Supporting Information

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SI Text

In our meta-analysis, we defined a competition–defense tradeoff as a negative correlation between resource limitation (the inverse of competitive ability) and consumer limitation (the inverse of resistance to consumers) for a group of species. We then used species-specific responses to resource addition and consumer removal as measures of limitation. This approach relies on the expectation that strong resource and consumer limitation translate into large responses following resource addition and consumer removal, respectively. The theoretical work from which the competition–defense tradeoff emerged supports these expectations. In these models, prey species compete for resources and experience predation by a shared consumer. Some species are better resource competitors (i.e., less limited by resources), whereas others are more resistant to predation (i.e., less limited by consumers). Both Holt et al. (1) and Leibold (2) have shown that densities of competing species change across a gradient of resource availability in predictable ways. When resources are scarce, only the species that is the best competitor for nutrients is present in the system. As resource supply increases, species that are inferior resource competitors (but better defended) invade and increase in density, at the expense of the superior resource competitors. These competitive but poorly defended species are favored when resources are scarce and consumer pressure is weak, whereas predation-resistant, poor resource competitors are dominant when resources are abundant and consumer pressure is high.

In addition to previous findings that lend support to our methods, we performed simulations to demonstrate explicitly that our approach is valid. Though there are countless ways to represent resource competition and predation in multispecies models, theoretical investigations of the competition–defense tradeoff have all used variations of the same model (1–4). We opted to use the formulation of Holt et al. (equation 10 in ref. 1), because their study is perhaps the most widely cited in support of the tradeoff:

$$\frac{dP}{dt} = P\left(a_1 b_1 N_1 + a_2 b_2 N_2 - c_p\right),$$

$$\frac{dN_1}{dt} = N_1\left(a_1^{'} b_1^{'} R - c_1^{'} - a_1 P\right),$$

$$\frac{dN_2}{dt} = N_2\left(a_2^{'} b_2^{'} R - c_2^{'} - a_2 P\right), \qquad \textbf{[S1]}$$

and

$$R = S - \frac{N_1}{b_1^{'}} - \frac{N_2}{b_2^{'}} - \frac{P}{b_p}.$$

A single consumer species P preys upon multiple species N_i with attack rates a_i and conversion efficiencies b_i, and experiences a density-independent mortality rate c_p. The competing prey species take up resource with affinities $a_i^{'}$ and conversion efficiencies $b_i^{'}$, and experience losses due both to predation and to density-independent mortality at rates $c_i^{'}$. All prey and consumer functional responses are linear with respect to their food sources. The system is assumed to be closed, so resource dynamics are determined by a simple mass balance constraint (i.e., the amount of free resource is equal to the total quantity of resource in the system S less the quantities of resource bound in prey and consumer populations).

Holt et al. (1) show that prey coexist if and only if there is a tradeoff between competitive ability and resistance to predation. More formally, the superior resource competitor must be more vulnerable to predation and must also support a higher density of consumers than the inferior resource competitor. A species' competitive ability is given by its R^* value:

$$R_i^* = \frac{c_i^{'}}{a_i^{'} b_i^{'}}. \qquad \textbf{[S2]}$$

As defined by Tilman (5), R^* is the resource concentration at equilibrium for a species grown in monoculture and in the absence of consumers. Species with low R^* values are better resource competitors (or are less limited by resource availability) than those with higher values.

Analogously, P^* is the consumer density a given species can support when grown in monoculture:

$$P_i^* = \frac{a_i^{'} b_i^{'} b_p}{a_i^{'} b_i^{'} + a_i b_p}\left(S - \frac{N_i^*}{b_i^{'}}\right) - \frac{b_p c_i^{'}}{a_i^{'} b_i^{'} + a_i b_p}, \qquad \textbf{[S3]}$$

where N^* is the prey species' own density at equilibrium. When resistance is the mechanism by which prey mitigate the impacts of predation, high values of P^* correspond to strong consumer limitation (i.e., susceptible prey support high consumer densities in monoculture and thus have high P^*, whereas resistant prey support few consumers and have low P^*). Thus, when the Holt et al. (1) tradeoff described above is operating, there is a negative correlation between prey species' R^* and P^* values.

We parameterized the system of equations (Eq. S1) with a tradeoff between competitive ability and defense for the two prey species. We incorporated resistance to predation for prey species 2 into the model by decreasing the consumer attack rate a_2. A cost to resistance was imposed by increasing this prey's density-independent death rate $c_2^{'}$. Thus, species 2 had high R^* and low P^*, and vice versa for species 1 (Fig. S1). We focus on resistance because it is the sole mechanism of plant defense that has been shown to promote coexistence in combination with resource competition (4). In contrast, a tradeoff between tolerance and competitive ability causes species to promote conditions that most limit their competitor, leading to alternative stable states.

