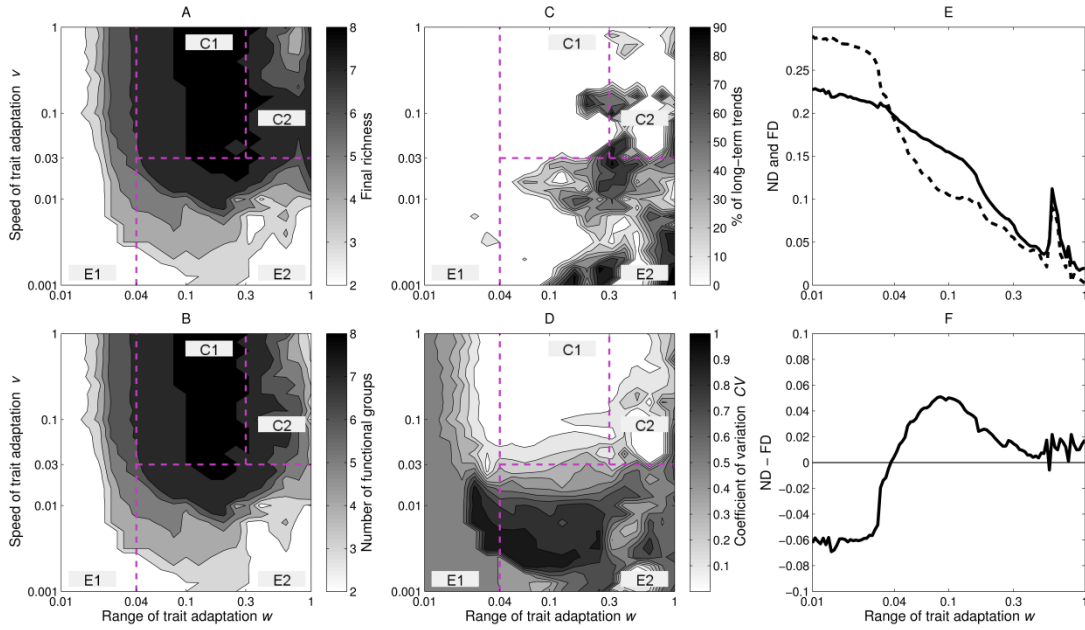


Figure 3. A) Summed final prey and predator species richness, B) summed number of prey and predator functional groups, C) percentage of remaining prey and predator species exhibiting long-term trends in their biomass dynamics and D) the mean coefficient of variation of prey and predator population dynamics during the last 10,000 time steps averaged over all initial conditions in dependence of the range (w) and speed (v) of trait adaptation for initially 4 prey and 4 predator species. Four regions exhibiting similar patterns are marked: 2 regions of extinction of numerous or all species (E1, E2) and 2 regions of species coexistence (C1, C2). E) Estimated time-averages of niche (ND , solid) and fitness differences (FD , dashed) among the 4 prey species and F) estimated net-stabilizing effects based on their difference for $v = 0.03$ in dependence of the range (w) of trait adaptation.

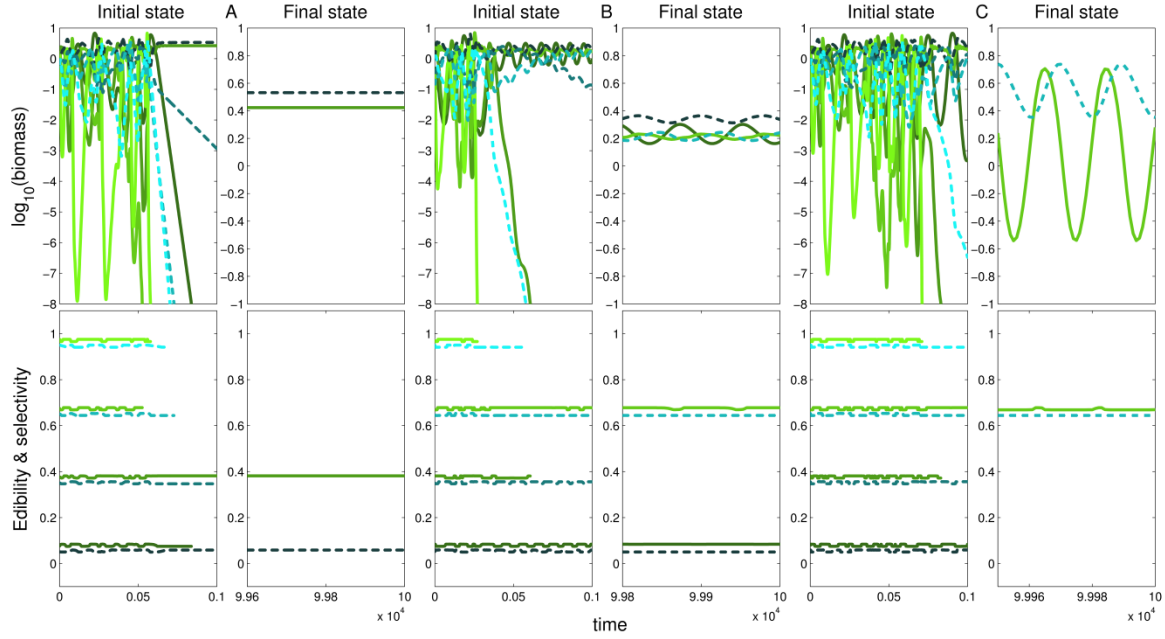


Figure 4. Biomass (top) and mean trait dynamics (bottom) for small ranges ($w=0.01$, cf. Fig. 3 A, region E1) and A) low ($v=10^{-2.5}$), B) moderate ($v=10^{-1.5}$) and C) high ($v=10^{-0.5}$) speed of trait adaptation, showing the initial (left panels) and final (right panels) state for four prey (colored green) and four predator species (colored blue). Initial edibility and selectivity increase from dark to light shades of colors (cf. Fig. 1). Note the different scales for the two time periods because of differences in the amplitudes and periods of the oscillations.

Slow trait adaptation did not promote species coexistence - Region E2

Low speed of trait adaptation ($v < 0.03$) resulted in a temporal mismatch between ecological and evolutionary processes preventing contemporary trait adjustments in response to selection, irrespective of w . As in region E1, this led to rapid exclusion of numerous species (Fig. 3 A) despite substantial trait changes over time (Fig. 5 A). However, 25% of the simulations exhibited supersaturated coexistence, i.e. the number of species in one trophic level exceeded the number of species in the other trophic level. In most cases two predators grazed on a single prey species (cf. Appendix E). Systems finally comprising only one prey and one predator species usually showed high frequency biomass oscillations that were superimposed upon low-frequency trait oscillations (Fig. 6 A). This led to periodic regime shifts in the biomass dynamics in which a predominance of fast oscillations alternated with slow ones. The temporally high amplitude oscillations within the fast component of the biomass dynamics corresponded to the prolonged occurrence of highly edible prey and highly selective predators with very high intrinsic growth and grazing rates (Fig. 6 A). The period of the low frequency part in the biomass oscillations strongly exceeded the sampling period and thus promoted the detection of long term trends that do not indicate prolonged transients of competitive exclusion in these systems (cf. Fig. 3, C; Fig. 6, A). For larger ranges of trait adaptation ($w > 0.04$) a transition from species poor (Fig. 3, A, region E2) to species rich (Fig. 3, A, regions C1 and C2) systems occurred at about $v \approx 0.03$, often characterized by irregular dynamics and long-term trends in species biomasses (Fig. 3, C).

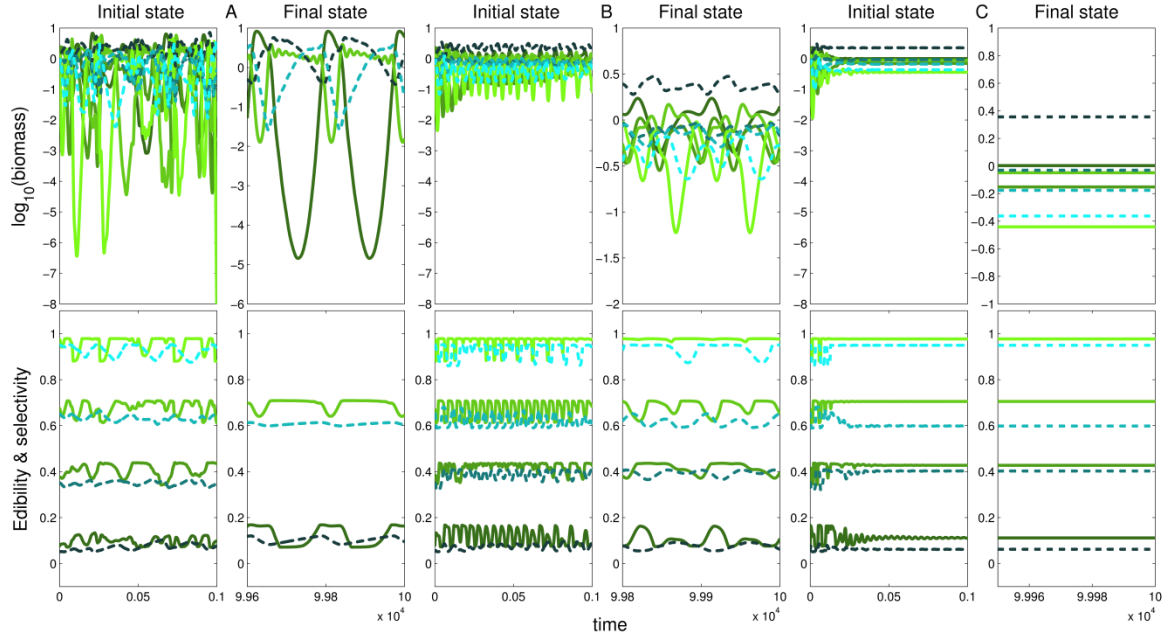


Figure 5. Biomass and mean trait dynamics as in Figure 4 but for moderately large ranges ($w=0.1$, cf. Fig. 3A, regions E2 and C1) and A) low ($v=10^{-2.5}$), B) moderate ($v=10^{-1.5}$) and C) high ($v=10^{-0.8}$) speed of trait adaptation.

