Supplementary Information

2 S.I.1. Testing for the effect of composition treatment on fecundity

We tested for the effect of composition treatment (solo / exotic-dominated / native-dominated / monoculture / control) on individual plant fecundity using a negative binomial model with the function manyglm from the package mvabund in R (Wang et al., 2012; R Development Core Team, 2016). We ran a separate GLM for each focal species. Given that our annual plant population model accounts for neighbour density and identity, we wanted to test whether composition treatment had a further effect on plant fecundity. We therefore included the effects of neighbour density and identity when testing for composition treatment.

10 For each focal species, the model formula was as described as follows:

11 Focal species fitness ~ $N_A + N_H + N_W + N_T + N_N +$ composition treatment

where N_A, N_H, N_W, N_T and N_N refer to the abundances of *A. calendula*, *H. glabra*, *W. acuminata*, *T. cyanopetala*, and all neighbours (combined) which were not any of the four focal species (N_N), respectively. Results from a Wald test on the model outputs for each focal species is presented in Supplementary Table 1. Composition treatment was only found to have a significant effect on *T. cyanopetala*, we hence felt comfortable not including composition treatment as an effect in our study.

18

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Supplementary Table 1.1: Walt test results and associated *p* values testing the effect of
neighbour density (N_A, N_H, N_W, N_T and N_N) and neighbourhood composition treatment
('Composition') on the individual fecundity of each focal species (measured as the number of
seeds produced). The Walt test was performed using the anova.manyglm function of the
mvabund package (Wang et al., 2012) on the results of a negative binomial glm. *p* values below
0.05 are bolded.

	A. calendula			H. glabra			W. acuminata			T. cyanopetala		
	df	Wald	р	df	Wald	р	df	Wald	р	df	Wald	р
	(df _{res})	test		(df _{res})	test		(df _{res})	test		(df _{res)}	test	
NA	1	0.610	0.534	1	0.051	0.959	1	0.338	0.757	1	1.684	0.150
	(250)			(273)			(272)			(223)		
N _H	1	1.362	0.177	1	1.637	0.126	1	1.300	0.195	1	1.922	0.098
	(249)			(272)			(271)			(222)		
N_W	1	3.012	0.007	1	5.694	0.001	1	2.177	0.031	1	2.309	0.042
	(248)			(271)			(270)			(221)		
NT	1	0.006	0.996	1	0.566	0.589	1	3.873	0.004	1	2.823	0.008
	(247)			(270)			(269)			(220)		
N_N	1	4.261	0.001	1	1.721	0.080	1	3.135	0.006	1	4.917	0.002
	(246)			(269)			(268)			(219)		
Comp	4	2.345	0.263	4	2.217	0.343	4	2.646	0.119	4	4.055	0.014
	(242)			(265)			(264)			(215)		

27 S.I.2. Estimating model parameters

In order to estimate the parameters for Eqs. 2-5 (in the main text), we fit a negative binomial generalised linear model to our observations of seed production for each of our four focal species separately. We did this regression in R (R Development Core Team, 2016), using the manyglm function from the mvabund package (Wang et al., 2012). For the baseline model (no environmental effect), the model formula was the following:

33 Fitness ~
$$\beta_0 + \beta_1 A + \beta_2 H + \beta_3 T + \beta_4 W + \beta_5 N$$

where 'Fitness' refers to our observations of seed production, β_0 is an intercept and 'A', 'H', 'T', 'W' and 'N' are the abundances of *A. calendula*, *H. glabra*, *T. cyanopetala*, *W. acuminata* and all other species in the immediate neighbourhood of the focal individual, respectively. β_0 gives us the value of $\tilde{\alpha}_i$ for intrinsic fitness in Eq. 3 (main text), whereas the coefficients for the abundances of each neighbour ($\beta_1 - \beta_5$) give us the equivalent interaction coefficients (α_{ii} and α_{ij} in Eqs. 4 and 5 in the main text).

