

# Supplementary Materials for

## Species coexistence through simultaneous fluctuation-dependent mechanisms

Andrew D. Letten,<sup>a,b\*</sup> Manpreet Dhami,<sup>a,c</sup> Po-Ju Ke,<sup>a</sup> & Tadashi Fukami<sup>a</sup>

<sup>a</sup>Department of Biology, Stanford University, Stanford, California, 94305-5020, USA

<sup>b</sup>University of Canterbury, Christchurch, New Zealand

<sup>c</sup>Biodiversity and Conservation, Landcare Research, Lincoln, New Zealand

\*To whom correspondence should be addressed; E-mail: [andrewletten@gmail.com](mailto:andrewletten@gmail.com)

### **This PDF file includes:**

Figs. S1 to S12

Tables S1 to S3

Supplementary text

# Supplementary figures

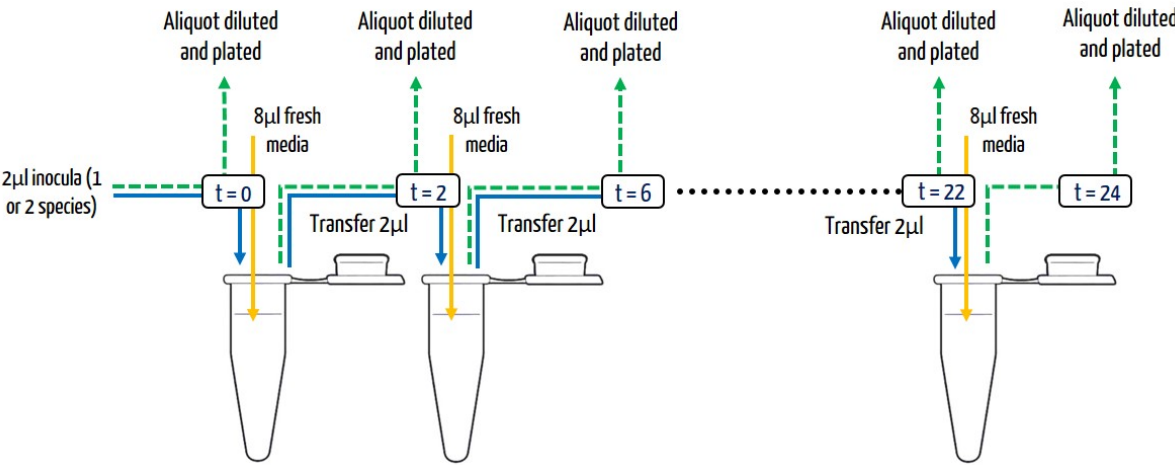


Figure S1: Illustration of the design of mixed- and mono-culture simulations and experiments.

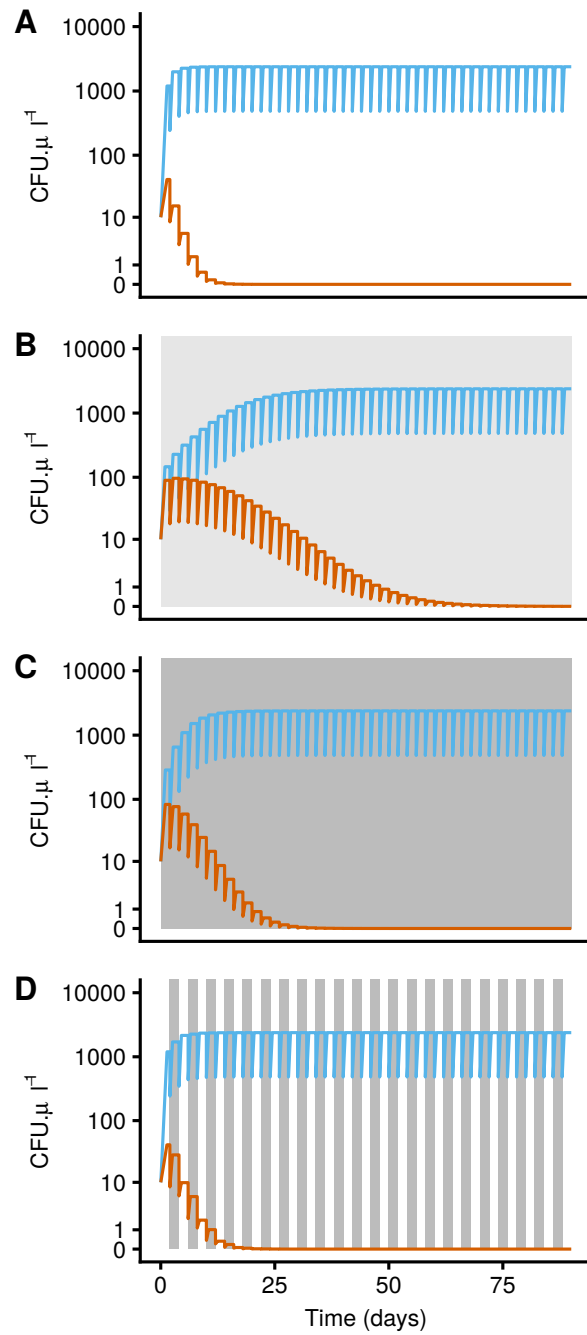


Figure S2: Simulated resource competition between *M. reukaufii* (blue) and *M. gruessii* (dark orange) at constant 10% (A), 30% (B), 50% (C) and fluctuating 10-50% (D) sucrose.