We used simulations, analogous to the two experimental manipulations used by the studies in our dataset, to show that species' responses to perturbations correctly correspond to their R^* and P^* values. To quantify consumer limitation, we reduced consumer density by increasing the consumer mortality rate c_p (Fig. S2A Lower, solid line). Likewise, to quantify resource limitation, we increased the total resource supply S (Fig. S2B Upper, solid line). Both c_p and S were increased to 10% above their basal levels beginning at $t = 250$, and held at those values for the duration of the simulations. We conducted these manipulations in separate simulations so as to measure resource and consumer limitation independently. For both manipulations, we quantified a species' response as the log ratio of its density following the perturbation to its density before the perturbation (defined at $t = 250$, when the system had equilibrated and resource supply and consumer mortality were still at their basal levels). We calculated log ratios for the entire postperturbation period of a simulation (from $t = 250$ to $t = 500$) to show how responses evolved through time.

Our expectations were confirmed by these simulations. When consumer mortality was increased, species 1 (higher P^*) benefited more than the resistant species as measured by log response

ratios (Fig. S2*A*). Though both species did increase initially, the release from consumer pressure drove a rapid and prolonged increase in the density of species 1. This release allowed species 1 to take up more of the available resource, which ultimately had a negative effect on its resource-limited competitor (Fig. 2*A* and Fig. S2*A*). In a similar manner, species 2 (higher R^*) benefited more than the better resource competitor when resource supply was increased (Fig. 2*B*). As resources became more available, species 2 was released from resource limitation and increased sharply. This caused a subsequent increase in consumer density, which drove down the density of species 1, the less-resistant prey (Fig. 2*B* and Fig. S2*B*).

To confirm that our finding did not rest solely on parameter selection, we conducted 1,000 simulations in which all parameters were drawn from uniform distributions ranging ±20% around their values in Fig. S2. We discarded simulations in which species did not coexist because they are not relevant to exploring species' relative limitation when a tradeoff maintains diversity. The species more limited by a given factor should always have a more positive response when the degree of limitation is reduced. Therefore, when consumer mortality was increased, we calculated the log response

of species 1 (susceptible to consumers) minus the log response of species 2 (resistant to consumers). Likewise, when resource supply was increased, we calculated the log response of species 2 (weak resource competitor) minus the log response of species 1 (strong resource competitor). All differences were calculated at the end of the simulation ($t = 500$). These differences should always be positive if the metrics used in our paper are supported by the model, and indeed that is what we found (Fig. S3).

From such simulations, we conclude that log response ratios to resource addition and consumer removal are valid metrics of resource and consumer limitation, respectively. Though the sign of a species' log response ratio did sometimes change over time, relative to one another, species' responses were always what we would expect. That is, the species more limited by a given factor always benefits more when that limitation is removed. For example, species 2 was resistant to predation, yet did have a brief positive response to consumer removal. Crucially, although, the response of species 1, the consumer-limited species, was always greater than that of species 2 throughout the postperturbation period (i.e., the blue curve in Fig. 2*A* is always above the green curve).

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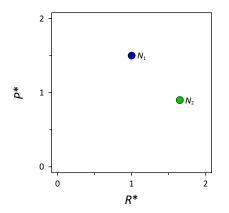
Fig. S1. R^* and P^* values of two species with a competition–defense tradeoff. Species 1 is the better competitor but is more susceptible to predation. Species 2 has greater resistance to consumers but is poorer at resource exploitation.
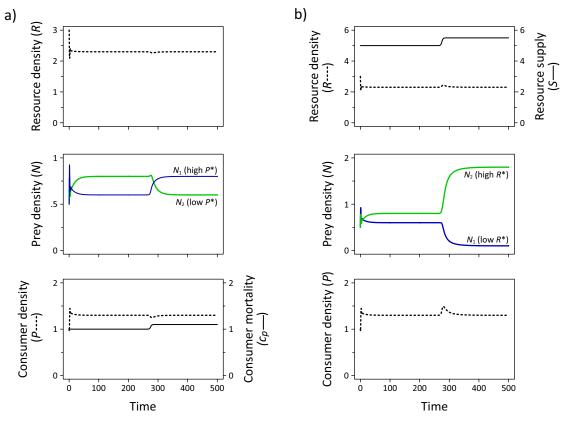

Fig. S2. Representative simulations of the Holt et al. model (Eq. S1) with perturbations in (*A*) consumer mortality and (*B*) resource supply. For both cases, we first allowed the system to equilibrate. To evaluate how limited species were by predation, we imposed an increase in consumer mortality c_p to 10% above its basal level (*A, Lower*). To evaluate resource limitation, we increased the resource supply S to 10% above its basal level (*B, Upper*). All other parameters in Eq. S1 were set to 1 except $a_2 = 0.5$, $c'_2 = 1.625$, and $S = 5$.
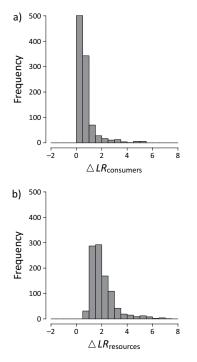
Fig. S3. Differences between species' log response ratio to (*A*) an increase in consumer mortality and to (*B*) an increase in resource supply when model parameters varied randomly. In *A*, the *x* axis is the response of species 1 (susceptible to consumers) minus the response of species 2 (resistant to consumers). In *B*, the *x* axis is the response of species 2 (weak resource competitor) minus the response of species 1 (strong resource competitor). Positive values indicate model support for our metrics of competitive ability and consumer resistance.
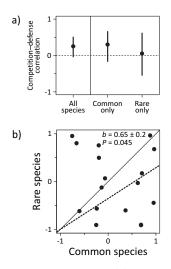