40 For our environmental models, the model formula was:

41 Fitness ~ $\beta_0 + \beta_1 abiotic + \beta_2 I(abiotic^2) + \beta_3 A + \beta_4 H + \beta_5 T + \beta_6 W + \beta_7 N + \beta_8 A: abiotic + \beta_9 H: abiotic$ $42 + <math>\beta_{10} T: abiotic + \beta_{11} W: abiotic + \beta_{12} N: abiotic + \beta_{13} A: I(abiotic^2) + \beta_{14} H: I(abiotic^2) + 43$ 43 $\beta_{15} T: I(abiotic^2) + \beta_{16} W: I(abiotic^2) + \beta_{17} N: I(abiotic^2)$

The effect of environmental variation is included by adding both a linear ('abiotic') and quadratic ('I(abiotic^2)') term, as well as an interaction between each of these and the neighbouring species (e.g. 'A:abiotic' and 'A:I(abiotic^2)'). We use the coefficients estimated above to calculate the parameters for intrinsic fitness:

48 (1)
$$\tilde{a}_i = \beta_0 - \frac{\beta_1^2}{4\beta_2}$$

$$49 \qquad (2) \tilde{b}_i = \beta_2$$

50 (3)
$$\dot{\xi}_i = \frac{-\beta_1}{2\beta_2}$$

51 Where β_0 in S.I. Eq. 1 refers to the intercept, and β_1 and β_2 refer to the coefficients estimated 52 for the terms 'abiotic' and 'I(abiotic^2)'. Substituting S.I. Eqs. 1-3 into Eq. 3 (main text), we get:

53 (4)
$$\lambda_i = e^{\beta_0 - \frac{\beta_1^2}{4\beta_2} + \beta_2 \left(\xi - \frac{-\beta_1}{2\beta_2}\right)^2}$$

54 Which simplifies to:

55 (5)
$$\lambda_i = e^{\beta_0 + \beta_1 \xi + \beta_2 \xi^2}$$

We proceed in the same manner for calculating the parameters for each of the interaction
coefficients. For example, with species *j* as *H. glabra* we get:

58 (6)
$$\bar{\alpha}_{ij} = \beta_4 - \frac{\beta_9^2}{4\beta_{14}}$$

59 (7) $\delta_{ij} = \beta_{14}$

60 (8)
$$\dot{\xi}_{ij} = \frac{-\beta_9}{2\beta_{14}}$$

61 Substituting S.I. Eqs. 6-8 into Eq. 5 (main text) simplifies to:

62 (9)
$$\alpha_{ij} = \beta_4 + \beta_9 \xi + \beta_{14} \xi^2$$

64 S.I.3. Estimates model parameters

65 Supplementary Figure 3.1: Summary graph of estimated parameters for the focal species A. 66 *calendula* varying along gradients of tree canopy cover, phosphorus and water availability. The top row (a-c) shows estimates of intrinsic fitness λ_i , and the second row (d-f) shows 67 intraspecific interaction strength α_{ii} (Eq. 4 in the main text). The three bottom rows show 68 how estimates of interspecific interaction strength α_{ii} (Eq. 5 in the main text) between A. 69 70 *calendula* and each of the other three focal species (g-i: *W. acuminata*; j-l: *T. cyanopetala*; m-o: *H. glabra*) vary along each gradient. In the graphs depicting interaction strength (d-o), any 71 72 value over 0 (in white) indicates competition, and any value below 0 (in grey) indicates 73 facilitation. Lines represent model fits and dotted lines give the simulated 95% confidence 74 intervals. The vertical dashed line present in the intrinsic fitness plots corresponds to the 75 maximum or minimum environmental value (as determined by fecundity rather than abundance) for *A. calendula* given by ξ_i . The darker ticks along the x axis indicate where 76 77 observations of fecundity collected along each environmental gradient.



80 <u>Supplementary Figure 3.2</u>: Summary graph of estimated parameters for the focal species *H*.