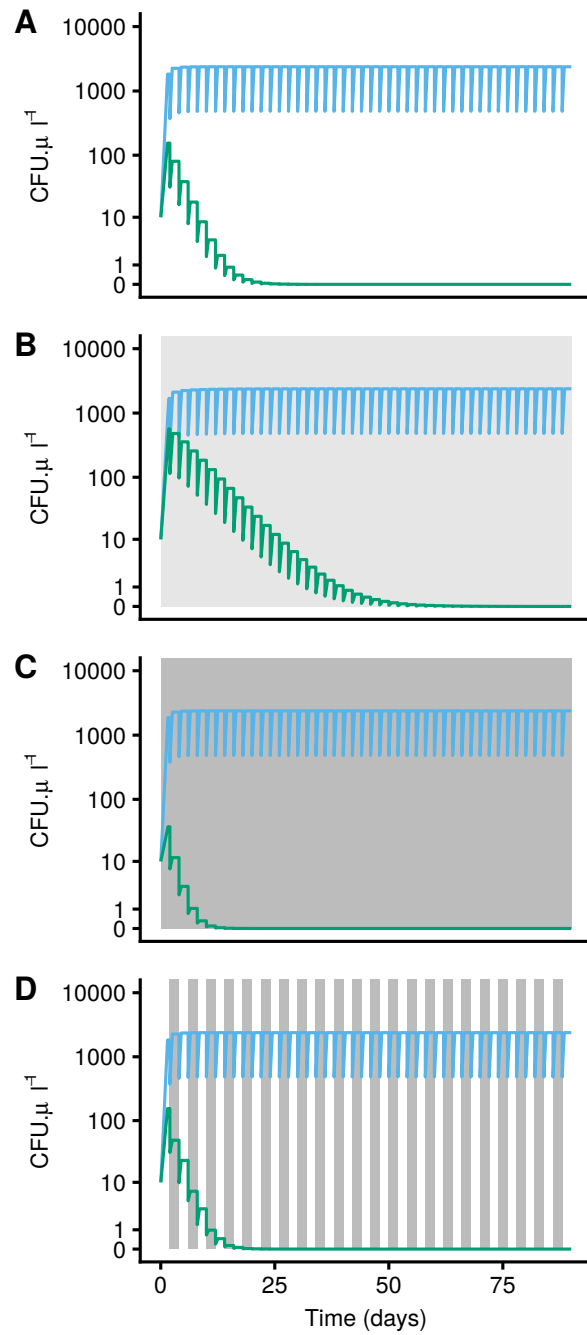


Figure S3: Simulated resource competition between *M. reukaufii* (blue) and *S. bombicola* (green) at constant 10% (A), 30% (B), 50% (C) and fluctuating 10-50% (D) sucrose.

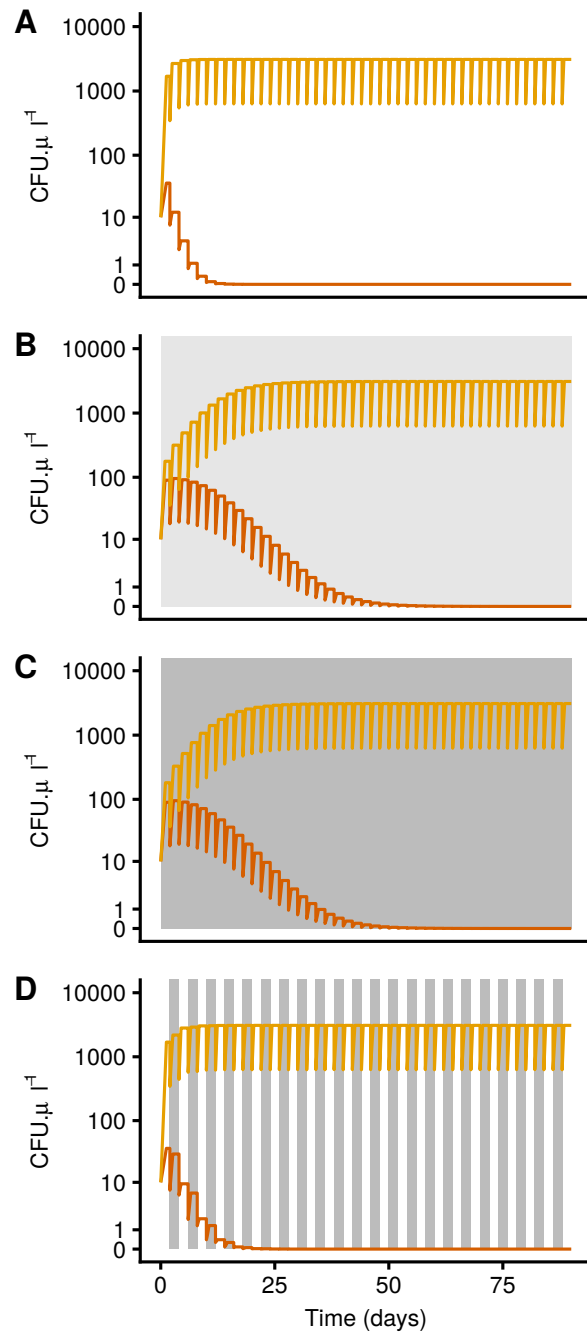


Figure S4: Simulated resource competition between *M. gruessii* (dark orange) and *M. koreensis* (light orange) at constant 10% (A), 30% (B), 50% (C) and fluctuating 10-50% (D) sucrose.

