Appendix 4

Parameter combinations tested

*We analyzed the model for each set of parameter combinations listed below at all of the same values of R_2, a_2 and $\beta_{1,2}$ presented in the results of the main text. The qualitative results for each set of parameters was consistent with those presented in the main text.

Table A1. Parameter combinations tested.

k_2	e	b	m
5000	0.65	1.16	0.54
5000	0.7	1.1	0.54
5000	0.7	1.16	0.5
5000	0.7	1.16	0.54
5000	0.7	1.16	0.56
5000	0.7	1.2	0.4
5000	0.7	1.3	0.5
5000	0.8	1.16	0.54
5000	0.8	1.3	0.5
6000	0.65	1.16	0.54
6000	1.7	0	0.54
6000	0.7	1.1	0.54
6000	0.7	1.16	0.5
6000	0.7	1.16	0.54
6000	0.7	1.16	0.56
6000	0.7	1.2	0.4
6000	0.7	1.3	0.5
6000	0.8	1.16	0.54
6000	0.8	1.3	0.5
7000	0.65	1.16	0.54
7000	0.7	1.1	0.54
7000	0.7	1.16	0.5
7000	0.7	1.16	0.54
7000	0.7	1.2	0.4
7000	0.7	1.3	0.5
7000	0.7	1.16	0.56
7000	0.8	1.16	0.54
7000	0.8	1.3	0.5

Appendix 5

Description of intersection in Fig. 5

The surfaces shown in Fig. 5 intersect when plant diversity reaches a maximum, regardless of whether or not herbivores are present, such that N_1:N_2 = N_2:N_1 = 1:1. These conditions are met in the current scenario when $\beta_{1,2} = \beta_{2,1}$, along a line where the proportional difference between R_2 and R_1 is equal to that between a_2 and a_1, or

$$\frac{R_2}{a_2} = \frac{R_1}{a_1} \tag{A8}$$

or

$$R_2 = \frac{a_2 R_1}{a_1} \tag{A9}$$

In other words, the surfaces intersect where both species are competitively equal and asymmetries in the attack rate favoring one species are proportional to asymmetries in the growth rate favoring the other species. Such an asymmetry in growth balances the direct effects of herbivory through apparent competition.

Appendix 6

Analogous effects of carrying capacity to growth rate in defensive tradeoffs

Carrying capacity–defense tradeoff

While differences in carrying capacity (k) are generally associated with differences in competition, favoring the species with the greater carrying capacity (Lotka 1925, Volterra 1926), their effects extend to the productivity, or the growth term in Eq. 5, of a species. Productivity increases with carrying capacity whenever the population biomass of a species is retained at a constant level by the actions of a consumer. Therefore, interspecific tradeoffs between carrying capacity and defense may be thought of in terms of plant growth or competition tradeoffs. As with the other tradeoffs, we consider the effects of this tradeoff independently of changes in other parameters, showing that such a tradeoff is not necessary for herbivores to increase plant diversity.

Unlike growth rate, a tradeoff with carrying capacity allows herbivores to increase plant diversity at any level of direct competitive asymmetry (β). To illustrate, consider the values of $\beta_{1,2}$ at which plant diversity is the same in the presence and absence of herbivores for each combination of k_i and a_i (Fig. A1A, see below for a description of these surfaces). The resulting surfaces hold the same qualitative properties described for the growth rate-defense tradeoff in Fig. 5. Thus, points occurring above one surface but below the other with respect to the $\beta_{1,2}$ axis represent the only conditions in which herbivores do not increase diversity. At points above or below both surfaces, with respect to the $\beta_{1,2}$-axis, competitive asymmetries are sufficiently strong that herbivores increase plant diversity by limiting the abundance of either plant species and, therefore, competition.