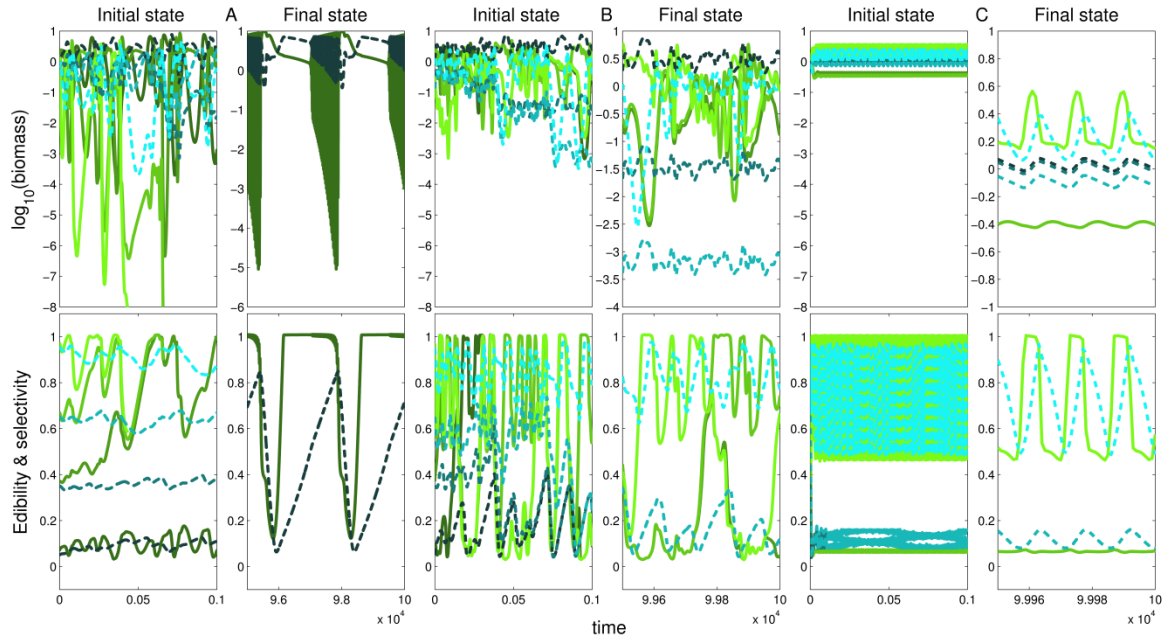


Figure 6. Biomass and mean trait dynamics as in Figure 4 but for large ranges ($w=1$, cf. Fig. 3A, regions E2 and C2) and A) low ($v=10^{-2.5}$), B) moderate ($v=10^{-1.5}$) and C) high ($v=10^{-0.5}$) speed of trait adaptation.

Constrained but fast trait adaptation promoted stable species coexistence - Region C1

Moderate ranges ($0.04 < w < 0.3$) and a sufficiently high speed ($v \geq 0.03$) of trait adaptation allowed species to make considerable and fast trait adjustments within their distinct ranges (Fig. 2, D) delaying or preventing species exclusion (Fig. 5). Higher values of v accelerated the

changes in traits relative to the changes in biomasses. This promoted stable coexistence of functionally different species as indicated by the rarity of long-term trends in their biomass dynamics (Fig. 3 C, region C1). Depending on w and v we found that the biomass and trait dynamics were either at equilibrium or oscillatory (Fig. 3, D). At equilibrium, the species composition reached a final state after unique shifts in their trait values whereas in case of oscillations species showed ongoing trait adjustments (Fig. 5 B, C).

The time-averaged niche differences, ND , and fitness differences, FD , among prey species both declined with w but the decrease in FD was more pronounced than that of ND . This gives rise to a net-increase in stabilizing mechanisms as indicated by $FD-ND$ (Fig. 3 E, F). In addition, for pronounced and regular oscillations, the trait values of the most edible prey cycled out of phase with that of the least edible prey implying that their trait values became temporally more similar or dissimilar (*correlation coefficient* $\rho \approx -0.75$; Fig. 5 B). This gave rise to a temporal interplay between niche- and fitness differences among prey species that stabilized their coexistence. Coadaptation was essential for coexistence as it ensured that fitness differences did not exceed the effect of niche differences (Fig. 3 E). Preventing coadaptation among prey or predator species by assigning constant trait values to some or all of them or assuming only non-adaptive random trait changes strongly reduced the final richness (for details see Appendix D).

Stable coexistence is further indicated by the low sensitivity of the species biomass dynamics to environmental stochasticity since neither low [final richness = 8 ± 0 ($v = 10^{-1.5}$); 8 ± 0 ($v = 10^{-1}$); 8 ± 0 ($v = 10^{-0.5}$)] nor high [final richness = 7.84 ± 0.55 ($v = 10^{-1.5}$); 8 ± 0 ($v = 10^{-1}$); 8 ± 0 ($v = 10^{-0.5}$)] levels of noise did substantially reduce the final richness below a value of 8, that is below the final richness obtained in the absence of noise.

When the trait ranges, i.e. niches, of neighboring species overlapped, i.e. $w > \Phi_i - \Phi_{i-1}$ for prey and $w > \Omega_j - \Omega_{j-1}$ for predators, species were able to cluster into functional groups with very similar trait values and highly synchronized biomass and trait dynamics. In systems comprising initially 16 prey and 16 predator species prey and predators formed functional groups that persisted throughout time (Fig. 7). This resulted in high final richness of 6 prey and 10 predators ($v = 10^{-1.5}$), 12 prey and 10 predators ($v = 10^{-1}$) and 12 prey and 10 predators ($v = 10^{-0.5}$) after $3 \cdot 10^5$ time steps. Interestingly, the 4 main functional groups formed within the prey and predator communities, respectively, exhibited very similar trait values to the ones shown for systems with initially 4 prey and 4 predator species. This suggests that our model system only allows stable coexistence of up to 4 prey and 4 predator species which is supported by the long-term trends present in the biomass dynamics of the remaining species. However, the very long persistence of many other species indicates strong equalizing mechanisms within functional groups. Indeed, the high trait similarity reduced the fitness differences of species within functional groups while maintaining trait and thus niche differences among species of different functional groups. The unequal number of final prey and predator species in the simulations with initially 16 prey and 16 predator species reveals that trait adaptation may enable

supersaturated coexistence. Indeed, trait adaptation strongly promoted stable supersaturated coexistence within the prey or predator community in systems with an unequal initial number of prey and predator species ($S_{\text{prey}}=6$ and $S_{\text{predators}}=2$ or $S_{\text{prey}}=2$ and $S_{\text{predators}}=6$; for details see Appendix E). The extent of supersaturated coexistence depended on the species' initial trait values. For example, trait adaptation allowed stable coexistence of 4 predator species on 2 prey species for $w=0.1$ when the prey had initially intermediate (Fig. 8, B) rather than extreme trait values (cf. Appendix E). However, we never observed stable supersaturated coexistence in the absence of trait adaptation irrespective of the initial trait values.

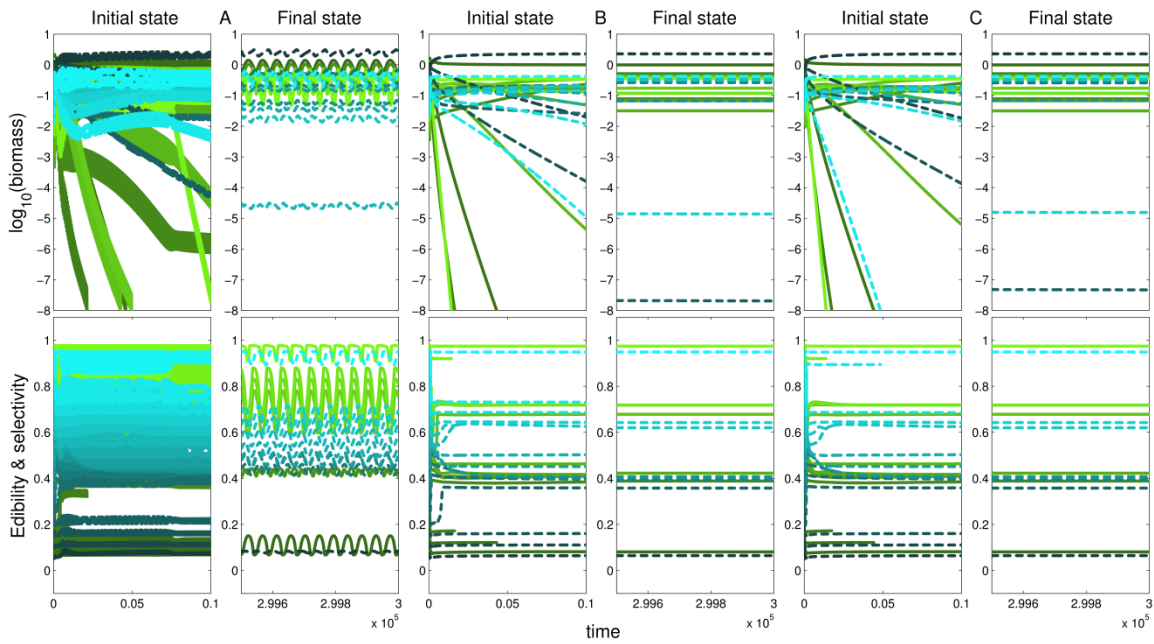


Figure 7. Biomass and mean trait dynamics as in Figure 5 but for initially 16 prey (colored green) and 16 predator species (colored blue) and for different high values of the speed of trait adaptation, A) $v=10^{-1.5}$, B) $v=10^{-1}$, C) $v=10^{-0.5}$ showing the first 10^4 (left panels) and last 500 time steps (right panels).

Large and fast trait adaptation promoted unstable coexistence - Region C2

Similar to region C1, the biomass and trait dynamics were either at equilibrium or oscillatory for higher values of w (>0.3) and v (>0.03) depending on their exact values (Fig. 3, D). However, in contrast to region C1, species often showed rather complex, irregular and high-amplitude biomass dynamics (Fig. 6 B, C) which frequently exhibited long-term trends suggesting prolonged transition periods of competitive exclusion (Fig. 3 C). This result is supported by very small values of ND and FD and lower final richness (Fig. 3 A, E). Hence, the species became functionally redundant sharing almost the same trait space and thus fitness landscape, i.e. the per-capita net-growth rate as a function of the trait value, so that the species were able to replace each other (Fig. 2, D). The system exhibited rather neutrally stable coexistence which is confirmed by the relatively high sensitivity of the biomass dynamics to environmental stochasticity. Independently of v , high levels of environmental noise

substantially reduced the final richness below a value of 8 which was the final richness obtained without noise [final richness= 5.88 ± 0.73 ($v=10^{-1.5}$); 4.52 ± 0.96 ($v=10^{-1}$); 5.40 ± 1.22 ($v=10^{-0.5}$)].