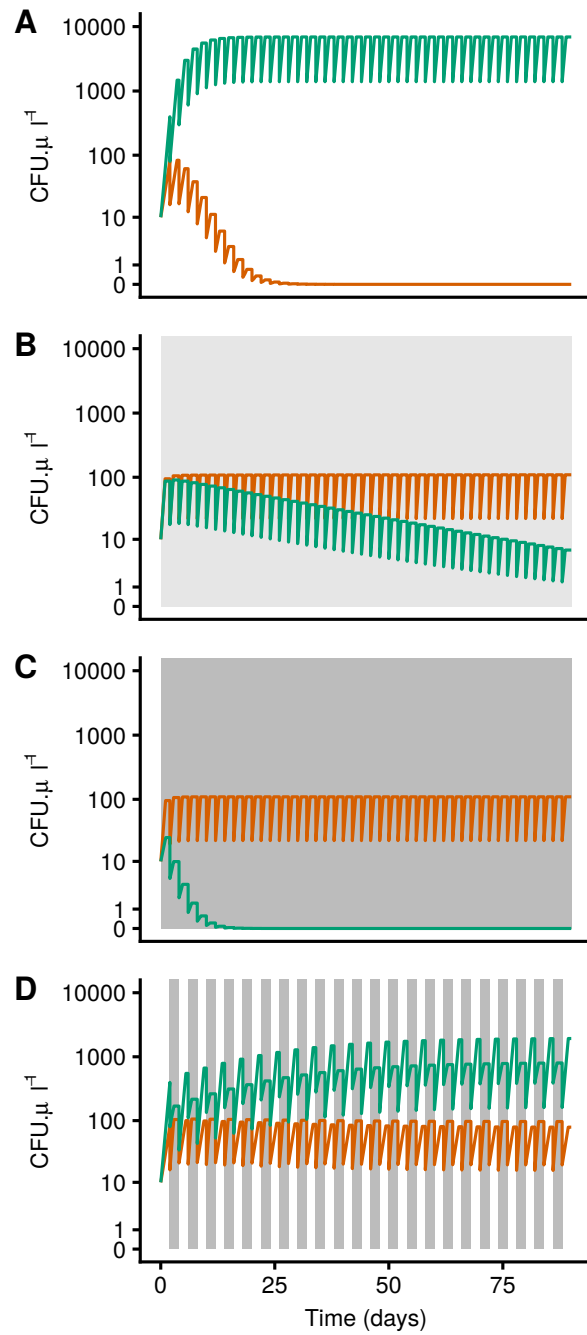


Figure S5: Simulated resource competition between *M. gruessii* (dark orange) and *S. bombicola* (green) at constant 10% (A), 30% (B), 50% (C) and fluctuating 10-50% (D) sucrose.

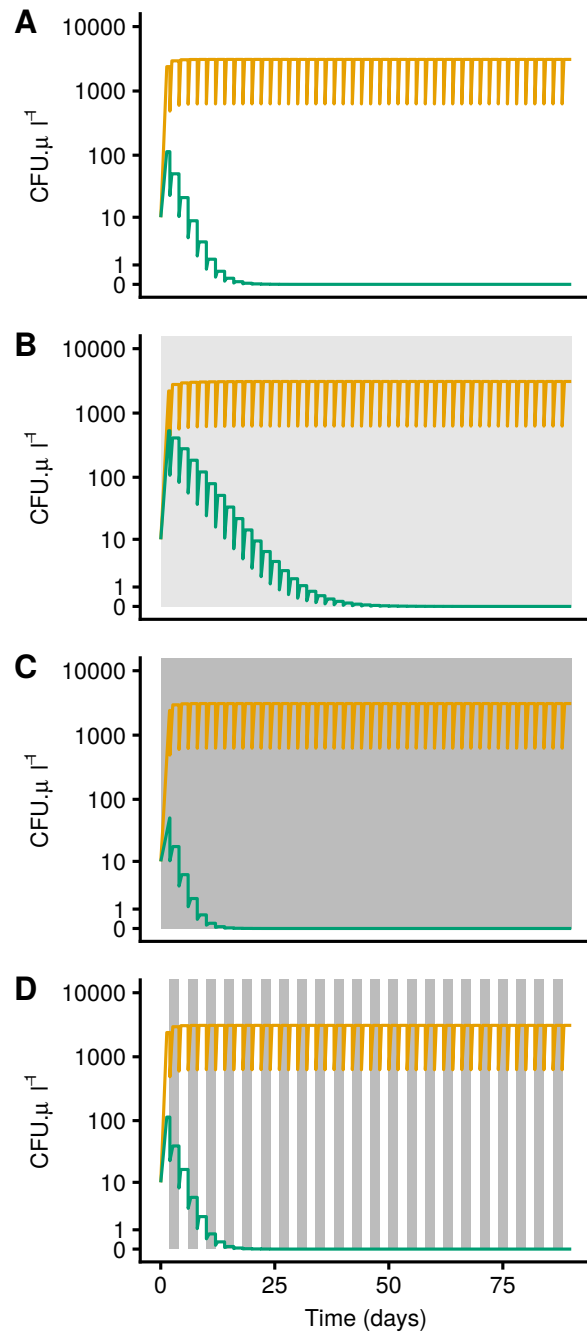


Figure S6: Simulated resource competition between *M. koreensis* (light orange) and *S. bombicola* (green) at constant 10% (A), 30% (B), 50% (C) and fluctuating 10-50% (D) sucrose.