81 *glabra* varying along gradients of tree canopy cover, phosphorus and water availability.

The top row (a-c) shows estimates of intrinsic fitness $\lambda_{i'}$ and the second row (d-f) shows 82 83 intraspecific interaction strength α_{ii} (Eq. 4 in the main text). The three bottom rows show how estimates of interspecific interaction strength α_{ii} (Eq. 5 in the main text) between *H. glabra* and 84 each of the other 3 focal species (g-i: *W. acuminata;* j-l: *T. cyanopetala*; m-o: *A. calendula*) vary 85 along each gradient. In the graphs depicting interaction strength (d-o), any value over 0 (in 86 87 white) indicates competition, and any value below 0 (in grey) indicates facilitation. Lines 88 represent model fits and dotted lines give the simulated 95% confidence intervals. The vertical 89 dashed line present in the intrinsic fitness plots corresponds to the maximum or minimum 90 environmental value (as determined by fecundity rather than abundance) for *H. glabra* given by ξ_i . The darker ticks along the x axis indicate where observations of fecundity collected along 91 92 each environmental gradient.



95 <u>Supplementary Figure 3.3</u>: Summary graph of estimated parameters for the focal species *T*.

96 *cyanopetala* varying along gradients of tree canopy cover, phosphorus and water availability.

97 The top row (a-c) shows estimates of intrinsic fitness λ_{i} , and the second row (d-f) shows 98 intraspecific interaction strength α_{ii} (Eq. 4 in the main text). The three bottom rows show how 99 estimates of interspecific interaction strength α_{ii} (Eq. 5 in the main text) between *T*. cyanopetala and each of the other 3 focal species (g-i: W. acuminata; j-l: H. glabra; m-o: A. 100 101 *calendula*) vary along each gradient. In the graphs depicting interaction strength (d-o), any 102 value over 0 (in white) indicates competition, and any value below 0 (in grey) indicates 103 facilitation. Lines represent model fits and dotted lines give the simulated 95% confidence 104 intervals. The vertical dashed line present in the intrinsic fitness plots corresponds to the 105 maximum or minimum environmental value (as determined by fecundity rather than abundance) for *T. cyanopetala* given by ξ_i . The darker ticks along the x axis indicate where 106 107 observations of fecundity collected along each environmental gradient.



110	Supplementary Figure 3.4: Summary graph of estimated parameters for the focal species <i>W</i> .
111	acuminata varying along gradients of tree canopy cover, phosphorus and water availability.
112	The top row (a-c) shows estimates of intrinsic fitness λ_i , and the second row (d-f) shows
113	intraspecific interaction strength α_{ii} (Eq. 4 in the main text). The three bottom rows show how
114	estimates of interspecific interaction strength α_{ij} (Eq. 5 in the main text) between W.
115	acuminata and each of the other 3 focal species (g-i: T. cyanopetala; j-l: H. glabra; m-o: A.
116	<i>calendula</i>) vary along each gradient. In the graphs depicting interaction strength (d-o), any
117	value over 0 (in white) indicates competition, and any value below 0 (in grey) indicates
118	facilitation. Lines represent model fits and dotted lines give the simulated 95% confidence
119	intervals. The vertical dashed line present in the intrinsic fitness plots (a -c) corresponds to
120	the maximum or minimum environmental value (as determined by fecundity rather than
121	abundance) for <i>W. acuminata</i> given by ${{{ \xi}_{i}}}$. The darker ticks along the x axis indicate where
122	observations of fecundity collected along each environmental gradient.



124 S.I.4. Scaling the interactions

In modern coexistence theory, Chesson (2000b) defined niche overlap and fitness differences
from the following Lotka-Volterra model:

127 (10)
$$\frac{1}{N_i} \frac{dN_i}{dt} = r_i \left(1 - \alpha_{ii} N_i - \alpha_{ij} N_j \right)$$

128 The rate of change in the abundance of species *i*, N_i , is determined by its intrinsic rate of 129 increase r_i . Here, the interaction coefficients α_{\perp} are directly proportional to the abundance of 130 competing individuals. In the case of our annual plant model (Eqs. 1 and 2 in the main text) 131 however, the α_{\perp} are also proportional to intrinsic fitness λ_i and to the germination rates g_i 132 and g_i .

