

Weis, J. J. and Vasseur, D. A. 2013. Differential predation drives overyielding of prey species in a patchy environment. – Oikos 000: 000–000.

Appendix A1

Equilibrium biomass

We solve for equilibrium population biomass of the resource (R^*), consumer species 1 (C_1^*) and species 2 (C_2^*), and the predator (P^*) from Eq. 1. Three sub-webs of the three-trophic level two-consumer food web emerge as stable equilibrium outcomes in our study. We derive these equilibria here.

In the simplest sub-web, the predator and one consumer are absent ($C_j^*, P^* = 0$) and equilibrium densities are given by Eq. A1.1.

$$C_i^* = k \left(\frac{uR_0}{m} - \frac{1}{a} \right) \quad (A1.1)$$

$$R^* = \frac{m}{ua_i}$$

In the simplest three-trophic level sub-web, one consumer is absent ($C_j^* = 0$) and resource, consumer, and predator equilibrium densities are given by Eq. A1.2.

$$P^* = \frac{\left(\frac{ua_i k R_0}{k + \frac{a_i d}{vb_i}} - m \right)}{b_i}$$

$$C_i^* = \frac{d}{vb_i}$$

$$R^* = \frac{kR_0}{k + \frac{a_i d}{vb_i}} \quad (A1.2)$$

When all four populations are present, equilibrium densities are given by Eq. A1.3.

$$\begin{aligned}
P^* &= \frac{m(a_2 - a_1)}{a_1b_2 - a_2b_1} \\
C_1^* &= \frac{kb_2 \left(\frac{R_0 u(a_2b_1 - a_1b_2)}{m(b_1 - b_2)} - 1 \right) - \frac{a_2d}{v}}{a_1b_2 - a_2b_1} \\
C_2^* &= \frac{kb_1 \left(\frac{R_0 u(a_1b_2 - a_2b_1)}{m(b_2 - b_1)} - 1 \right) - \frac{a_1d}{v}}{a_2b_1 - a_1b_2} \\
R^* &= \frac{m(b_2 - b_1)}{u(a_1b_2 - a_2b_1)}
\end{aligned} \tag{A1.3}$$

Appendix A2

Outcomes of consumer competition and predation

We explore the outcome of predator mediated coexistence of two consumer prey species through a tradeoff between resource uptake (a_i) and resistance to predation (b_i) by varying the parameter values of consumer 2 (a_2 and b_2 , Eq. 1). Competition between the competitors results in qualitatively different outcomes across $a_2 - b_2$ parameter space (Fig. 2, Table 2). The boundaries of these outcomes across $a_2 - b_2$ parameter space can be found from inequalities based on equilibrium solutions for biomass for the component populations (Supplementary material Appendix A1).

At equilibrium, not all sets of consumer 2 parameters ($a_2 < a_1$, $b_2 < b_1$) result in positive growth of consumer 2 in the presence of consumer 1. Setting the solution for C_2^* greater than zero in Eq. A1 defines the parameters for which consumer 2 can maintain a population at equilibrium in the presence of consumer 1 (Eq. A2.1).

$$b_2 < \frac{-a_2(b_1^2 R_0 kuv) + b_1^2 kmv + a_1 b_1 dm}{a_1 dm + b_1 kmv - a_1 b_1 R_0 kuv} \tag{A2.1}$$

If the inequality in Eq. A2.1 is false, consumer 2 is inviable, and we do not consider the parameters further (outcome I in Fig. 2).

Within the parameter space where consumer 2 can invade consumer 1 in the presence of a predator population (defined by Eq. A2.1), the area of parameter space for which consumer 2 is an 'edible' prey and can support a stable predator population in monoculture is defined by setting the solution for P^* greater than zero in Eq. A1.2 with the parameters set for consumer 2 (Eq. A2.2).

$$b_2 > -\frac{a_2 dm}{kv(m - a_2 R_0 u)} \quad (\text{A2.2})$$

If the inequality in Eq. A2.2 is false, we assume that the predator population goes extinct in the three-trophic level consumer 2 monoculture. For parameter values where Eq. A2.2 is false we record predator equilibrium biomass as zero ($P^* = 0$), and calculate consumer 2 (C_2^*) and resource (R^*) equilibrium biomass according to Eq. A1.1 in the three-trophic level consumer 2 monoculture.