Assuming differences in $\beta_{1,2}$ between species are unrelated to differences in k_2 and a_2, the effect of herbivores on plant diversity may be found by drawing a plane in Fig. A1A parallel to the k_2–a_2 plane. The portion of the plane existing above or below both surfaces with respect to the $\beta_{1,2}$-axis indicates the conditions within which herbivores may increase plant diversity. Increasing $\beta_{1,2}$ increases the number of combinations of k_2 and a_2 at which herbivores counteract asymmetric competition and increase plant diversity (Fig. A1B–G). However, increasing $\beta_{1,2}$ also decreases the value of k_2 at which species 1 is excluded in the absence of herbivores (inequality 3 and Euq. A10). As a result, combinations of k_2 and a_2 at which herbivores increase diversity by preventing exclusion shift towards lower values of k_2 as we increase $\beta_{1,2}$. With this shift also comes a change in how the tradeoff between carrying capacity and defense, or a lack thereof, affects plant diversity.

A tradeoff between carrying capacity and defense occurs in the upper-left and lower-right portions of Fig. A1B–G. When competition is symmetric (i.e. $\beta_{1,2} = \beta_{2,1}$), herbivores may have positive or negative effects on plant diversity regardless of the presence or nature of a tradeoff between carrying capacity and defense (e.g. Fig. A1D). However, as competition becomes increasingly asymmetric, the regions in which herbivores reduce diversity shift along the k_2 axis, altering the proportion of points in which herbivores increase diversity within each quadrant. Consequently, at very low or high values of $\beta_{1,2}$, herbivores will nearly always increase plant diversity in the absence of a tradeoff, increasing the relative mass of species 1 or 2, respectively (Fig. A1B, F–G).

As with the growth rate–defense tradeoff, herbivores increase plant diversity whenever they counteract the negative effects of competition. In our simulation, the effects of apparent competition on plant diversity are relatively minor as the herbivore holds both plant populations well below their carrying capacities (e.g. Fig. 2B). As a result, both plant species have similar, though unequal, population growth rates regardless of their carrying capacities when herbivores are present. Inequalities remain as population growth (*dN*/*dt*) remains slightly lower for the species with the lower carrying capacity. Thus, for herbivores to increase diversity as much as possible at any given value of k_2, they must slightly prefer the faster growing species, or the species with the greater carrying capacity as shown by the nearly vertical ridge in Fig. A1B–G. However, the effects of apparent competition on plant diversity are fairly negligible compared to the direct effects of competition associated with different carrying capacities.

The strongest effects of replacing one plant species with another possessing a different carrying capacity on plant diversity occur as herbivores counteract the direct effects of competition. In the absence of herbivores, asymmetries in carrying capacity allow one plant species to achieve a greater mass than the other. Herbivores may balance the plant masses through consumption, easing the effects of interspecific competition and thus appearing to increase plant diversity, regardless of whether or not carrying capacity tradesoff with plant defense. Consequently, although herbivores maximize diversity when herbivory is relatively indiscriminant (with the exception of slightly favoring the faster growing species), they may still increase diversity while preferring the 'maladapted' species with the lower carrying capacity (upper-right and lower-left portions of Fig. A1B–G).