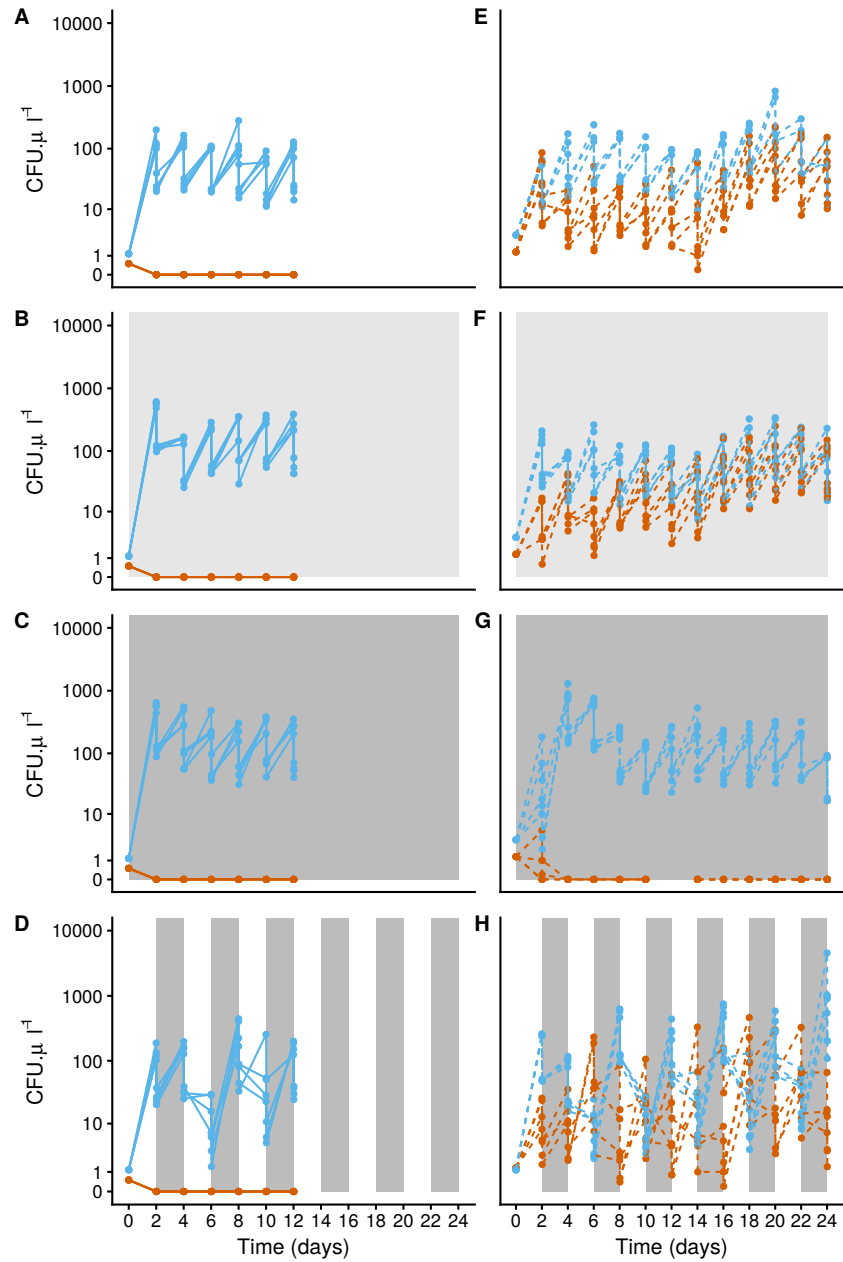


Figure S7: Mixed (solid lines) and monoculture (dashed lines) times-series for *M. guessii* (dark orange) and *M. reukaufii* (blue) at constant 10% (A,E), 30% (B,F), 50% (C,G) and fluctuating 10-50% (D,H) sucrose. Due to rapid exclusion of *M. guessii*, mixed culture assays were terminated after 12 days.



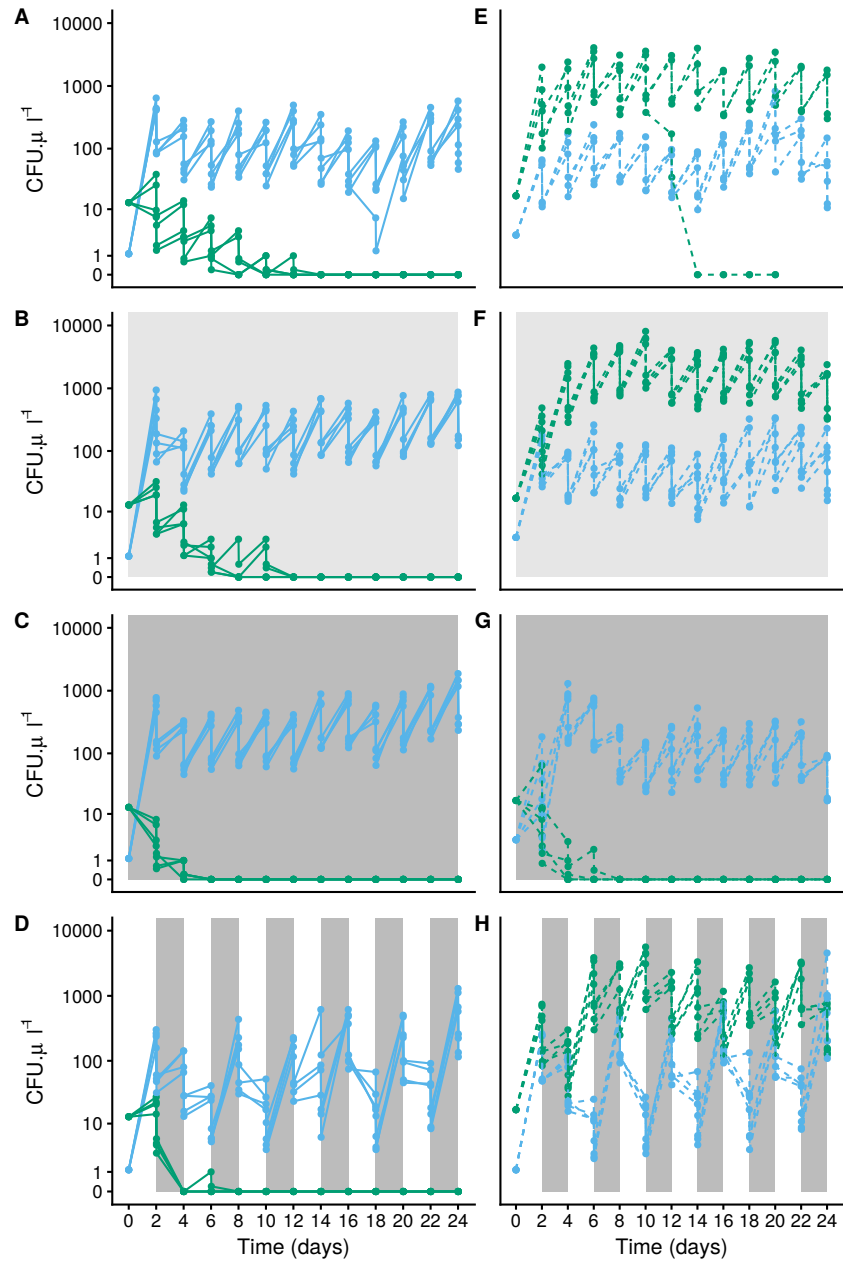


Figure S8: Mixed (solid lines) and monoculture (dashed lines) times-series for *S. bombicola* (green) and *M. reukaufii* (blue) at constant 10% (A,E), 30% (B,F), 50% (C,G) and fluctuating 10-50% (D,H) sucrose.