Fig. S4. Tradeoffs tend to be stronger among the rarest species in a community. (*A*) Mean competition–defense correlations did not differ significantly regardless of whether all species were included in the correlation, or whether only common or rare species were included. However, (*B*) competition–defense correlations within each study were consistently lower for rare species than for common species. The fitted line (dashed) falls below the 1:1 line (solid; the expected relationship if correlations for common and rare species within a study were equal on average). The *P* value is for the test that the estimated slope equals 1.
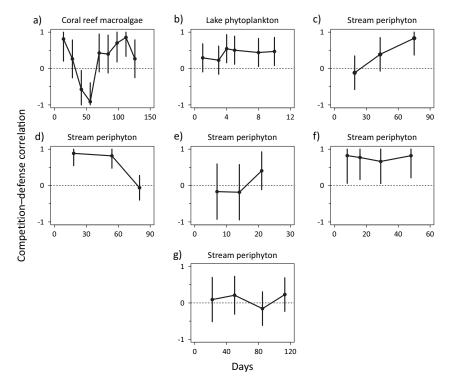
Fig. S5. Competition–defense correlations (±SE) over time for studies with time-series data. SEs are symmetrical, but are truncated for presentation in the cases for which bars fall outside the range of the correlation coefficient. Data are from (*A*) Thacker et al. (1); (*B*) Perez-Martinez and Cruz-Pizarro (2); (*C*) Steinman et al. (3); (*D*) Sumner and McIntire (4); (*E*) Walton et al. (5); (*F*) Steinman (6); and (*G*) Steinman et al. (7). See Studies Used in the Meta-Analysis for full citations.

Table S1.   Definitions of variables

Variable	Definition
Ecological characteristics	
System type	The habitat of the study (freshwater, marine, or terrestrial)
Organismal complexity	A broad classification of study organism (single cellular or multicellular)
Resource	The resource that was manipulated (light, nitrogen, or phosphorous, and in combinations)
Consumer	A broad classification of the type of consumer that was manipulated (invertebrate or vertebrate)
Experimental characteristics	
Study venue	The experimental location of the study (laboratory, field, or mesocosm)
Community assembly	The way in which the community was formed (artificial or natural)
Response variable	The way in which species' responses were measured (e.g., percent cover or biomass)
Duration	The number of days after treatments were imposed when response variable measured
Treatment definitions	
Control	Unfertilized and with consumers present
Resource addition	Fertilized and with consumers present
Consumer removal	Unfertilized and with consumers reduced or removed
Species-level variables	
Resource response	Log ratio of abundance in resource addition treatment to abundance in control treatment
Consumer response	Log ratio of abundance in consumer removal treatment to abundance in control treatment
Community-level variables	
Community size	No. of species in a study
Evenness	Species evenness for a given treatment
Richness	Species richness for a given treatment
Competition–defense correlation	Correlation between resource response and consumer response

Table S2. Test statistics for fixed categorical effects

Factor	Q	df	P
System type	3.87	2	0.144
Organismal complexity	0.88	1	0.347
Resource	3.48	4	0.481
Consumer	1.28	1	0.257
Study venue	0.31	2	0.854
Community assembly	0.29	1	0.588
Response variable	0.25	3	0.970

Q statistics are approximately χ^2 distributed with degrees of freedom (df).

Table S3. Test statistics for overall residual heterogeneity within levels of categorical effects

Factor	Q	df	P
Overall	95.35	35	
System type			
Terrestrial	49.05	9	<0.001
Freshwater	26.21	17	0.071
Marine	23.12	7	0.002
Organismal complexity			
Multicellular	43.19	10	<0.001
Single cellular	50.41	24	0.001
Resource			
Light (L)	1.70	3	0.637
Nitrogen (N)	19.33	2	<0.001
Phosphorous (P)	1.98	2	0.372
N + P	65.17	23	<0.001
L + N + P	2.96	1	0.085
Consumer			
Vertebrate	19.73	6	0.003
Invertebrate	74.08	28	<0.001
Study venue			
Laboratory	15.50	8	0.050
Field	51.38	22	<0.001
Mesocosm	30.57	3	<0.001
Community assembly			
Natural	56.02	22	<0.001
Artificial	41.78	12	<0.001
Response variable			
Biomass	34.88	5	<0.001
Percent cover	32.08	13	<0.001
Abundance	7.38	9	0.597
Biovolume	23.33	5	<0.001

Q statistics are approximately χ^2 distributed with degrees of freedom (df).