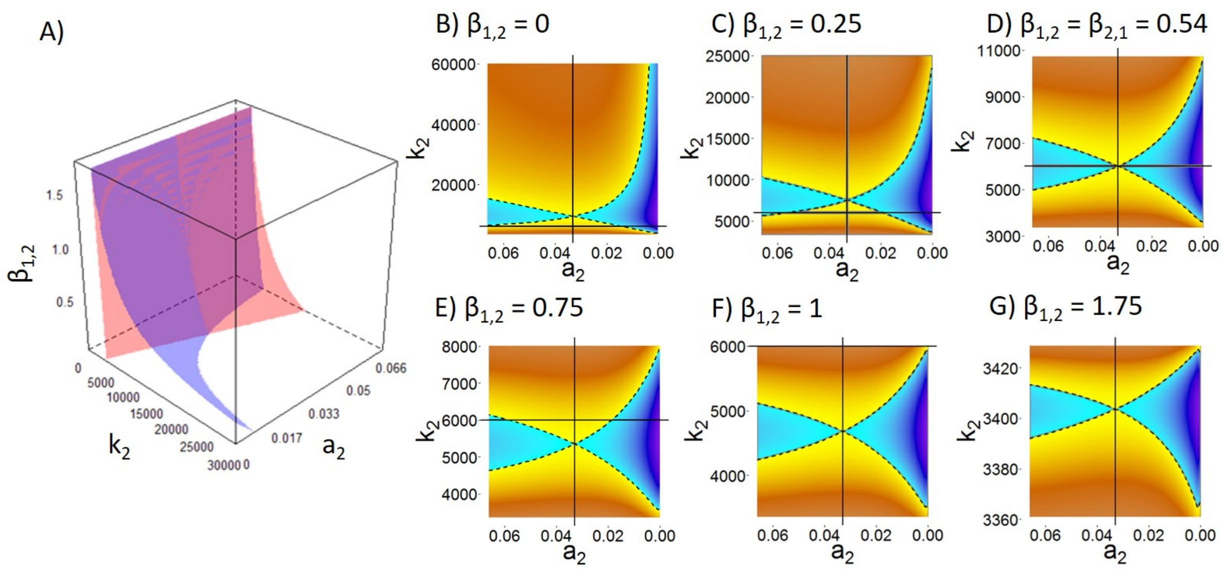

Figure A1. Carrying capacity–defense tradeoff effects on species diversity. (A) Values of $\beta_{1,2}$ (i.e. the per unit mass effect of plant 2 on plant 1 relative to the effect of plant 1 on itself) at which herbivores have no effect on species diversity in relation to the carrying capacity for and attack rate on species 2. All other parameters are as listed in Table 1. The axis for k_2 is reversed with values increasing from right to left to aid viewing. The effects of herbivores on plant diversity, represented as the difference in species diversity (e^{Sh}) in the presence and absence of herbivores, are shown when (B) species do not compete, or $\beta_{1,2} = 0$, (C) $\beta_{1,2} = 0.25$, (D) $\beta_{1,2} = \beta_{2,1} = 0.54$ as in Table 1, (E) $\beta_{1,2} = 0.75$, (F) $\beta_{1,2} = 1$, and (G) $\beta_{1,2} = 1.75$. Note the difference in scale for panels B-G (see text for explanation). Changes in plant diversity are shown using the same scale as in Fig. 4.

Competition–defense tradeoff at different carrying capacities

Herbivores produce analogous results on plant diversity in the presence or absence of a competition–defense tradeoff when considered at different carrying capacities as when considered at different growth rates (e.g. Fig. 6). Consider the effects of replacing one species with another possessing a different competition coefficient ($\beta_{j,i}$) and/or attack rate (a_i) while holding the carrying capacity constant at different levels and setting $R_1 = R_2$. We may determine the effects of herbivores on plant diversity for this tradeoff at different values of k_2 by drawing a plane in Fig. A1A parallel to the $\beta_{1,2}$–a_2 plane. In order for both species to coexist in the absence of herbivores, k_2 must occur above the point where the two surfaces intersect perpendicular to the $\beta_{1,2}$-axis (Eq. A10). At this minimum plane, herbivores increase diversity for all points that permit stable coexistence in their absence (Fig. A2A). As we consider combinations of $\beta_{1,2}$ and a_2 at greater values of k_2, regions within which herbivores decrease diversity appear, shifting towards smaller values of $\beta_{1,2}$ (Fig. A2). Stronger competitive asymmetries at greater values of k_2 limit the maximum value of $\beta_{1,2}$ where the two species coexist in the absence of herbivores, accounting for the changing scale in Fig. A2 (see below for description of surfaces in Fig. A1A). However, regardless of the value of k_2, there exist points that allow herbivores to increase plant diversity regardless of a competition–defense tradeoff.