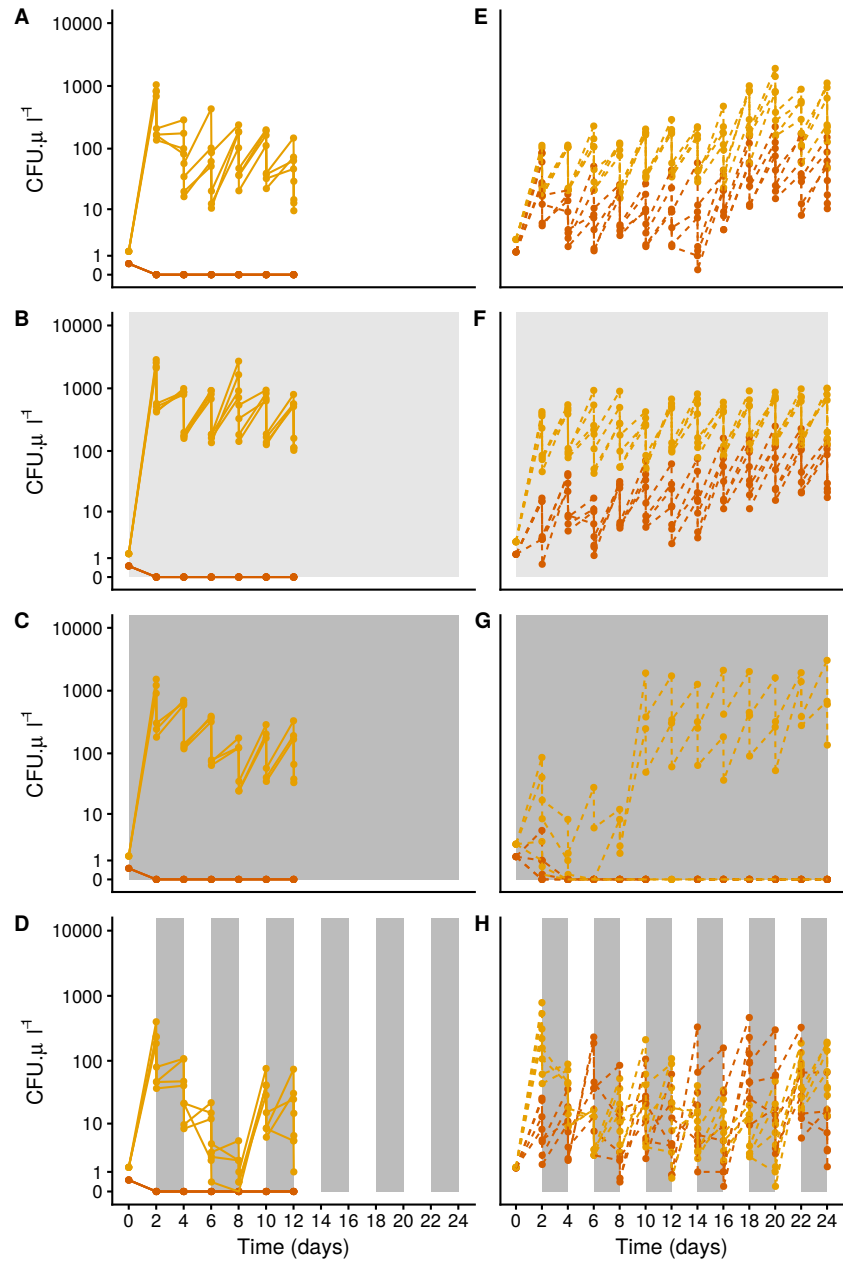


Figure S9: Mixed (solid lines) and monoculture (dashed lines) times-series for *M. gruessii* (dark orange) and *M. koreensis* (light orange) at constant 10% (A,E), 30% (B,F), 50% (C,G) and fluctuating 10-50% (D,H) sucrose. Due to rapid exclusion of *M. gruessii*, mixed culture assays were terminated after 12 days.

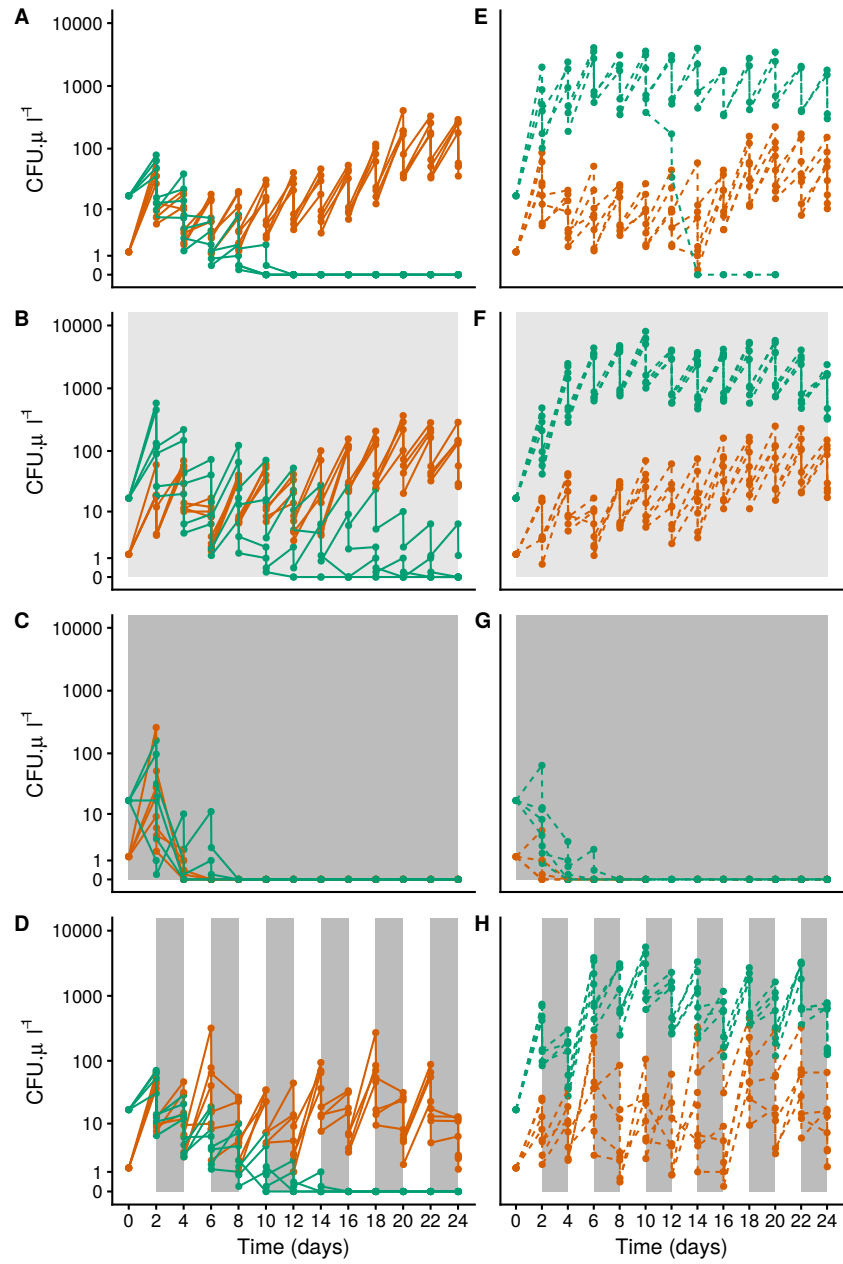


Figure S10: Mixed (solid lines) and monoculture (dashed lines) times-series for *S. bombicola* (green) and *M. gruessii* (dark orange) at constant 10% (A,E), 30% (B,F), 50% (C,G) and fluctuating 10-50% (D,H) sucrose.