In order to calculate niche overlap and fitness differences, we rescale the α_{i} 's in our model to 133 134 more closely resemble those in Chesson's Lotka-Volterra model. This step means that the 135 interaction coefficients are no longer proportional to intrinsic fitness or germination rates and 136 are instead directly proportional to the abundance of competing individuals (see Appendix A 137 in Godoy & Levine, 2014 for a similar approach). This approach involves including intrinsic 138 fitness and germination rates into the rescaled interaction coefficients (α') in such a way that 139 these variables are cancelled out when we replace the α s in our annual plant population 140 model with α'_{μ} and simplify.

141 We define β_i as the loss rate of seeds in the seed bank, and η_i as the productivity, i.e. the 142 annual seed production per seed lost from the seed bank.

143 (11) $\beta_i = 1 - (1 - g_i)(s_i)$

144 (12) $\eta_i = \frac{\lambda_i g_i}{\beta_i}$

145 We can then rescale the α_{μ} by defining α'_{μ} :

146 (13)
$$\alpha_{ii}' = \frac{g_i \alpha_{ii}}{ln(\eta_i)} = \frac{g_i (\bar{\alpha}_{ii} + \delta_{ii} (\xi - \xi_{ii})^2)}{ln(\eta_i)}$$

147 and

148 (14)
$$\alpha_{ij}' = \frac{g_j \alpha_{ij}}{\ln(\eta_i)} = \frac{g_j (\overline{\alpha}_{ij} + \delta_{ij} (\xi - \xi_{ij})^2)}{\ln(\eta_i)}$$

This allows us to rewrite our annual plant population model such that the α'_ have an
analogous effect on plant fitness as the interaction coefficients in Chesson's original Lotka Volterra model:

152 (15)
$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - \beta_i) + \beta_i \eta_i e^{-ln(\eta_i)(\alpha'_{ii}N_{i,t} + \alpha'_{ij}N_{j,t})}$$

To confirm that these rescaled interaction coefficients in this annual plant model are similarly meaningful, we can check that they verify the invasibility criterion, such that for species *i* to invade species *j* when *j* is at equilibrium, *j* must limit itself more than it limits $i (\alpha'_{jj} > \alpha'_{ij})$. First, we determine \dot{N}_{j} , the density of species *j* when it is at equilibrium and in the absence of species *i*:

158 (16)
$$\dot{N}_j = \frac{\ln(\eta_j)}{g_j \alpha_{jj}}$$

159 We then substitute \dot{N}_j for $N_{j,t}$ in our annual plant model (Eq. 1 in the main text), rewriting it to 160 include β_i and η_i and assuming that there are no competing individuals of species *i*:

161 (17)
$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - \beta_i) + \beta_i \eta_i e^{-\alpha_{ij} g_j \frac{\ln(\eta_j)}{g_j \alpha_{jj}}}$$

162 This gives us the growth rate of species *i*, which must be over 1 for it to invade:

163 (18)
$$1 < (1 - \beta_i) + \beta_i \eta_i e^{-\alpha_{ij} g_j \frac{\ln(\eta_j)}{g_j \alpha_{jj}}}$$

164 which simplifies to:

165 (19)
$$\frac{g_j \alpha_{jj}}{\ln(\eta_j)} > \frac{g_j \alpha_{ij}}{\ln(\eta_i)}$$

S.I.5. Defining niche overlap and fitness differences

168 Chesson (2012) defined niche overlap as:

169 (20)
$$\rho = \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{jj}\alpha_{ii}}}$$