The $a_2 - b_2$ parameter space in which consumer 2 outcompetes consumer 1 in the presence of the predator is defined by setting the solution for C_1^* less than zero in Eq. A1.1 (Eq. A2.3).

$$0 > b_2^2(kmv - a_1 R_0 kuv) + b_2(a_2 dm - b_1 kmv + a_2 b_1 R_0 kuv) - a_2 b_1 dm \quad (\text{A2.3})$$

If the inequality in Eq. A2.3 is true, we assume that consumer 1 goes extinct in the three-trophic level polyculture. Where Eq. A2.3 is true we set consumer 1 equilibrium biomass as zero ($C_1^* = 0$), and calculate predator, consumer 2, and resource equilibrium biomass according to Eq. A1.2 in the three-trophic level polyculture.

Appendix A3

Food web stability analysis

Here we analyze the local stability of the equilibrium biomass values of the consumer monoculture and polyculture food webs outlined in Supplementary material Appendix A1

No predator

When the predator and one consumer are absent ($C_j^*, P^* = 0$), the Jacobian matrix for the equilibrium values of consumer and resource biomass (Eq. A1.1) is shown in Eq. A3.1.

$$J(R^*, C_i^*) = \begin{bmatrix} -k - a_i C_i^* & -\frac{m}{u} \\ u a_i C_i^* & 0 \end{bmatrix} \quad (\text{A3.1})$$

Analytical solutions for the eigenvalues for Eq. A3.1 are shown in Eq. A3.2.

$$\lambda_1 = \frac{-a_i k R_0 u - \sqrt{k} \sqrt{4m^3 - 4am^2 R_0 u + a_i^2 k R_0^2 u^2}}{2m}$$
$$\lambda_2 = \frac{-a_i k R_0 u + \sqrt{k} \sqrt{4m^3 - 4am^2 R_0 u + a_i^2 k R_0^2 u^2}}{2m} \quad (\text{A3.2})$$

The first eigenvalue λ_1 is a negative real number for all parameter values considered. The second eigenvalue λ_2 is a negative real number for all conditions given that the inequality in Eq. A3.3 is true.

$$a_i > \frac{m}{R_0 u} \quad (\text{A3.3})$$

Equation A3.3 is true for the fixed parameter values of consumer 1 ($a_1 = 1.5$, Table 1). Equation A3.3 is true for consumer 2 given $a_2 > 0.2$. Across parameter values explored in our analysis, both eigenvalues for this sub-web are negative real numbers and equilibrium consumer monocultures in the absence of the predator are locally stable.

Monocultures with predator

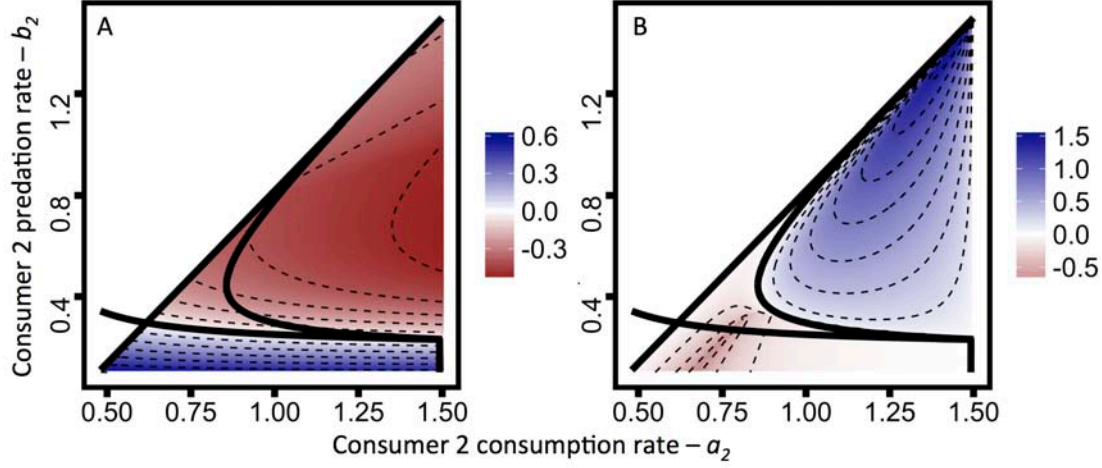
In the three-trophic level food web where one consumer is absent ($C_j^* = 0$), the Jacobian matrix for the equilibrium values of predator, consumer, and resource biomass in consumer monoculture (Eq. A1.2) is shown in Eq. A3.4.