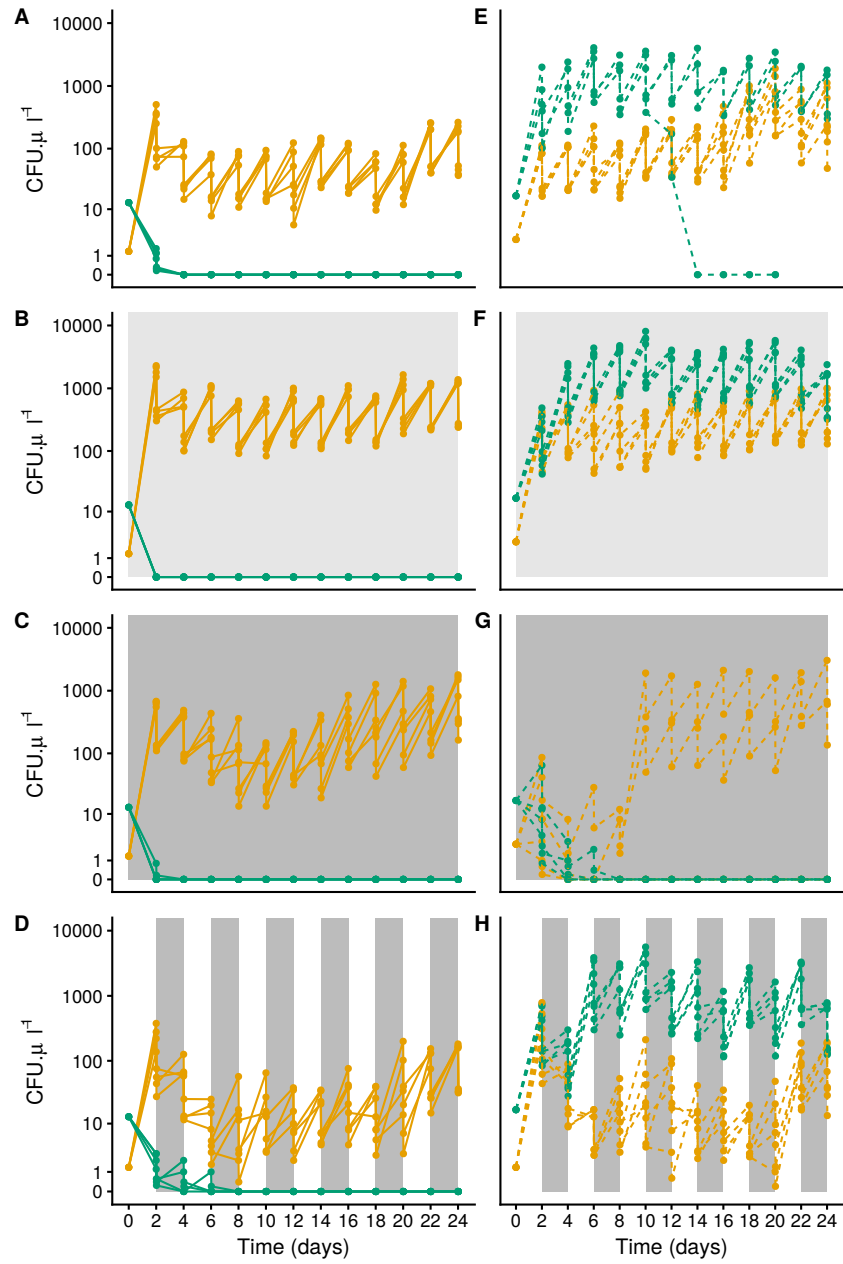


Figure S11: Mixed (solid lines) and monoculture (dashed lines) times-series for *S. bombicola* (green) and *M. koreensis* (light orange) at constant 10% (A,E), 30% (B,F), 50% (C,G) and fluctuating 10-50% (D,H) sucrose.