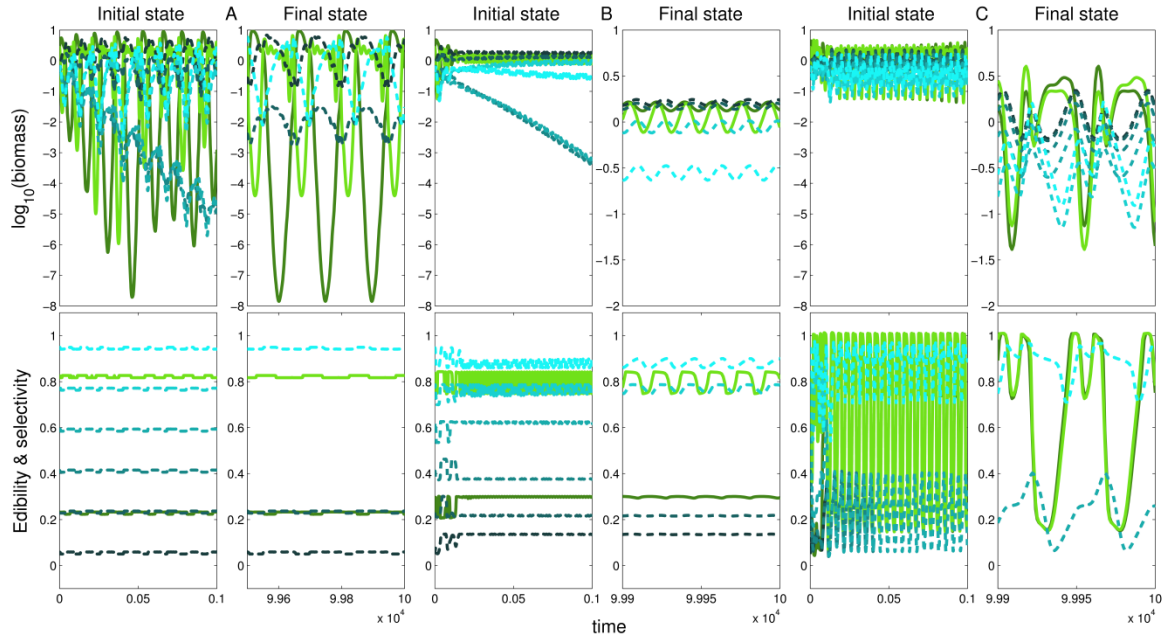


Figure 8. Biomass (top) and mean trait dynamics (bottom) for moderate speed ($v=10^{-1}$) and A) small ($w=0.01$), B) intermediate ($w=0.1$) and C) large ($w=1$) ranges of trait adaptation, showing the initial (left panels) and final (right panels) state for initially two prey (colored green) and six predator species (colored blue). Initial edibility and selectivity increase from dark to light shades of colors (cf. Fig. 1). In contrast to the results shown in Appendix E, the prey species exhibited intermediate rather than extreme initial trait values. In A) one of the less selective predators has a negative long-term trend in its biomass dynamics suggesting prolonged competitive exclusion.

For very large ranges of trait adaptation ($w \approx 1$) the 4 prey and 4 predator species clustered into functional groups reducing fitness differences among species of the same functional group (compare region C2 of Fig. 3 A and B). Such a formation of functional groups was temporally variable for moderate values of v (Fig. 6 B) and usually persisted throughout time for higher values of v (Fig. 6 C, Fig. 9). The remaining prey species formed 1 or 2 functional groups, whereas the predators split into up to 3 functional groups. If only a single functional group remained the temporal changes in its mean trait value covered the whole trait space (Fig. 9 A, C). In contrast, the individual traits of 2 or 3 remaining prey or predator functional groups partitioned the trait space almost equally (Fig 6 C, Fig. 9 B). The formation of functional groups in our model occurred consistently and independently of the initial trait values of the species (results not shown).

The clustering of species into different functional groups suggests the maintenance of stabilizing niche differences within the prey and predator communities. This is supported by the fact that low levels of environmental stochasticity were usually not sufficient to reduce the final richness during the simulation period [final richness= 7.72 ± 0.46 ($v=10^{-1.5}$); 8 ± 0 ($v=10^{-1}$);

8 ± 0 ($v=10^{-0.5}$)] below a value of 8. However, in contrast to region C1, coexistence depended much more on the recurrent trait oscillations within a functional group as indicated by the unequal number of prey and predator functional groups giving rise to supersaturated coexistence based on temporal niche differences (Fig. 6; Fig. 9). Indeed, 33% of the simulations exhibited supersaturated coexistence, typically with four prey species grazed upon by three predators (cf. Appendix E). Furthermore, trait adaptation enabled a clustering of species on the trait axes that allowed for supersaturated coexistence of up to 6 prey and 2 predator species or 2 prey and 6 predator species when running simulations with an unequal initial number of prey and predator species ($S_{\text{prey}}=6$ and $S_{\text{predators}}=2$ or $S_{\text{prey}}=2$ and $S_{\text{predators}}=6$; Fig. 8, C; Appendix E). The increase in final richness demanded higher values of v for higher values of w ($w>0.3$) than for intermediate values of w ($0.04 \leq w \leq 0.3$) (cf. Fig. 3 A) where several prey and predator species frequently survived already with $v>0.003$ (Fig. 5 A).

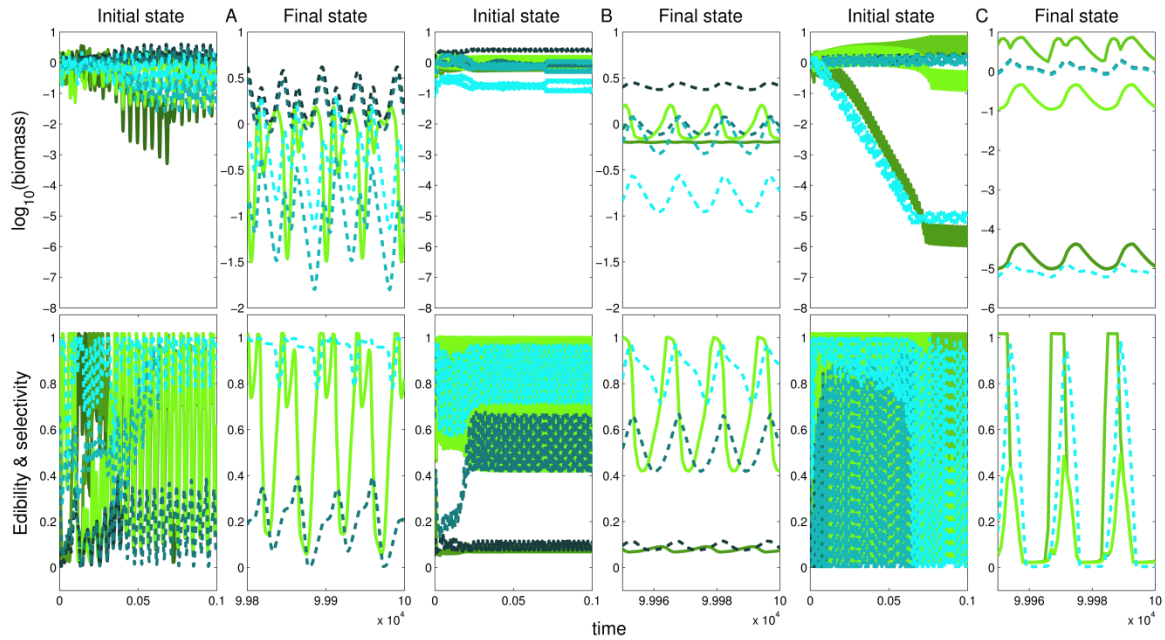


Figure 9. Biomass and mean trait dynamics as in Figure 6 but for different high values of the speed of trait adaptation, A) $v=10^{-1}$, B) $v=10^{-0.7}$, C) $v=1$.

Discussion

Species are able to adjust their traits in response to selection and recent studies showed that such frequently neglected trait adaptation may strongly stabilize population dynamics and species coexistence (Abrams 2000; Abrams 2006c; Vasseur et al. 2011; Mougi 2013). However, these studies restricted trait adaptation to one trophic level and allowed species to change their trait values over the entire trait space of the community. The first assumption neglects the potential of prey and predator species to mutually adjust their defensive and offensive strategies to each other (Lankau 2011). The second assumption disregards that species generally differ in their functional traits and thus abilities to cope with different environmental conditions, likely giving rise to stabilizing niche differences (Taper and Case 1992; Tilman

2004). Hence we used an innovative model approach that allows for simultaneous coadaptation within and among trophic levels to investigate the influence of the range (w) and the speed (v) of trait adaptation on coexistence in multispecies predator and prey communities.

In general, our results show that narrow and slow trait adaptation led to low final richness whereas sufficiently large and fast trait adaptation yielded higher final richness. Species coexistence was stable when trait adaptation was restricted to species-specific limits maintaining trait and thus niche differences among species. Species coexistence was rather neutrally stable when all species could attain almost the same trait values preventing strong niche-differentiation. We thus demonstrate that coadaptation among prey and predators can lead to recurrent changes in defense and offense traits that provide novel stabilizing and equalizing effects which is in line with theoretical considerations of Lankau (2011) and will be discussed below. We describe our results in terms of species coexistence but they hold equally well for the coexistence of clones in asexually reproducing populations and thus the maintenance of their genetic diversity.

Small and slow trait adaptation did not enable species coexistence - Regions E1 and E2

When the range of trait adaptation was strongly constrained ($w < 0.04$) species exhibited considerable niche differences that promoted coexistence mostly by selective predation on fast growing prey and resource partitioning among predators. However, high time-averaged niche differences implied also high time-averaged fitness differences. Thus, in the absence of trait adaptation the niche differences were not sufficient to compensate for the large fitness differences yielding fast exclusion of most species. Finally, usually one prey and one predator species survived showing either oscillatory or stable dynamics depending on the remaining prey and predator traits. Cyclic predator-prey dynamics require a sufficiently strong non-linearity in the predator's functional response so that it reaches half of its maximum at prey densities well below the prey's carrying capacity, K (Abrams 2006c). This was given in our model for highly selective predators (half-saturation constant $H \approx 1$) but not for non-selective predators ($H \approx 8$, $K = 10$). Our results confirm that trait adjustments which are slow compared to the ecological dynamics are insufficient to promote the maintenance of species-rich communities (Vasseur et al. 2011; Mougi 2013).