170 Chesson & Kuang (2008) defined the average fitness difference as:

171 (21)
$$\frac{\kappa_j}{\kappa_i} = \frac{\alpha_{ij}}{\alpha_{jj}} \left(\frac{1}{\rho}\right) = \sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}}$$

172 We can begin by substituting the interaction coefficients in S.I.5. Eq. 20 and 21 with our rescaled α' (S.I.4. Eqs. 13 – 14). The same approach is used by Godoy & Levine (2014), though 173 174 they are able to simplify their expressions such that niche overlap becomes a function of the 175 unscaled interaction coefficients, and fitness differences, a function of the unscaled interaction 176 coefficients and the seed productivities of species *i* and *j*. Here, we use a different annual plant 177 population model which requires a different rescaling of the interaction coefficients, and this 178 simplification is no longer applicable. We therefore continue to use the rescaled interaction coefficients α'_{μ} throughout our study. 179

- 180 Our expressions, however, are still not mathematically tractable if any of the α' s hold a
- 181 negative value (indicating a facilitative interaction). We therefore remove the square root and

exponentiate the α'_{μ} such that facilitative interactions can be accounted for and ρ and $\frac{\kappa_j}{\kappa_j}$ don't 182

blow-up when any α'_{μ} in the denominator reaches 0. 183

184 In Chesson's framework, niche overlap reflects the ratio of inter- to intra specific interactions, 185 whereas fitness differences reflect how species differ in their relative responses to 186 interactions. Importantly, our exponentiated values hold the same meaning as above since the 187 inequality in S.I.4. Eq. 19 still holds as:

188 (22)
$$e^{\frac{g_j \alpha_{jj}}{\ln(\eta_j)}} > e^{\frac{g_j \alpha_{ij}}{\ln(\eta_i)}}$$

190 **S.I.6. Predicting coexistence**

191 When all rescaled interaction coefficients α_{n}' were competitive, we were able to calculate 192 traditional measures of niche overlap (ρ) and fitness differences ($\frac{\kappa_{j}}{\kappa_{i}}$) as defined by Chesson 193 (2000b) and Chesson & Kuang (2008). We did this by substituting the interaction coefficients 194 in his expressions with our rescaled α_{n}' as shown in equations 23 and 24 below:

195 (23)
$$\rho = \sqrt{\frac{\alpha_{ij} \cdot \alpha_{ji} \cdot }{\alpha_{ii} \cdot \alpha_{jj} \cdot }}$$

196 (24)
$$\frac{\kappa_j}{\kappa_i} = \sqrt{\frac{\alpha_{ij} \cdot \alpha_{ii} \cdot}{\alpha_{jj} \cdot \alpha_{ji} \cdot}}$$

197 Coexistence between a pair of species is predicted when $\rho < \frac{\kappa_j}{\kappa_i} < \frac{1}{\rho}$. Supplemental Table 2 198 shows how often we were able to calculate traditional niche overlap and fitness differences 199 from our predictions of interaction coefficients, and when those calculations resulted in 200 predicted coexistence.

Supplementary Figures 6.1 and 6.2 are two examples of the patterns we observed in terms of the relative contributions of niche overlap and fitness differences to coexistence among focal species pairs in this study. In Supp. Fig 6.1, *H. glabra* and *W. acuminata* move further away from the space where coexistence is predicted (defined by the grey cone) as phosphorus concentration increases. In Figure 6.2, niche overlap and fitness differences between *W. acuminata* and *H. glabra* shift non-monotypically as tree canopy cover increases, eventually predicting coexistence in highly shaded plots.