The competition coefficient trades off with defense in the upper-left and lower-right portions of Fig. A2. In these and all other regions of the graph, herbivores again increase plant diversity when consumption sufficiently counteracts the negative effects of competition. As herbivores reduce the mass of both plant populations, they ease the effects of competition in all portions of Fig. A2. However, increasing the attack rate on the competitively dominant species allows herbivores to increase diversity to a greater degree. Consequently, as asymmetry in *k* increases, introducing herbivores is more likely to increase diversity in the absence of a tradeoff as competition may still be counteracted despite stronger preferential attack. Thus, introducing herbivores to a plant community can increase diversity irrespective of differences in carrying capacity or the presence of a competition–defense tradeoff.

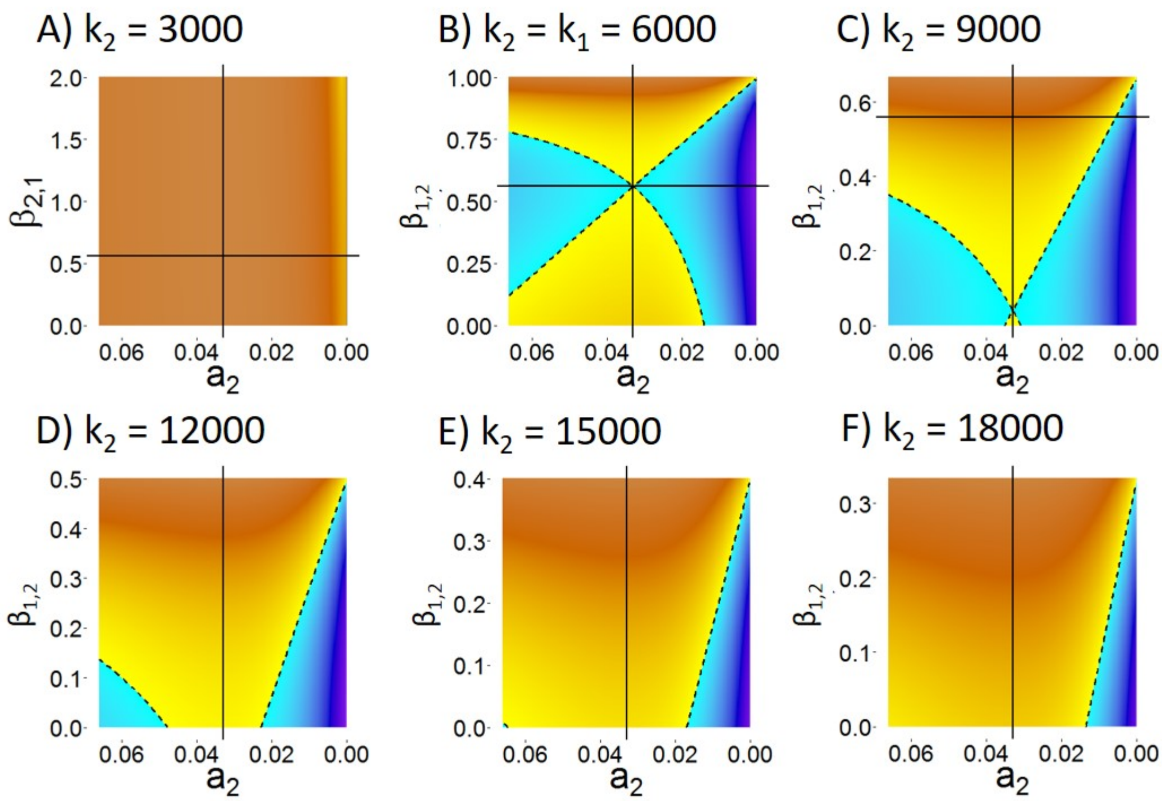

Figure A2. Competition–defense tradeoff effects on species diversity at different carrying capacities. The values of k_2 (carrying capacity of species 2) at which herbivores have no effect on species diversity in relation to the competition coefficient of and attack rate on species 2 can be viewed in Fig. A1A. The effects of herbivores on plant diversity, represented as the difference in species diversity (e^{Sh}) in the presence and absence of herbivores, are shown when (A) $k_1 = 3000$, (B) $k_1 = k_2 = 6000$ as in Table 1, (C) $k_1 = 9000$, (D) $k_1 = 12000$, (E) $k_1 = 15000$, and (F) $k_1 = 18000$. Note the difference in scale in panels B–G (see text for explanation). The axis for a_2 is reversed with values increasing from right to left to aid viewing. Changes in plant diversity are shown using the same scale as in Fig. 4.