Constrained and fast trait adaptation promoted stable species coexistence - Region C1

Sufficiently large ($0.04 < w < 0.3$) and fast ($v \geq 0.03$) trait adaptation allowed considerable trait adjustments in response to selection resulting in a strong dampening of the biomass oscillations and stable coexistence of functionally different prey and predators. The prevailing characteristics of the prey community selected for predator traits more suitable for exploiting the dominant prey. The subsequently enhanced grazing pressure on the dominant prey was accompanied by a release in the grazing pressure on rare prey promoting their recovery. In addition, coadaptation among prey species stabilized their coexistence further by allowing the

well edible prey to defend themselves against predation and the less edible prey to increase their competitive abilities, both of which increases the fitness of the different prey species at low densities (cf. Appendix D). These trait and biomass changes in the prey community, in turn, improve the food supply for the rare predators. Hence, coadaptation in defense and offense traits may stabilize coexistence by reducing the strength of pairwise trophic interactions at low densities (cf. Kokkoris et al. 2002; Imura et al. 2003; Bolnick et al. 2011) and enhancing it at high densities. This gives rise to negative frequency dependence that prevents overexploitation of the prey and long periods of starvation of the predators.

Beyond stabilizing coexistence via (temporal) niche differentiation trait adaptation also equalized species performances in our model by allowing a reorganization of pairwise trophic interactions that alters their strength. For example, highly selective predators were able to broaden their prey spectrum whereas prey species enhancing their growth rate became accessible to more predators. Both promoted an increased connectivity between the two trophic levels that reduced fitness differences. Our result is in line with findings from food web models where the presence of adaptive foragers strongly promoted species persistence when the overall connectivity was sufficiently high (Kondoh 2003; Uchida et al. 2007; Heckmann et al. 2012).

The stabilizing and equalizing effects of trait adaptation in our model are in line with previous model results (Tirok and Gaedke 2010; Bauer et al. 2014) where additional stabilizing and equalizing mechanisms were *a priori* introduced to ensure coexistence of multiple prey and predator species. Their functional response was similar to a type III functional response, and all predators were able to consume a certain amount of less edible prey buffering more selective predators from extinction when prey composition shifted towards less edible species. As a result, our species biomass dynamics for higher values of v and w look very similar to those of Tirok and Gaedke (2010) and Bauer et al. (2014). However, in contrast to a functional type III response where the negative frequency dependence arises instantaneously at low densities, the reduction in grazing pressure on rare prey and the enhancement of grazing of rare predators in our model occur with time-lags that are inversely proportional to v . This is in line with previous studies where higher speed of trait adaptation was needed to promote coexistence in consumer-resource models (Abrams 2006c; Vasseur et al. 2011; Mougi 2013).

Our results also show that coadaptation among prey and predator species promoted coexistence by allowing species to cluster into functional groups influencing both stabilizing and equalizing mechanisms at the same time. Coexistence was stabilized by reducing fitness differences among species of the same functional group while maintaining niche differences among species of different functional groups. This result is in line with recent discussions that both niche differences and neutrality jointly act to maintain species rich communities (Bonsall et al. 2004; Vergnon et al. 2009). Hence, two contrasting windows of opportunity exist for species to coexist: being functionally sufficiently different or being sufficiently similar (Scheffer and van Nes 2006). In the first case, weak equalizing mechanisms are compensated for by strong stabilizing mechanisms whereas in the second case strong equalizing mechanisms

promote coexistence in the absence of strong stabilizing mechanisms. In line with Scheffer and van Nes (2006) we show that trait adaptation may enable a self-organization of species' traits on the trait axes that promotes coexistence via the formation of functional groups, i.e. the generation of stable clusters of similar species on the trait axes. However, in contrast to Scheffer and van Nes (2006), in our model species clusters arose on an ecological time scale enabling species coexistence even without additional stabilizing mechanisms such as density-dependent losses. Although coexistence within functional groups was not stable, species co-occurred for a very long time. Indeed, in the absence of stabilizing niche differences, equalizing mechanisms can reduce fitness differences and thus slow down but not prevent competitive exclusion in the long run (Chesson 2000). Furthermore, stabilizing mechanisms acting within functional groups need only to be small in order to allow coexistence and might be easily realized in natural systems through higher dimensional trade-offs (Clark et al. 2010).

When trait adaptation was sufficiently high and restricted to species-specific limits we observed both equilibrium and non-equilibrium dynamics which suggests that trait adaptation can stabilize coexistence via unique shifts and via ongoing redistribution of trait values. At equilibrium coexistence is enabled without further trait adjustments (e.g. evolution) whereas ongoing trait changes promote coexistence due to a mutual interplay between biomass and trait dynamics (i.e. eco-evolutionary dynamics or biomass-trait feedbacks). Hence, when predator and prey biomasses oscillated different trait values were favored at different times. Since all species continuously adapted their trait values in response to selection the trait oscillations (ongoing coadaptation) were directly and inseparably related to the cycles in predator-prey biomasses. This is in line with findings from an experimental system of two competing plant species (Lankau and Strauss 2007) where coexistence was based on frequency dependent selection (Vasseur et al. 2011). In this case trait adaptation and species diversity generated a feedback loop that maintained each other.

Depending on the current selection pressure trait divergence or trait convergence dominated the trait changes within the prey community leading to out-of-phase cycles between the trait values of more and less edible prey species in our model. For example, a dominance of selective predators selected for lower edibility within well edible and higher edibility within less edible species giving rise to trait convergence. In contrast, a dominance of rather non-selective predators promoted character divergence within the prey community since well edible prey species changed their edibility towards higher values and less edible prey species towards lower trait values. Therefore, two strategies temporally emerged within the prey community, either becoming defended or growing faster giving rise to temporal changes in niche and fitness differences (cf. Appendix D).

Hence, the recurrent convergence and divergence of species' traits causes an interesting interplay between equalizing and stabilizing mechanisms as trait distances change: when traits are similar species have similar fitness but low niche differences and vice versa. Thus, when stabilizing niche differences (here differences in grazing pressure) weakened, trait and thus

fitness differences (here in intrinsic growth rates) decreased reducing the risk of competitive exclusion. Conversely, trait distances among species increased if stabilizing mechanisms were strong, compensating for reduced equalizing mechanisms. This way, the contribution of equalizing and stabilizing mechanisms was time-dependent in systems with non-equilibrium dynamics. Our result is in line with recent findings of trait convergence towards a single strategy or trait divergence towards complementary strategies under competition for nutritionally essential (MacArthur and Levins 1967; Abrams 2000; Fox and Vasseur 2008) or substitutable (Lundberg and Stenseth 1985; Abrams 2000; Vasseur and Fox 2011) resources. However, these studies considered the long-term behavior of the trait dynamics whereas our model reveals that trait convergence or divergence may vary temporally as a result of a biomass-trait feedback. Hence, based on the precondition that stable coexistence requires intraspecific competition to be on average larger than interspecific competition but not at every moment in time (cf. Vasseur et al. 2011), coexistence is promoted by the species potential to be sometimes more similar (neutral theory) or different (niche theory).

Large and fast trait adaptation promoted neutrally stable coexistence - Region C2

For larger ranges of trait adaptation ($w > 0.3$) a transition from stable (niche differentiated) to rather neutrally stable (equalized) species coexistence occurred. Systems falling within this transition zone were usually marked by irregular biomass dynamics. The relatively low final richness and high sensitivity to environmental noise suggest a reduction of stabilizing mechanisms. However, for very high values of w the species shared a common range of trait adaptation allowing them to dynamically cluster into a single or a few different functional groups. In our model, at least two specialized prey or predator strategies emerged, suggesting the maintenance of stabilizing mechanisms based on self-organized niche partitioning. Interestingly, the number of functional groups within the prey community usually differed from the one within the predator community giving rise to supersaturated coexistence, i.e. the number of coexisting species exceeds the number of limiting resources. For example, in one case, only one prey strategy was supported in the long run whereas two strategies, i.e. being either highly selective or non-selective, emerged within the predator community. The two predator functional groups coexisted by specializing on prey differing in their edibility and the oscillations in the trait values of the single prey functional type provided temporal opportunities for them to succeed.

Hence, the potential for trait adaptation gives rise to biomass-trait feedbacks that enable supersaturated coexistence. This directly corresponds to the generally debated importance of internally driven fluctuations in resource and consumer densities for maintaining species rich communities (Huisman and Weissing 1999; Huisman et al. 2001). Biomass fluctuations promoted coexistence in consumer-resource-models where two consumers differed in their functional responses and competed for a common resource (Armstrong and McGehee 1980; Abrams and Holt 2002) and in a predator-prey model where the predator grazed on a genetically

variable prey species (i.e. two specialists) and a phenotypic plastic prey species (i.e. the generalist) (Yamamichi et al. 2011). In these examples a dominant competitor altered the environment in a way that allowed the other competitor to recover. For example, specialist consumers may promote cyclic predator-prey dynamics, enabling invasion by the generalist consumer which is superior when the prey composition fluctuates (Abrams 2006a; Abrams 2006c; Holt et al. 2013).

Up to now, several studies emphasized that supersaturated coexistence is very sensitive to the chosen parameter values (Schippers et al. 2001), likely unstable (Roelke and Eldridge 2008) and that complex dynamics are not a likely mechanism to maintain high levels of genetic diversity (Jones et al. 2009). We challenge this point of view by showing that trait adaptation may enable stable supersaturated species coexistence in a wide parameter space by providing novel stabilizing and equalizing effects based on trait fluctuations. This finding is supported by our sensitivity analysis as neither changes in bottom-up (K) nor top-down control (d) altered the general patterns (cf. Appendix C). Therefore, it is the inherent flexibility of species that makes their coexistence robust against environmental fluctuations. Indeed, low levels of environmental noise did not destabilize coexistence. Hence, studies like Huisman and Weissing (1999) that show the potential for coexistence given the right parameter combinations are conservative, since trait adaptation is ubiquitous in natural systems and would find these and possibly more configurations that succeed. In summary, trait adaptation may enable species coexistence even if the number of limiting factors is smaller than the number of species and thus may contribute to resolve the paradox of the plankton (cf. Appendix E).