$$J(R^*, C_i^*, P^*) = \begin{bmatrix} -k - a_i C_i^* & -a_i R^* & 0 \\ u a_i C_i^* & u a_i R^* - m - b_i P^* & -b_i C_i^* \\ 0 & v b_i P^* & v b_i C_i^* - d \end{bmatrix} \quad (\text{A3.4})$$

Analytical solutions for the eigenvalues of Eq. A3.4 are lengthy, and we focus on numerical solutions of eigenvalues to understand the stability of this sub-web. For the fixed parameters of consumer 1 ($a_1 = 1.5$, $b_1 = 1.5$, Table 1), the first two eigenvalues are complex numbers with the real component -0.44 . The third eigenvalue is the real number -0.44 . The equilibrium biomass of the three-trophic level food web with a consumer 1 monoculture is locally stable. Across the variable parameters of consumer 2, the dominant eigenvalue (most positive real component) of the consumer 2 monoculture tends to decrease as the predation rate on consumer 2 (b_2) increases (Fig. A3.1A). Here, the dominant eigenvalue is negative and equilibrium biomass is locally stable for parameter values where consumer 2 is ‘edible’ and can maintain a predator population at equilibrium in monoculture (where the inequality in Eq. A2.2 is true, Fig. 2).

Where consumer 2 is inedible the predator population goes extinct, the dominant eigenvalue is positive (Fig. A3.1A), and the three-trophic level food web is unstable. In our analyses, if the predator goes extinct in the three-trophic level sub-web with consumer 2, we record predator density as zero ($P = 0$) and measure consumer 2 and resource equilibrium biomass according to the two-trophic level sub-web equilibrium solutions (Eq. A1.1). As we have shown, equilibrium values for the all consumer 2 parameter values we consider are locally stable (Eq. A3.3).

Figure C1. Dominant eigenvalues in a three-trophic level food web. Real components of dominant eigenvalues are represented by color, red for negative values and blue for positive values. Dashed lines clarify contour of eigenvalues across consumer 2 parameter space. Solid lines show transition boundaries between outcomes of competition in the full polyculture food web (Figure 2). A. Dominant eigenvalue in the three-trophic level consumer 2 monoculture sub-web. B. Dominant eigenvalue in the three-trophic level consumer polyculture food web.



Polyculture with predator

For the full food web, the Jacobian matrix for predator, consumer, and resource biomass (Eq. A1.3) is shown in Eq. A3.5.

$$J(R^*, C_1^*, C_2^*, P^*) = \begin{bmatrix} -k - (a_1 C_1^* + a_2 C_2^*) & -a_1 R^* & -a_2 R^* & 0 \\ ua_1 C_1^* & ua_1 R^* - m - b_1 P^* & 0 & -b_1 C_1^* \\ ua_2 C_2^* & 0 & ua_2 R^* - m - b_2 P^* & -b_2 C_2^* \\ 0 & vb_1 P^* & vb_2 P^* & v(b_1 C_1^* + b_2 C_2^*) - d \end{bmatrix} \quad (\text{A3.5})$$

Analytical solutions of the eigenvalues for Eq. A3.5 are lengthy and we focus on numerical solutions to analyze the local stability of equilibrium values. For parameter values of consumer 2 where consumers coexist (Fig. 2, outcome II), the dominant eigenvalue of the Jacobian matrix in Eq. A3.4 is negative and equilibrium biomass of the food web is locally stable (Fig. A3.1B).

Where consumer 1 goes extinct (Fig. 2, outcome III), defined by the inequality in Eq. B3, the dominant eigenvalue is positive, and the three-trophic level polyculture food web is unstable. In our analysis, if consumer 1 goes extinct, we record consumer 1 equilibrium biomass as zero ($C_1 = 0$) and measure predator, consumer 2, and resource equilibrium biomass according to the

three-trophic level monoculture sub-web equilibrium solutions (Eq. A1.2). As we have shown, equilibrium values for this sub-web for parameter values of consumer 2 that result in the competitive exclusion of consumer 1 (Fig. 2, outcome III) are locally stable (Fig. A3.1A).