Derivation and description of carrying capacity–defense tradeoff intersections in Fig. A1A

The surfaces shown in Fig. A1A intersect when

$$\beta_{1,2} = \frac{k_1\left(1+\beta_{2,1}\right)}{k_2} - 1 \tag{A10}$$

A derivation for this equation is provided below. Thus, to maintain a perfect balance between N_1 and N_2, $\beta_{1,2}$ must be inversely proportional to k_2. In other words, increasing the maximum achievable mass for a species must accompany a decrease in its competitive ability (and vice versa) to prevent its competitor from declining. This balance between N_1 and N_2 shown in Eq. A10 only applies in the presence of herbivores when herbivory is indiscriminant, or when $a_1 = a_2$ (see below for derivation).

The surfaces shown in Fig. A1A are limited to conditions in which both plant species may stably coexist in the absence of herbivores (inequality 3). Extending the surfaces beyond these bounds would be meaningless as only one plant species would occur in the absence of herbivores so that herbivores would always increase diversity. Consequently, we may rearrange inequality 3 to find the conditions within which the surfaces in Fig. A1A are bound:

$$\frac{k_1}{\beta_{1,2}} > k_2 > k_1\beta_{2,1}. \tag{A11}$$

Thus, as we increase $\beta_{1,2}$, we must also decrease k_2 to maintain coexistence, hence the different scales in Fig. 6. Additionally, k_2 must be greater than the value on the right of the inequality to maintain stable coexistence. As k_1 and $\beta_{2,1}$ are constant, we may only increase $\beta_{1,2}$ until the values on the left and right of the inequality are equal. In Fig. A1A, this limit is represented as the second, horizontal intersection of the two surfaces at the top of the graph.

Calculation 1: Intersection parallel to the $\beta_{1,2}$-k_2 *plane (Eq. A10)*

Given that $N_1 = N_2 = N$, $R_1 = R_2 = R$, and $H = 0$ (*i.e.* herbivores are absent)

$$\frac{dN_1}{dt} = 0 = R\left(1 - \frac{N + N\beta_{1,2}}{k_1}\right) - \left(\frac{NHa_1}{1 + bN\sum_j a_j}\right)$$

$$\frac{dN_2}{dt} = 0 = R\left(1 - \frac{N + N\beta_{2,1}}{k_2}\right) - \left(\frac{NHa_2}{1 + bN\sum_j a_j}\right)$$

$$R\left(1 - \frac{N + N\beta_{1,2}}{k_1}\right) - \left(\frac{NHa_1}{1 + bN\sum_j a_j}\right) = R\left(1 - \frac{N + N\beta_{2,1}}{k_2}\right) - \left(\frac{NHa_2}{1 + bN\sum_j a_j}\right)$$

$$\frac{N + N\beta_{1,2}}{k_1} = \frac{N + N\beta_{2,1}}{k_2}$$

$$\frac{N(1 + \beta_{2,1})}{k_1} = \frac{N(1 + \beta_{1,2})}{k_2}$$

$$\frac{1 + \beta_{1,2}}{k_1} = \frac{1 + \beta_{2,1}}{k_2}$$

$$\beta_{1,2} = \frac{k_1(1 + \beta_{2,1})}{k_2} - 1$$

Calculation 2: Intersection parallel to the a_2-k_2 *plane*

Given that $N_1 = N_2 = N$, $R_1 = R_2 = R$, but herbivores are present ($H \neq 0$)

$$R\left(1-\frac{N+N\beta_{1,2}}{k_1}\right)-\left(\frac{NHa_1}{1+bN\sum_j a_j}\right)=R\left(1-\frac{N+N\beta_{2,1}}{k_2}\right)-\left(\frac{NHa_2}{1+bN\sum_j a_j}\right)$$