Conclusions

We used an innovative multi-species predator-prey model that allowed for simultaneous coadaptation among all prey and predator species. The model was parametrized for a distinct planktonic system but has very general properties. We demonstrate that the naturally ubiquitous but so far mostly neglected trait adaptation strongly increases the number of coexisting species, in particular when realistically restricted to species-specific limits. Both niche differences and neutrality jointly acted to maintain species rich communities. Coadaptation among prey or predators yielded functional groups as species formed clumps along the trait axes. This reduced fitness differences among species of the same functional group while maintaining niche differences between species of different functional groups. Hence, species coexistence may arise from both, high trait similarities (resulting in ecological equivalence) and dissimilarities (resulting in niche differences) among species. In addition, coadaptation resulted in an ongoing convergence and divergence of species traits giving rise to a time-dependent balance between equalizing and stabilizing mechanisms. In contrast to previous studies, the emergent feedback between biomass and trait fluctuations enabled supersaturated coexistence for a broad range of potential trait adaptation and parameters.

We conclude that the mismatch between the naturally observed species richness and theoretical predictions partly arises from assigning too rigid, temporally invariant mean values to the species' traits that underlie theory. Accepting the potential for trait changes as actual properties of natural systems allows to explain stable or supersaturated species coexistence for a broad range of environmental conditions. Hence, trait adaptation may be an important reason for the empirical evidence of high species richness in both aquatic and terrestrial systems.

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Appendix A: v scales the time-scale of trait dynamics relative to population dynamics

$$\frac{dR_{p_i}}{dt} = \sum_{k=1}^s \frac{\partial R_{p_i}}{\partial P_k} \cdot \frac{\partial P_k}{\partial t} + \sum_{j=1}^s \frac{R_{p_i}}{\partial C_j} \cdot \frac{\partial C_j}{\partial t} + \sum_{k=1}^s \frac{\partial R_{p_i}}{\partial \varphi_k} \cdot \frac{\partial \varphi_k}{\partial t} + \sum_{j=1}^s \frac{\partial R_{p_i}}{\partial \omega_j} \cdot \frac{\partial \omega_j}{\partial t} \quad (\text{A1})$$
$$\begin{aligned} \frac{d\bar{R}_p}{dt} &= \frac{d}{dt} \left(\sum_{i=1}^S p_i \cdot R_{p_i} \right) = \sum_{i=1}^S \frac{d}{dt} (p_i \cdot R_{p_i}) = \sum_{i=1}^S \left[\frac{dp_i}{dt} \cdot R_{p_i} + p_i \cdot \frac{dR_{p_i}}{dt} \right] \\ &= \sum_{i=1}^S \left[\frac{dp_i}{dt} \cdot R_{p_i} \right] + \sum_{i=1}^S \left[p_i \cdot \left(\sum_{k=1}^S \frac{\partial R_{p_i}}{\partial p_k} \cdot \frac{\partial p_k}{\partial t} + \sum_{j=1}^S \frac{\partial R_{p_i}}{\partial C_j} \cdot \frac{\partial C_j}{\partial t} \right) \right] + \sum_{i=1}^S \left[p_i \cdot \left(\sum_{k=1}^S \frac{\partial R_{p_i}}{\partial \varphi_k} \cdot \frac{\partial \varphi_k}{\partial t} + \sum_{j=1}^S \frac{\partial R_{p_i}}{\partial \omega_j} \cdot \frac{\partial \omega_j}{\partial t} \right) \right] \quad (\text{A2}) \end{aligned}$$
$$\left(v \cdot \sum_{i=1}^S \left[p_i \cdot \left(\sum_{k=1}^S \frac{\partial R_{p_i}}{\partial \varphi_k} \cdot \frac{\partial R_{p_i}}{\partial \varphi_i} + \sum_{j=1}^S \frac{\partial R_{p_i}}{\partial \omega_j} \cdot \frac{\partial R_{C_j}}{\partial \omega_j} \right) \right] \right) \quad \text{Adaptive evolution or phenotypic plasticity}$$

$$\left(\sum_{i=1}^S \left[\frac{\partial p_i}{\partial t} \cdot R_{p_i} \right] + \sum_{i=1}^S \left[p_i \cdot \left(\sum_{k=1}^S \frac{\partial R_{p_i}}{\partial P_k} \cdot \frac{\partial P_k}{\partial t} + \sum_{j=1}^S \frac{\partial R_{p_i}}{\partial C_j} \cdot \frac{\partial C_j}{\partial t} \right) \right] \right) \quad \begin{array}{c} \text{Species sorting} \\ \text{Ecological interactions} \end{array}$$

(A3)

Hence, ν scales the relative time-scale of trait and biomass dynamics, and thus any increase in ν will increase the rate of change of the species' trait values relative to changes in their biomasses. For simplicity, we dropped the boundary function B from the expression above.

Appendix B: Modelling trait adaptation within species-specific limits

To describe the temporal development of the species' mean trait values, \bar{x} , we adopted a general formula proposed by Abrams (2010) that is rooted in quantitative genetics:

$$d\bar{x}/dt = \nu(\bar{x}) \cdot \partial R(x)/\partial x|_{x=\bar{x}} + B(\nu, \bar{x}) \quad (\text{B1})$$

The function ν scales the rate of trait adaptation relative to the species' population dynamics, R is the species' per capita net growth rate and B is the boundary function representing non-adaptive trait changes that restrict the trait values to the ecologically feasible trait range. The sign $|_{x=\bar{x}}$ denotes the evaluation of the species' fitness-gradient $\partial R/\partial x$ at its mean trait value. Although this approach has been used primarily for traits with a genetic basis and thus for the representation of adaptive evolution (Lande 1982; Taper and Case 1985; Dieckmann and Law 1996), it may also be used to account for changes in the mean trait value via adaptive phenotypic plasticity (Abrams 2010; Mougi et al. 2011; Mougi and Iwasa 2011).

When considering trait changes within species-specific limits, the rate of change of \bar{x} has to slow down and finally approach zero when it approaches the extremes. This has frequently been achieved by making ν itself dependent on \bar{x} (Abrams 1999; Tien and Ellner 2012). However, \bar{x} only uniquely determines the variance of the trait distribution when trait changes are based on shifts in the relative abundance of two extreme phenotypes. Nevertheless, since we consider a continuous quantitative trait, we assumed ν to be constant and thus independent of \bar{x} (cf. Schreiber et al. 2011; Vasseur et al. 2011). Hence, we restricted the trait range by including a boundary function B in eq. B1 that accounts for non-adaptive trait changes following Abrams and Matsuda (2004) (cf. eq. 10). It depends on both \bar{x} and ν satisfying the properties proposed by Abrams (2010): it is large and positive (or negative) when \bar{x} approaches its minimum (or maximum) and it is very small for intermediate trait values. In accordance with theoretical studies of evolutionary biology (Saloniemi 1993) we slightly modified the framework of Abrams (2010) to make B dependent on ν . This is reasonable since species with high values of ν , reflecting a large standing trait variation, already comprise a high share of phenotypes which perceive the constraints of the boundary of the ecologically feasible trait range. This slows down adaptation. Below we provide a mathematical derivation for such a boundary function.

Consider a continuous quantitative trait that is restricted to a finite range because of physical or biological limits. For example, prey species cannot be less than inedible or more

than entirely edible restricting the biologically feasible trait range between 0 (0% edible) and 1 (100% edible). To reflect this, one may assume that a species' fitness becomes increasingly negative when its trait value passes the biologically feasible extremes. This property is captured by the following general differential equation describing the per-capita rate of change of the biomass of a subpopulation n with a particular trait value x .

$$1/n(x) \cdot dn(x)/dt = f(x, N) - g(x, N) + \mathcal{G}(x) \quad (\text{B2})$$

where f and g are the gross growth rate and death rate and $N = \int n(x)dx$ the total biomass of the population. The function \mathcal{G} restricts changes in the mean trait values to the biologically feasible range by assuming \mathcal{G} to be (approximately) zero within this range and to become increasingly negative for trait values approaching or passing the extreme trait values. One such function for the interval $[0, 1]$ is given by:

$$\mathcal{G}(x) = -\log(\sin(\pi x))/\pi \quad (\text{B3})$$

Note that the rate of change of N and \bar{x} are given by

$$1/N \cdot dN/dt = 1/N \cdot \int dn(x)/dt dx = 1/N \cdot \int n(x) \cdot [f(x, N) - g(x, N) + \mathcal{G}(x)] dx \quad (\text{B4a})$$

$$d\bar{x}/dt = d(1/N \cdot \int n(x)x dx)/dt = 1/N \cdot \int dn(x)/dt \cdot (x - \bar{x}) dx \quad (\text{B4b})$$

Following the approach of quantitative genetics (Lande 1982; Abrams et al. 1993) we now assume normally distributed trait values with a low and constant additive genetic variance. This way, we can approximate eq. B4 by:

$$1/N \cdot dN/dt = [f(x, N) - g(x, N) + \mathcal{G}(x)] \Big|_{x=\bar{x}} \quad (\text{B5a})$$

$$d\bar{x}/dt = v \cdot \partial(dN/Ndt)/\partial x \Big|_{x=\bar{x}} \quad (\text{B5b})$$

According to eq. B5 we get:

$$d\bar{x}/dt = v \cdot [\partial(f(x, N) - g(x, N))/\partial x \Big|_{x=\bar{x}} + \partial(\mathcal{G}(x))/\partial x \Big|_{x=\bar{x}}] \quad (\text{B6a})$$

$$= v \cdot \partial(f(x, N) - g(x, N))/\partial x \Big|_{x=\bar{x}} + v \cdot \partial(\mathcal{G}(x))/\partial x \Big|_{x=\bar{x}} \quad (\text{B6b})$$

$$=: v \cdot \partial(dN'/N'dt)/\partial x \Big|_{x=\bar{x}} + B(v, \bar{x}) \quad (\text{B6c})$$

where $dN'/N'dt$ corresponds to the species' average per-capita rate of change that is based solely on its ecologically relevant gross growth and death processes. The second term of eq. B6 corresponds to the boundary function B which yields a large positive and negative slope of the fitness landscape around the minimum and maximum trait values of the ecologically feasible trait range. This way, B can be viewed as part of the whole fitness landscape (eq. B6), determining the range over which biological interactions may change the landscape. Hence, v influences how fast trait changes approach the boundaries but not the boundaries of the fitness landscape themselves. Building on eq. B3 a boundary function that limits trait adaptation to the biologically feasible range, i.e. $[0, 1]$, is given by:

$$B(v, x) = -v \cdot \tan(\pi/2 \cdot (2 \cdot x - 1)) \quad (\text{B7})$$

Since we partly consider very small ranges of trait adaptation in our model in which \bar{x} is already close to the extreme trait values, we added an exponent s to eq. 10 (main text) to make our boundary function more stiff, thereby reducing confounding effects between \bar{x} and B in these cases. Hence, with $B(v, x) = v \cdot \partial \mathcal{G}(x) / \partial x$ we included a limiting function $\mathcal{G}(x)$ into eqns. 7 and 8 describing trait adaptations of the prey and predator species. We dropped this term from eqns. 1 and 2 since it has a negligible effect on the rate of biomass change over the vast majority of the trait range but would slow down numerical integration.