Appendix A4

Multivariate parameter space

Here we explore broader variation in the independent parameters (Table 1) of our three-trophic level ‘diamond shaped consumer resource food web (Eq. 1). We calculate equilibrium biomass for 10 000 randomly chosen parameter sets using the ordinary differential equation solver (NDSolve) in Mathematica set to a maximum of 10 000 time steps (Fig. A4.1). We also provide an interactive analysis of consumer yield across this multivariate parameter space that allows point-by-point calculations of deviations from relative yield for each consumer i (ΔRY_i), non-transgressive overyielding (D_T), and transgressive overyielding (D_{max}) in the two-patch region (Fig. D2). The file (Weis and Vasseur Fig. A4.2.cdf) can be downloaded from the online appendix and a free computable document format (.cdf) player and browser plugin is available from Wolfram Mathematica at www.wolfram.com/cdf-player/.

In Fig. A4.1 and Fig. A4.2 we require that consumer 1 has a higher per capita resource uptake rate than consumer 2 ($a_1 > a_2$), but is more susceptible to predation than consumer 2 ($b_1 > b_2$), and explore a range of consumer 2 parameter values for a given set of consumer 1 values (Table 1). We consider a broader range of consumer 1 per capita resource uptake rates (a_1) ranging from highly efficient consumers $a_1 = 10$ to highly inefficient consumers $a_1 = 0.1$ (Table 1). Similarly we consider a range of uptake rates of the predator on consumer 1 (b_1 from 0.1 to 10). We assume that a value of 1 for per capita death rates (d and m) and resource turnover rates (k) represent the high boundary of turnover in an ecosystem and allow a range of lower values for

these parameters with a minimum set near zero at 0.05. Similarly we assume that a value of 1 for conversion rates between trophic levels (v and u) represents a high boundary of conversion efficiency and allow a range of lower values for these parameters with a minimum set near zero at 0.05.

Of the initial 10 000 randomly chosen parameter sets, 2252 resulted in the stable coexistence of the two consumers in the predator patch (Fig. 2, outcome II), and 476 resulted in the competitive exclusion of consumer 1 (Fig. 2, outcome III). Of the outcome II parameter sets, D_{max} was positive in 60%, confirming that the direction and magnitude of transgressive overyielding in outcome II parameter space depends on parameter values (Fig. A4.1). In contrast, D_{max} was positive for all but 4 of the 476 outcome III parameter sets (<1%) (Fig. A4.1). D_{max} values for these four sets of parameters are actually long-term transient values from parameter sets where consumers were competitively very similar ($a_1 \approx a_2$ and/or $b_1 \approx b_2$) and not completely excluded in one or both patches by the end of 10 000 time steps. Overall, this analysis confirms that transgressive overyielding is predominantly positive in outcome III parameter space. In general, the direction and magnitude of D_{max} was not sensitive to the values of any other single parameter relative to the outcome of consumer competition (Fig. A4.1). D_{max} is constrained to values near zero with high values of a_2 and b_2 (Fig. A4.1, panel C and D) primarily because of consumer 1 and consumer 2 are more likely to be competitively similar at these values given the constraints ($a_1 > a_2$ and $b_1 > b_2$).