Model type	Environmental variable	N total	N coexistence	N predicted	Details
Baseline	NA	12	8	0	
Environmental	Canopy	251	59	3	H.glabra & W. acuminata
	Phosphorus	82	18	0	
	Water	24	9	1	A. calendula & T. cyanopetala

Supplementary Table 6.1: Summary of our predicted coexistence outcomes. Model type refers to the model formulation described in the Methods under "Model framework". 'N total' refers to the total number of observations made, 'N coexistence' is the number of observations where coexistence outcomes can be predicted (in other words, when all interactions are competitive) and 'N predicted' is the number of observations for which we did predict coexistence to occur

213 $(\rho < \frac{\kappa_j}{\kappa_i} < \frac{1}{\rho}).$

Parameters for the baseline model are fixed across the environmental gradient. This is why there are only 12 total observations (1 for each species pair). In the environmental models, intrinsic fitness (λ_i) and all interaction coefficients (α'_{n}) can vary, such that predictions are calculated whenever a species pair shares the same environmental context (i.e. when they share a given value for any one environmental variable (ξ)). We limited our predictions to environmental values to the environmental space for which we had observational data (excluding the modelled tails evident in S.I.3. Figs. 3.1-3.4).

Supplementary Figure 6.1: Coexistence plot between Hypochaeris glabra and Waitzia 221 *acuminata*. Niche overlap (ρ) is plotted on the x- axis, and fitness differences $\binom{\kappa_j}{\kappa_j}$ on the y- axis. 222 The region of the graph where these species are predicted to coexist is shown in grey and is 223 defined by the inequality $\rho < \frac{\kappa_j}{\kappa_i} < \frac{1}{\rho}$. Each dot represents a prediction for a given value of 224 ground phosphorus, with dots increasing in size as phosphorus concentration increases. 225

226

227



Hypochaeris glabra – Waitzia acuminata

Supplementary Figure 6.2: Coexistence plot between *Waitzia acuminata* and *Hypochaeris* glabra. Niche overlap (ρ) is plotted on the x- axis, and fitness differences $\left(\frac{\kappa_{j}}{\kappa_{i}}\right)$ on the y- axis. The region of the graph where these species are predicted to coexist is shown in grey and is defined by the inequality $\rho < \frac{\kappa_{j}}{\kappa_{i}} < \frac{1}{\rho}$. Each dot represents a prediction for a given value of tree canopy cover, with dots increasing in size as canopy cover increases. In addition, dots are numbered in increasing value of tree canopy cover to better illustrate the threshold observed between values 7 and 8.



Waitzia acuminata – Hypochaeris glabra

236 S.I.7. Niche overlap and fitness differences

Supplementary Figure 7.1: Predicted variation in our analogues of niche overlap (ρ , Eq. 11 in the main text) in black, and fitness differences ($\frac{\kappa_j}{\kappa_i}$, Eq. 12 in the main text) in grey, along each environmental gradient between *A. calendula* and the other three focal species. The two lines for each expression represent predicted values for each of the two reserves, which had different germination and seed survivability rates (see main Methods).



Supplementary Figure 7.2: Predicted variation in our analogues of niche overlap (ρ , Eq. 11 in the main text) in black, and fitness differences ($\frac{\kappa_j}{\kappa_i}$, Eq. 12 in the main text) in grey, along each environmental gradient between *H. glabra* and the other three focal species. The two lines for each expression represent predicted values for each of the two reserves, which had different germination and seed survivability rates (see main Methods).



Supplementary Figure 7.3: Predicted variation in our analogues of niche overlap (ρ , Eq. 11 in the main text) in black, and fitness differences ($\frac{\kappa_j}{\kappa_i}$, Eq. 12 in the main text) in grey, along each environmental gradient between *T. cyanopetala* and each of the three other focal species. The two lines for each expression represent predicted values for each of the two reserves, which had different germination and seed survivability rates (see main Methods).



Supplementary Figure 7.4: Predicted variation in our analogues of niche overlap (ρ , Eq. 11 in the main text) in black, and fitness differences ($\frac{\kappa_j}{\kappa_i}$, Eq. 12 in the main text) in grey, along each environmental gradient between *W. acuminata* and the other three focal species. The two lines for each expression represent predicted values for each of the two reserves, which had different germination and seed survivability rates.



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