Appendix C: Sensitivity analysis

To test the robustness of our results with respect to parameter changes we conducted numerical simulations comprising a full-factorial combination of 11 carrying capacities ($K \in [5, 6, \dots, 15]$) and 11 death rates of the predators ($d \in [0.1, 0.11, \dots, 0.2]$) simulating changes in the bottom-up regulation and top-down control of the prey. We analyzed 3 different predator-prey systems differing in the species' range of trait adaptation ($w \in [10^{-2}, 10^{-1}, 10^0]$).

The influence of w on species coexistence was largely independent of the parameters varied (Fig. C1). For $w=10^{-2}$ usually one prey and one predator species survived at the end of the simulation independent of K and d , except for a combination of low values of K and low or very high values of d . At very high values of d , predators suffered from low food availability and high mortality leading to their exclusion and neutrally stable coexistence of some prey species at their carrying capacity. Coexistence was neutrally stable since any small perturbation would promote the replacement of the less edible species by the most edible species which are the competitive superior in the absence of predators. In contrast, low values of d often prevented selective predators from exhibiting strong biomass declines during periods of starvation reducing their risk of extinction.

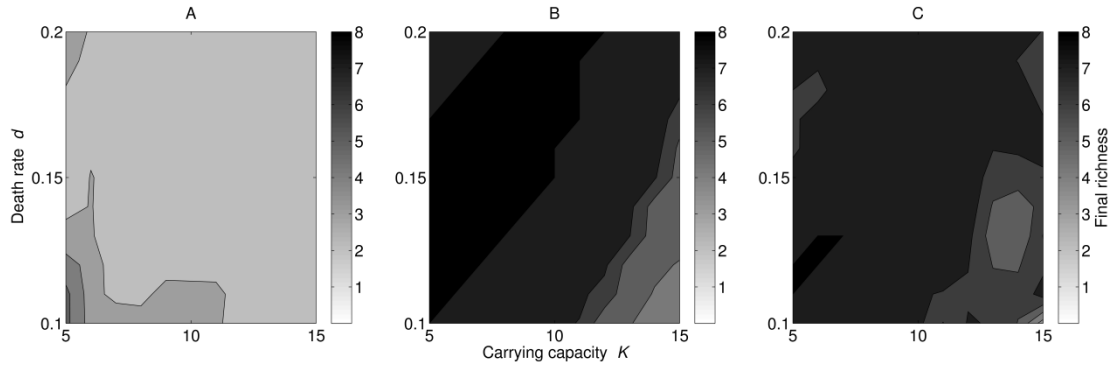


Figure C1. Final richness summed over the prey and predator communities depending on the prey's carrying capacity (K) and the predator's death rate (d) for $S=4$, $v=10^{-1.5}$ and $w=10^{-2}$ (A), $w=10^{-1}$ (B) and $w=10^0$ (C).

For $w=10^{-1}$ and $w=1$ final richness was always high except for a combination of high values of K and low values of d . In this case, an increased top-down control and a synchronization of the prey species by non-selective predators destabilized population and community dynamics. As a result, many prey and predator species were excluded. Hence, coadaptation strongly increased the parameter range where generalist and specialist consumers can coexist which is in line with findings from Abrams (2006) considering trait adaptation only at one trophic level.

Despite the positive influence of trait adaptation on species coexistence for a wide range of parameters our results also indicate that we can expect a decrease in final richness of prey and predator species when increasing or decreasing K . This leads to a humped-shaped dependency of final richness on the carrying capacity K (Fig. C1, B; cf. Leibold 1996). For very low values of K prey biomass is frequently too low to support the food demands of the less selective predators leading to their extinction. As a consequence, the system will get locked in a state of inedible prey species promoting further extinctions of more edible prey species and the more selective predators. In contrast, very high values of K strongly improve the performance of less selective predators compared to more selective ones initially promoting the exclusion of more selective predators and ultimately of less edible prey species because the costs for their defense do not pay off.

The general framework underlying our model was also analyzed with respect to the role of various other parameters including the maximum growth rate (r_{max}) of the prey, the maximum grazing rate (g) of the predators and the parameters b and c determining the feeding interactions between predator and prey species (Tirok and Gaedke 2010; Tirok et al. 2011; Bauer et al. 2014). The results from their sensitivity analyses are assumed to hold for our case as well.

Appendix D: Coadaptation within and among trophic levels jointly promotes coexistence

We provide here a more detailed evaluation of the mechanisms underlying species coexistence in our multispecies predator and prey communities in region C1 of our simulation results, combining numerical simulations and analytical considerations.

First, we evaluated the importance of coadaptation within and among trophic levels for coexistence numerically by analyzing our model for cases where only a subset of prey or predator species were able to adapt their trait values in response to selection. We simulated all possible combinations with 0 to 8 adaptive species for 25.000 time steps which was usually enough to reach quasi-equilibrium. We further compared the effects of adaptive to non-adaptive trait changes by considering situations where the trait values changed only randomly irrespective of what the other species were doing. We modeled non-adaptive trait changes by modifying equations 7 and 8 in the following way:

$$\frac{d\varphi_i}{dt} = v \cdot (n(0,1) + B(\varphi_i, \Phi_i)) \quad (D1)$$

$$\frac{d\omega_j}{dt} = v \cdot (n(0,1) + B(\omega_j, \Omega_j)) \quad (D2)$$

where the term $n(0,1)$ represents random numbers that were drawn independently from a normal distribution with mean and standard deviation equal to 0 and 1 for each time step and differential equation prior to numerical integration. Hence, trait changes followed additive white noise.

Increasing the number of adaptive species increased final richness in our model (Fig. D1; Fig. D2). In particular, final richness was maximized when at least 6 species and thus at least 2 prey and predator species were adaptive irrespective of the species identities. This suggests that coadaptation within and among trophic levels interacted to promote species-rich communities in our model. In contrast, non-adaptive trait changes did not increase final richness but often promoted the exclusion of all species (Fig. D1; Fig. D2).

We further disentangled the relative importance of coadaptation within and among trophic levels on coexistence. First, to evaluate the role of coadaptation within a trophic level, we allowed only the prey or the predators to change their traits. Second, to evaluate the effect of coadaptation between the two trophic levels, we allowed trait adaptation in both the prey and the predator communities, but all prey and all predator species had to change their traits in concert and thus in response to a common selection pressure. This was achieved by changing equations 7 and 8 in the following way:

$$\frac{d\varphi_i}{dt} = v \cdot \left(\sum_{k=1}^s \left(p_k \cdot \frac{\partial R_{p_k}}{\partial \varphi_k} \right) + B(\varphi_i, \Phi_i) \right) \quad (D3)$$

$$\frac{d\omega_j}{dt} = v \cdot \left(\sum_{k=1}^s \left(p_k \cdot \frac{\partial R_{C_k}}{\partial \omega_k} \right) + B(\omega_j, \Omega_j) \right) \quad (D4)$$

Hence, all species change their trait values according to the biomass-weighted (p_k) average of the species-specific fitness gradients thereby preventing coadaptation within a trophic level. To ensure synchronous trait dynamics during the entire simulation time we started all simulations

with trait values equal to $\varphi_i = \Phi_i - w \cdot (\Phi_i - 0.5)$ for prey and $\omega_j = \Omega_j - w \cdot (\Omega_j - 0.5)$ for predators, respectively.

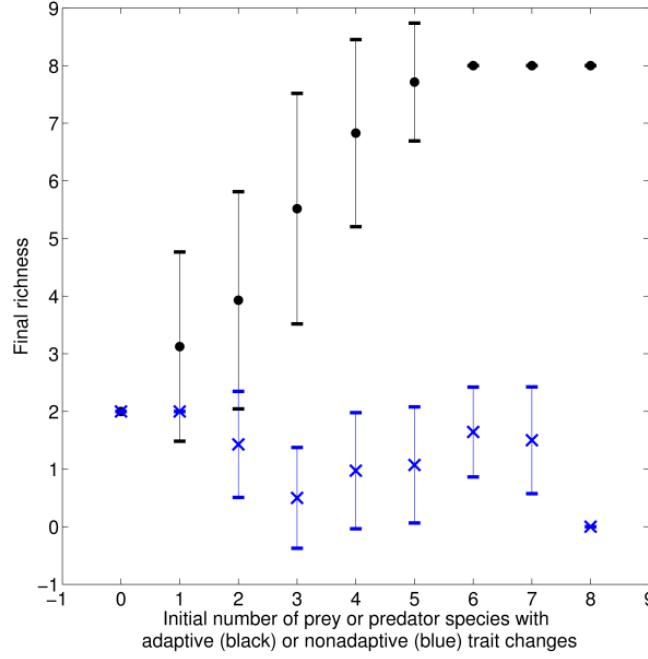


Figure D1. Average and standard deviation of summed final prey and predator richness in relationship to the initial number of species which are able to adjust their mean trait values in response to selection (black dots) or which exhibit random trait changes (blue crosses).

Our results show that coadaptation within and among trophic levels similarly promoted final richness. When only the prey or the predators could adapt final richness decreased from 8 ± 0 (mean \pm std; $n=25$) to 5.5 ± 0.9 or 5.8 ± 0.7 , respectively (Fig. D3 A, B). When coadaptation within a trophic level was absent final richness decreased to 4.8 ± 1.5 (Fig. D3 C).

The numerical results can be more clearly understood by considering the equations underlying the trait and biomass dynamics. The partial derivatives given in eq. 7 and eq. 8 of the main text denote the fitness gradients of the species evaluated at their respective mean trait values. Their analytical expressions provided below show how the feedback between biomass and trait dynamics promotes species coexistence.