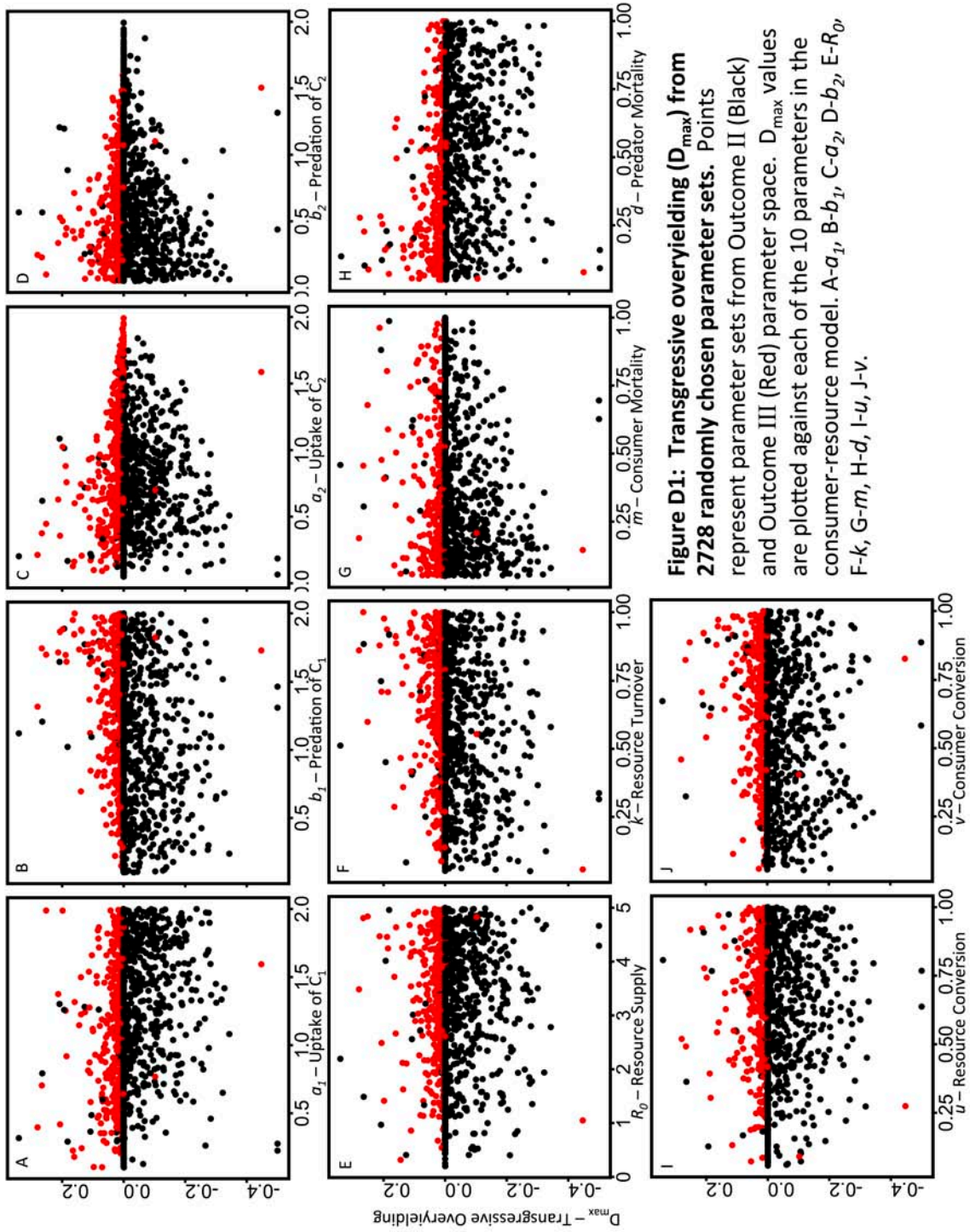


Figure D1: Transgressive overyielding (D_{\max}) from 2728 randomly chosen parameter sets. Points represent parameter sets from Outcome II (Black) and Outcome III (Red) parameter space. D_{\max} values are plotted against each of the 10 parameters in the consumer-resource model. A- a_1 , B- b_1 , C- a_2 , D- b_2 , E- R_0 , F- k , G- m , H- d , I- u , J- v .

Readers can further explore the conclusion that levels of overyielding are dependent upon the outcome of consumer competition by varying any single parameter in the interactive Fig. A4.2. In Fig. A4.2, the boundaries between the outcomes of consumer competition vary depending on the values of each parameter, which can be demonstrated in $a_2 - b_2$ parameter space (compare boundaries in Fig. A4.2 to Fig. 2).

Figure A4.2. (The file (Weis and Vasseur Fig. A4.2.cdf) can be downloaded from the online appendix and a free computable document format (.cdf) player and browser plugin is available from Wolfram Mathematica at www.wolfram.com/cdf-player/). Outcomes of competition and overyielding. This interactive plot allows readers to manipulate parameter values. The tabs can be moved to manipulate individual parameter values. Selecting a point on the figure with a mouse click will display deviations from relative yield (ΔRY_i), non-transgressive overyielding (D_T), and transgressive overyielding (D_{max}) for that point in $a_2 - b_2$ parameter space in the two-patch region (compare results to Fig. 4A–C). In Fig. A4.2, blue shows outcome I of consumer competition (Fig. 2). Gray shows outcome II, where light gray represents an ‘edible’ consumer 2 and dark gray represents an ‘inedible’ consumer 2. Red shows outcome III of consumer competition.