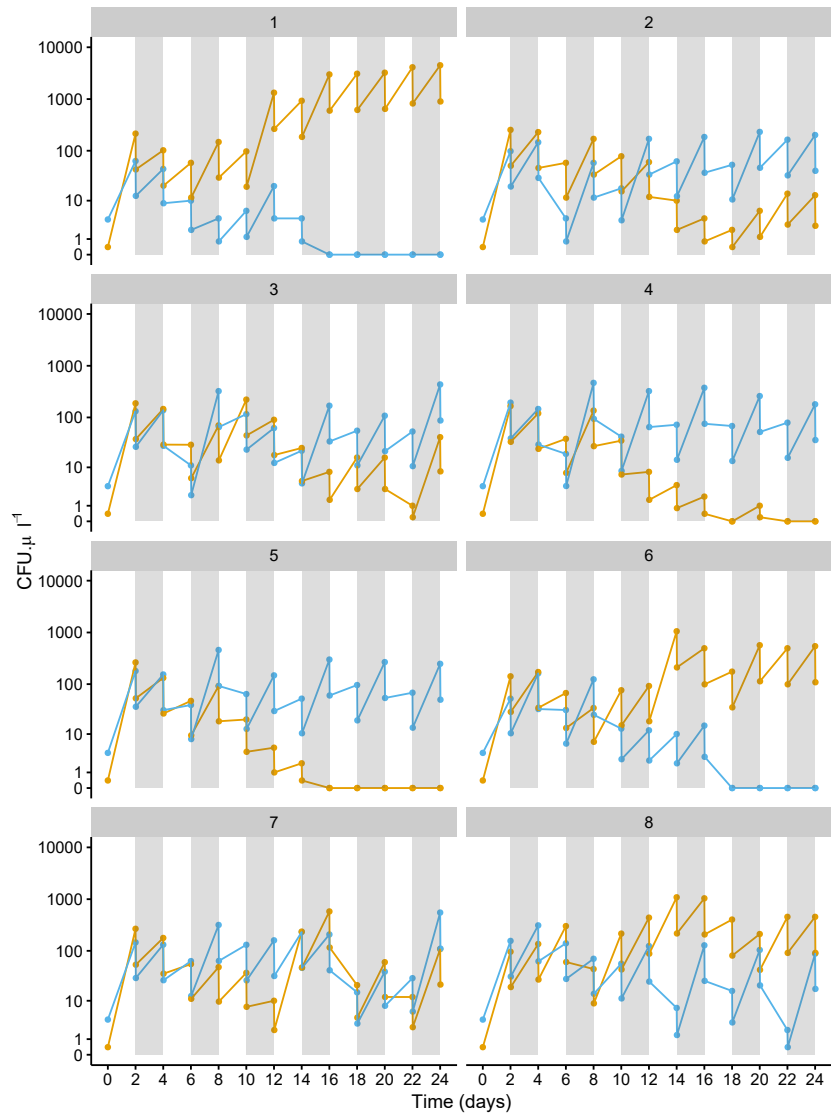


Figure S12: Replicated experiment. Mixed culture times-series for *M. koreensis* (light orange) and *M. reukaufii* (blue) under fluctuating 10-50% (D) sucrose.

## Supplementary tables

Table S1: Model parameters and  $R^*$  for each species at each sucrose concentration ( $R^* = \frac{DK}{\mu_{max} - D}$ , where  $D = 0.03352 \text{ hr}^{-1}$ ).

Species	Sucrose (%)	$K$ (mM)	$\mu_{max}$ ( $\text{hr}^{-1}$ )	$Q$ (mM)	$R^*$
<i>M. koreensis</i>	10	0.0058	0.1741	0.0009	0.0014
	30	0.0029	0.1305	0.0009	0.0010
	50	0.0365	0.1219	0.0009	0.0140
<i>M. reukaufii</i>	10	0.0047	0.1469	0.0011	0.0014
	30	0.0067	0.1225	0.0011	0.0025
	50	0.0084	0.1409	0.0011	0.0026
<i>S. bombicola</i>	10	0.0048	0.0772	0.0004	0.0037
	30	0.0083	0.0966	0.0004	0.0044
	50	0.0021	0.0349	0.0004	0.0526
<i>M. gruessii</i>	10	0.0169	0.0442	0.0245	0.0530
	30	0.0003	0.0992	0.0245	0.0002
	50	0.0426	0.0930	0.0245	0.0240

Table S2: Contribution of  $\Delta I$  and  $\Delta N$  to invader growth rate for all species pairs in all treatments, alongside simulation predictions and experimental outcomes. Experimental results inconsistent with model predictions are bolded.  $\Delta I$  boxes greyed-out under constant treatments to indicate there is no storage effect in the absence of environmental fluctuations.

Treatment	Species pair	$r_{inv}$	$\Delta I$	$\Delta N$	Predicted outcome	Observed outcome
Fluctuating	Mr Mk	0.00073 0.000065	0.00092 0	-0.00092 0.0013	coexist	coexist*
	Mr Mg	0.05 -0.017	0.0054 0.0011	-0.032 0.06	Mg excluded	Mg excluded
	Mr Sb	0.065 -0.021	0.0048 -0.00091	-0.027 0.065	Sb excluded	Sb excluded
	Mk Mg	0.055 -0.017	0.01 0.0021	-0.033 0.059	Mg excluded	Mg excluded
	Mk Sb	0.06 -0.021	-0.00074 0.0000074	-0.029 0.064	Sb excluded	Sb excluded
	Mg Sb	0.018 0.0029	0.011 0.0088	-0.0037 0.0043	coexist	<b>Sb excluded</b>
	Mr Mk	-0.005 0.006		0.021 -0.02	Mr excluded	Mr excluded
	Mr Mg	0.08 -0.02		-0.023 0.08	Mg excluded	Mg excluded
	Mr Sb	0.03 -0.016		-0.039 0.053	Sb excluded	Sb excluded
	Mk Mg	0.1 -0.025		-0.029 0.1	Mg excluded	Mg excluded
	Mk Sb	0.042 -0.019		-0.054 0.076	Sb excluded	Sb excluded
	Mg Sb	-0.015 0.026		0.019 -0.007	Mg excluded	<b>Sb excluded</b>
Constant 10	Mr Mk	-0.0024 0.0023		0.007 -0.0068	Mr excluded	Mr excluded
	Mr Mg	0.0073 -0.0061		-0.014 0.015	Mg excluded	Mg excluded
	Mr Sb	0.0089 -0.0073		-0.017 0.019	Sb excluded	Sb excluded
	Mk Mg	0.01 -0.008		-0.02 0.022	Mg excluded	Mg excluded
	Mk	0.012		-0.023	Sb excluded	Sb excluded
	Constant 30	Mr Mk	-0.0024 0.0023		0.007 -0.0068	Mr excluded
Mr Mg		0.0073 -0.0061		-0.014 0.015	Mg excluded	Mg excluded
Mr Sb		0.0089 -0.0073		-0.017 0.019	Sb excluded	Sb excluded
Mk Mg		0.01 -0.008		-0.02 0.022	Mg excluded	Mg excluded
Mk		0.012		-0.023	Sb excluded	Sb excluded

	Sb	-0.0091		0.026		
	Mg	0.0014		-0.0026		
	Sb	-0.0014		0.0029	Sb excluded	Sb excluded
Constant 50	Mr	0.0068		-0.02		
	Mk	-0.0057		0.022	Mk excluded	<b>coexist</b> <sup>†</sup>
	Mr	0.02		-0.033		
	Mg	-0.012		0.043	Mg excluded	Mg excluded
	Mr	0.1		-0.0032		
	Sb	-0.025		0.078	Sb excluded	Sb excluded
	Mk	0.011		-0.017		
	Mg	-0.0083		0.02	Mg excluded	Mg excluded
	Mk	0.081		-0.0038		
	Sb	-0.023		0.053	Sb excluded	Sb excluded
	Mg	0.053		-0.0028		
	Sb	-0.02		0.031	Sb excluded	<b>Non-persistence</b>

\* coexistence in 3 out of 4 replicates in original experiment and 4 out of 8 replicates in follow-up experiment;  
† coexistence in 3 out of 4 replicates.