The fitness gradient of prey species i is given by (for parameters see Table 1):

$$\frac{\partial R_{P_i}}{\partial \varphi_i} = \left(1 - \frac{\sum_{z=1}^S P_z}{K} \right) \cdot (r_{\max} - r_{\min}) - \sum_{j=1}^S \frac{g_{\max} \cdot C_j \cdot b \cdot q(\varphi_i, \omega_j) \cdot \left(\sum_{z=1}^S q(\varphi_z, \omega_j) \cdot P_z - (q(\varphi_i, \omega_j) \cdot P_i) + H(\omega_j) \right)}{\left(e^{b(\varphi_i - c \cdot \omega_j)} + 1 \right) \cdot \left(\sum_{z=1}^S q(\varphi_z, \omega_j) \cdot P_z + H(\omega_j) \right)^2} \quad (D5)$$

In the presence of strong grazing pressure by non-selective predators the second term of eq. D5 will be negligible. Hence, changes in the mean trait values of the prey will be mainly driven by the first term promoting shifts towards higher edibility increasing the prey's competitiveness. In contrast, a high prey biomass close to the carrying capacity K combined with a substantial predation pressure of selective predators will favor trait changes within prey species towards

lower edibility based on the second term of eq. D5. This reduces the grazing pressure on the prey buffering them from extinction.

The fitness gradient of predator species j is given by:

$$\frac{\partial R_{C_j}}{\partial \omega_j} = e \cdot g_{\max} \cdot \left[\frac{P_i \cdot \frac{-c \cdot b \cdot q(\varphi_i, \omega_j)}{e^{b \cdot (\varphi_i - c \cdot \omega_j)} + 1}}{\left(\sum_{z=1}^s q(\varphi_i, \omega_j) \cdot P_z + H(\omega_j) \right)} - \frac{P_i \cdot q(\varphi_i, \omega_j) \cdot \left(\sum_{z=1}^s \frac{-c \cdot b \cdot q(\varphi_i, \omega_j)}{e^{b \cdot (\varphi_i - c \cdot \omega_j)} + 1} \cdot P_z - (H_{\max} - H_{\min}) \right)}{\left(\sum_{z=1}^s q(\varphi_i, \omega_j) \cdot P_z + H(\omega_j) \right)^2} \right] \quad (D6)$$

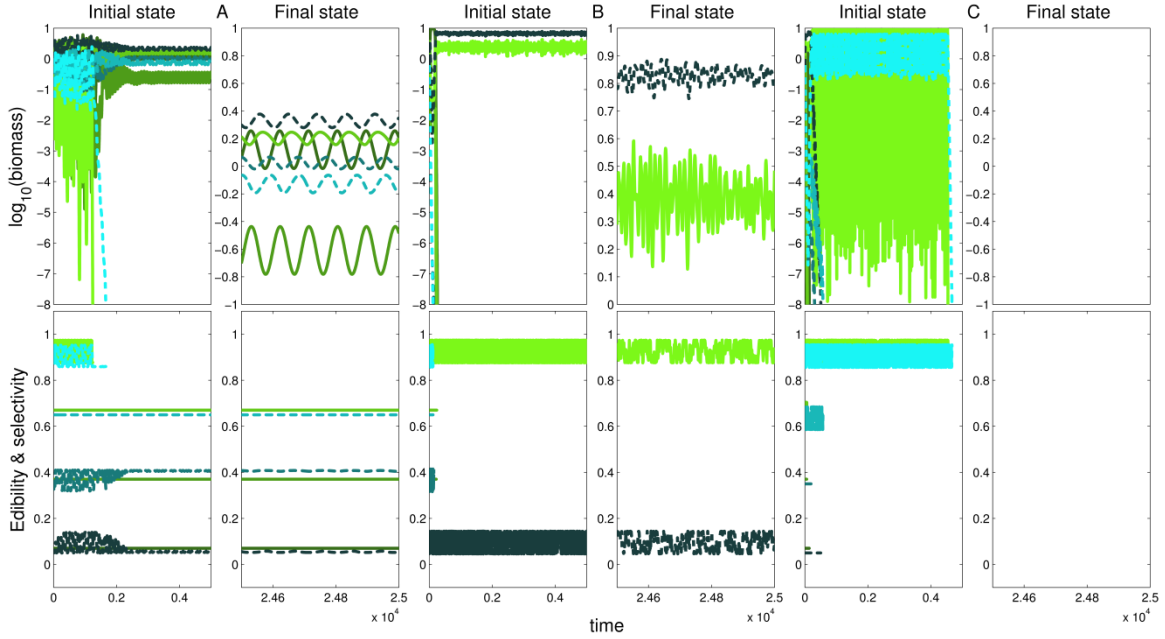


Figure D2. Biomass (top) and trait dynamics (bottom) for intermediate values of the range ($w=0.1$) and speed ($v=10^{-1.5}$) of trait adaptation for adaptive (A) or non-adaptive (B, C) trait changes within 4 species, showing the first 5000 time steps (left panels) and last 500 time steps (right panels) for four prey (green) and four predator species (blue). Initial edibility and selectivity increase from dark to light shades of colors (cf. Fig. 2). In C, all prey or predator species were excluded.

In the presence of well edible prey the second term of eq. D6 will promote changes in the traits of the predators towards higher selectivity. This arises from a dominant influence of the slope of the trade-off between half-saturation constant and selectivity. In contrast, if less edible prey species dominate the prey community the derivative of the preference function in both terms of eq. D6 will jointly favor trait changes towards lower values of ω . This increases the grazing pressure on the dominant prey thereby reducing periods of food shortage. Hence, coadaptation among prey and predators gives rise to negative frequency and density dependence promoting stable species coexistence.

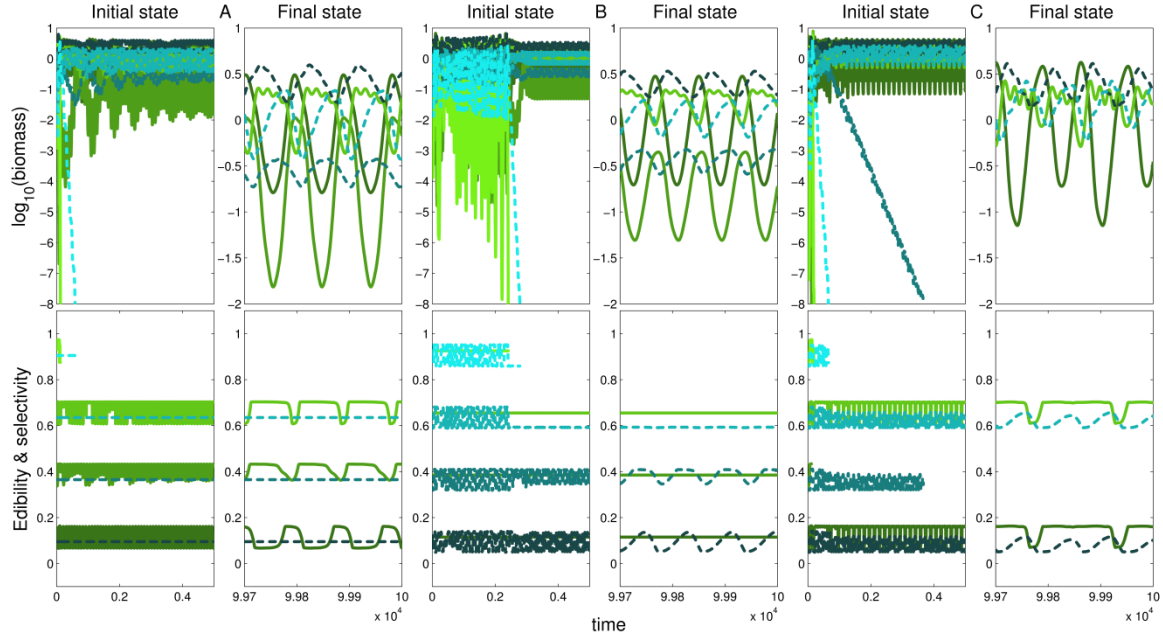


Figure D3. Biomass (top) and mean trait dynamics (bottom) for intermediate values of the range ($w=0.1$) and speed ($v=10^{-1.5}$) of trait adaptation allowing trait changes only within A) the prey or B) the predators and C) only between the prey and predators (trait changes within predator and prey communities synchronized), showing the first 5000 time steps (left panels) and last 300 time steps (right panels) for four prey (green) and four predator species (blue). Initial edibility and selectivity increase from dark to light shades of colors (cf. Fig. 1).

In addition, considering the equations underlying the biomass dynamics in the prey community reveals that coadaptation among prey allows a temporal convergence and divergence of traits that gives rise to temporal changes in niche and fitness differences among prey species. The rate of change of the i -th prey species biomass can be expressed as:

$$\frac{dP_i}{dt} = r(\varphi_i) \cdot \left(1 - \sum_{z=1}^S P_z / K\right) \cdot P_i - \eta(\varphi_i) \cdot P_i = (r(\varphi_i) - \eta(\varphi_i)) \cdot \left(1 - \sum_{z=1}^S P_z / K \cdot \left(1 - \frac{\eta(\varphi_i)}{r(\varphi_i)}\right)\right) \cdot P_i \quad (D7)$$

with

$$\eta(\varphi_i) = g_{\max} \cdot \sum_{j=1}^S q_{i,j} / \left(\sum_{z=1}^S q_{z,j} \cdot P_z + H_j \right) \quad (D8)$$

being the per capita death rate of the i -th prey species caused by grazing (cf. eq. 1). This formulation shows how trait adaptation can increase a prey species' effective capacity and thus its (direct or apparent) competitive ability either by increasing its growth rate or reducing its death rate giving rise to environment-dependent temporal convergence or divergence of prey species traits (Fig. D3 A). A dominance of highly selective predators promotes shifts towards lower and higher trait values in more and less edible prey species, respectively (trait convergence). The opposite and thus divergence among prey species' traits happens when moderately selective species dominate the predator community.

Appendix E: Trait adaptation promotes stable supersaturated coexistence

The paradox of the plankton questions how a large number of phytoplankton species can coexist in a rather homogeneous environment while all compete for the same few limiting resources (Hutchinson 1961). We show that trait adaptation may help to resolve this paradox as it strongly promotes supersaturated coexistence, where the number of species exceeds the number of limiting factors.

In the main text, we presented simulation results using an equal number of initial prey and predator species. Without trait adaptation (region E1, cf. Fig. 3), we never observed supersaturated coexistence (Fig. E1, A). In contrast, when species were sufficiently able to adapt their trait values in response to selection the final richness in one trophic level often exceeded the richness in the other one. In regions E2 and C2 (cf. Fig. 3) 25% and 33% of the simulations showed such a supersaturated coexistence (Fig. E1, B, D).

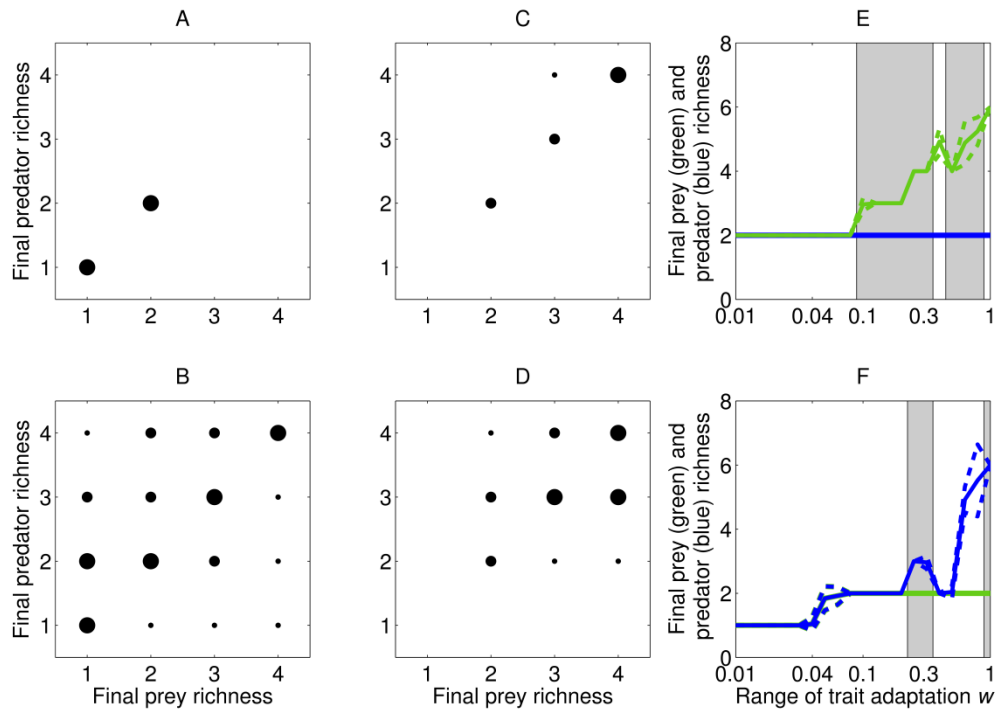


Figure E1. A-D) Final prey versus final predator richness for parameter regions E1 (A), E2 (B), C1 (C) and C2 (D) (cf. Fig. 3 main text). The relative frequency is indicated by large ($100\% \geq p > 10\%$), intermediate ($10\% \geq p > 1\%$) or small dot sizes ($p \leq 1\%$). E-F) Average (solid line) and standard deviation (dashed line) of final prey (green) and predator richness (blue) depending on the range of trait adaptation w for $v=0.1$ and initially 2 predator and 6 prey species (E), respectively 6 predator and 2 prey species (F). Grey shaded areas mark parameter regions of stable supersaturated prey (E) respectively predator (F) coexistence, that is prey and predator species do not exhibit long-term trends independent of the initial conditions.

Furthermore, starting with the same initial richness of prey and predator species may strongly underestimate the potential for trait adaptation to generate supersaturated coexistence. For example, in region C1 all prey and predator species were usually maintained preventing the possibility of supersaturated coexistence (Fig. E1, C). Hence, we present here additional

simulations with an unequal initial number of prey ($S_{\text{prey}}=6$) and predators ($S_{\text{predators}}=2$) for $v=0.1$, 25 different initial conditions and 21 different values of w ($[10^{-2}, 10^{-1.9}, \dots, 10^0]$). Supersaturated prey coexistence occurred from $w=0.1$ onwards and final prey richness strongly increased with w (Fig. E1, E; Fig. E2). In the absence of trait adaptation, two prey species with similar trait values coexisted as each of them was limited by a different predator (Fig. E2, A). In contrast, sufficiently large ranges of trait adaptation allowed for stable supersaturated coexistence of several functionally different prey species where each prey species was temporally limited by one of the two predators (Fig. E2, B). We obtained similar results when conducting the corresponding simulations with initially two prey and six predator species. In the absence of trait adaptation, usually one predator and one prey survived (Fig. E3, A). Supersaturated predator coexistence occurred from $w=0.25$ onwards where each predator species was temporally limited by one of the two prey species (Fig. E3, B).

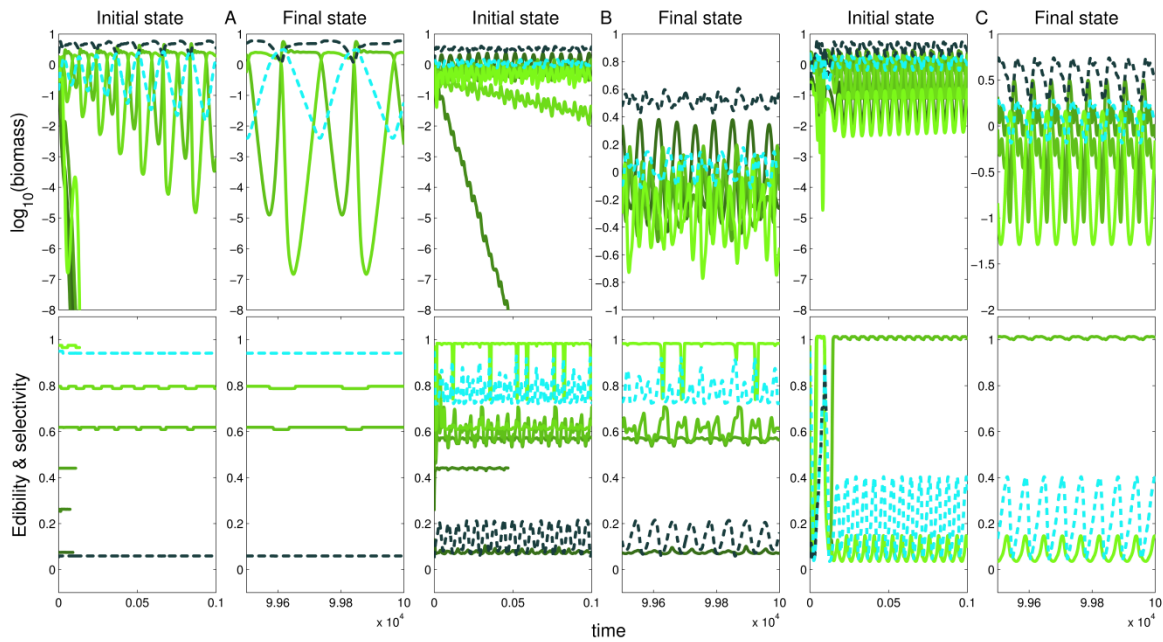


Figure E2. Biomass (top) and mean trait dynamics (bottom) for moderate speed ($v=10^{-1}$) and A) small ($w=0.01$), B) intermediate ($w=0.25$) and C) large ($w=1$) ranges of trait adaptation, showing the initial (left panels) and final (right panels) state for initially six prey (colored green) and two predator species (colored blue). Initial edibility and selectivity increase from dark to light shades of colors (cf. Fig. 1). Note the different scales for the two time periods because of differences in the amplitudes and periods of the oscillations during the transients and the final states.

In accordance with the results described in the main text, very large ranges of trait adaptation enabled prey and predators to cluster into functional groups thereby allowing a large number of prey species or predator species to coexist on a few limiting factors (Fig. E1; Fig. E2, C; Fig. E3, C). Hence, trait adaptation may strongly facilitate supersaturated coexistence in natural systems such as zoo- and phytoplankton communities.

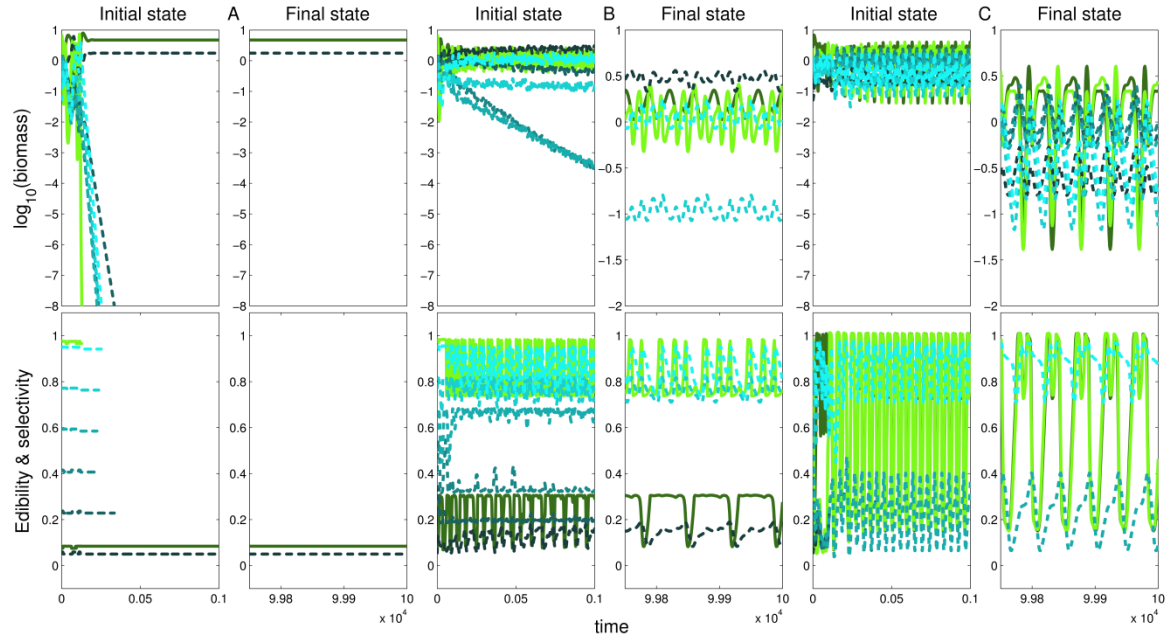


Figure E3. Biomass (top) and mean trait dynamics (bottom) for moderate speed ($v=10^{-1}$) and A) small ($w=0.01$), B) intermediate ($w=0.25$) and C) large ($w=1$) ranges of trait adaptation, showing the initial (left panels) and final (right panels) state for initially two prey (colored green) and six predator species (colored blue). Initial edibility and selectivity increase from dark to light shades of colors (cf. Fig. 1).

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