Table S3: Scaling factor adjusted contribution of  $\Delta I$  and  $\Delta N$  to invader growth rate for all species pairs in all treatments.  $\Delta I$  boxes greyed-out under constant treatments to indicate there is no storage effect in the absence of environmental fluctuations.

Treatment	Species pair	$r_{inv}$	$q_{ir}$	$adjusted-\Delta I$	$adjusted-\Delta N$	
Fluctuating	Mr	0.00073	0.33	0.00021	-0.072	
	Mk	0.000065	3	(0) 2.4e-05	0.22	
	Mr	0.05	0.49	0.0029	-0.047	
	Mg	-0.017	1.9	0.0013	0.15	
	Mr	0.065	4.8	0.026	0.037	
	Sb	-0.021	0.21	-0.001	-0.019	
	Mk	0.055	1.6	0.013	-0.018	
	Mg	-0.017	0.62	0.0017	0.019	
	Mk	0.06	16	0.08	0.22	
	Sb	-0.021	0.069	-0.00098	-0.034	
	Mg	0.018	9.9	0.061	0.15	
	Sb	0.0029	0.1	0.0045	-0.02	
	Constant 10	Mr	-0.005	0.69		-0.021
		Mk	0.006	2.9		0.19
Mr		0.08	0.95		-0.02	
Mg		-0.02	2		0.19	
Mr		0.03	1.9		-0.0016	
Sb		-0.016	1.1		0.06	
Mk		0.1	1.4		-0.025	
Mg		-0.025	1.4		0.15	
Mk		0.042	2.71		0.02	
Sb		-0.019	0.74		0.019	
Mg		-0.015	1.9		0.059	
Sb		0.026	1		-0.007	
Constant 30	Mr	-0.0024	2.1		0.12	
	Mk	0.0023	0.94		-0.012	
	Mr	0.0073	25		1.53	
	Mg	-0.0061	0.082		-0.065	
	Mr	0.0089	1		-0.016	
	Sb	-0.0073	2		0.1	
	Mk	0.01	11		0.67	
	Mg	-0.008	0.18		-0.057	
	Mk	0.012	0.48		-0.055	
	Sb	-0.0091	4.2		0.33	
Mg	0.0014	0.042		-0.063		

	Sb	-0.0014	48		3.2
	Mr	0.0068	0.31		-0.074
	Mk	-0.0057	6.4		0.58
	Mr	0.02	0.34		-0.067
	Mg	-0.012	5.5		0.51
	Mr	0.1	16		0.0096
	Sb	-0.025	0.13		-0.013
Constant 50	Mk	0.011	1.1		-0.0094
	Mg	-0.0083	1.7		0.076
	Mk	0.081	57		0.045
	Sb	-0.023	0.04		-0.021
	Mg	0.053	50		0.04
	Sb	-0.02	0.044		-0.019

## Supplementary text

### Derivation of scaling factors

In this section we describe the derivation of the scaling factors,  $q_{ir}$ . As in [1], we start by defining the competitive effects experienced by each species  $j$  when species  $i$  is invading,  $\mathcal{C}_{j\setminus i}$ , as:

$$\mathcal{C}_{j\setminus i} = -r_j(E_j^*, C_{j\setminus i}). \quad (\text{S1})$$

Here,  $E_j^*$  is the baseline environment and is typically set as the central value of  $E_j(t)$ . Then, the scaling factors,  $q_{ir}$ , are defined as follows:

$$q_{ir} = \frac{\partial \mathcal{C}_{i\setminus i}}{\partial \mathcal{C}_{r\setminus i}}. \quad (\text{S2})$$

For our model, if we set  $E_j^*$  as the mean value  $\overline{\mu_{max_j}}$ , we arrive at the following expression:

$$\mathcal{C}_{j\setminus i} = D - E_j^*/C_j = D - \frac{\overline{\mu_{max_j}}R}{K_j + R}. \quad (\text{S3})$$

To derive  $q_{ir}$  for our model, we turn to equation (SI.16) in [2] since an explicit formula for  $\mathcal{C}_{i\setminus i}$  as a function of  $\mathcal{C}_{r\setminus i}$  cannot be easily found. With this approach, we derived  $q_{ir}$  as follows:

$$q_{ir} = \frac{\partial \mathcal{C}_{i\setminus i}}{\partial \mathcal{C}_{r\setminus i}} = \frac{\partial \mathcal{C}_{i\setminus i}/\partial R}{\partial \mathcal{C}_{r\setminus i}/\partial R} = \frac{\overline{\mu_{max_i}}\overline{K_i}}{\overline{\mu_{max_r}}\overline{K_r}} \times \frac{(\overline{K_r} + \overline{R_r})^2}{(\overline{K_i} + \overline{R_r})^2}. \quad (\text{S4})$$

We used the mean value of  $K_j$  as the half-saturation constant varies with environmental variability in our model. More importantly, we used the mean resource level set by the resident,  $\overline{R_r}$ , instead of its respective  $R^*$ . This is because in our system the pulsing of resources set by the resident results in a mean resource level set by the resident that is slightly greater than expected based on each species  $R^*$ . According to the small-variance assumption of [1], this choice should be immaterial assuming  $\overline{R_r}$  and  $R^*$  differ by  $O(\sigma^2)$ . Nevertheless, as we found in this work, we expect this assumption to break down in many empirical contexts. We refer to this derivation of the scaling factors as semi-analytical as the mean resource level set by the resident is obtained through numerical simulation.

## References

- [1] Chesson P (1994) Multispecies competition in variable environments. *Theoretical Population Biology* 45(3):227–276.
- [2] Ellner SP, Snyder RE, Adler PB (2016) How to quantify the temporal storage effect using simulations instead of math. *Ecology Letters* 19(11):1333–1342.