Rearrange and combine terms

$$R\left(1-\frac{N+N\beta_{1,2}}{k_1}\right)-R\left(1-\frac{N+N\beta_{2,1}}{k_2}\right)=\left(\frac{NHa_1}{1+bN\sum_j a_j}\right)-\left(\frac{NHa_2}{1+bN\sum_j a_j}\right)$$

$$R\left(\frac{N+N\beta_{2,1}}{k_2}-\frac{N+N\beta_{1,2}}{k_1}\right)=\left(\frac{NHa_1-NHa_2}{1+bN\sum_j a_j}\right)$$

Factor

$$rN\left(\frac{1+\beta_{2,1}}{k_2}-\frac{1+\beta_{1,2}}{k_1}\right)=NH\left(\frac{a_1-a_2}{1+b(a_1+a_2)}\right)$$

$$\frac{rN}{NH}\left(\frac{1+\beta_{2,1}}{k_2}-\frac{1+\beta_{1,2}}{k_1}\right)=\frac{a_1-a_2}{1+b(a_1+a_2)}$$

Substitute for $\beta_{1,2}$ from calculation 1

$$\frac{R}{H}\left(\frac{1+\beta_{2,1}}{k_2}-\frac{1+\frac{k_1(1+\beta_{2,1})}{k_2}-1}{k_1}\right)=\frac{a_1-a_2}{1+b(a_1+a_2)}$$

Combine

$$\frac{R}{H}\left(\frac{1+\beta_{2,1}}{k_2}-\frac{k_1(1+\beta_{2,1})}{k_2k_1}\right)=\frac{a_1-a_2}{1+b(a_1+a_2)}$$

$$\frac{R}{H}(0)=\frac{a_1-a_2}{1+b(a_1+a_2)}$$

Rearrange

$$0=\frac{a_1-a_2}{1+b(a_1+a_2)}$$

$$0=a_1-a_2$$

$$a_2=a_1$$

Appendix 7

Logistic growth model

Our model in the main text assumes that biomass can regrow rapidly (at rate ≈ R_i when N_i is small) from unmodeled stored energy. To assess the dependence of our results on this regrowth assumption, we also considered a model in which we neglect stored energy and instead assume simple logistic growth of aboveground biomass (i.e. with growth rate ≈ r_iN_i when N_i is small),

$$\frac{dN_i}{dt} = r_iN_i\left(1 - \frac{N_i + N_j\beta_{i,j}}{k_i}\right) - \left(\frac{N_iHa_i}{1 + bN_ia_i + bN_ja_j}\right) \tag{A12}$$

The equation for herbivore mass remains as shown in Eq. 6.

Following Eq. A12 and 6, the equilibria for a system with two plant species and a shared herbivore are:

$$N_1^* = \frac{a_2r_1 - a_1r_2 + \left(\frac{m}{a_2(c - mb)}\right)\left(\frac{a_1r_2}{k_2} - \frac{a_2r_1\beta_{1,2}}{k_1}\right)}{\frac{r_1}{k_1}\left(a_2 - a_1\beta_{1,2}\right) + \frac{a_1r_2}{a_2k_2}\left(a_1 - a_2\beta_{2,1}\right)} \tag{A13}$$

$$N_2^* = \frac{1}{a_2}\left(\frac{m}{c - mb} - a_1N_1^*\right) \tag{A14}$$

$$H^* = \frac{cr_1\left(1 - \frac{N_1^* + \beta_{1,2}N_2^*}{k_1}\right)}{a_1(c - mb)} \tag{A15}$$

We used these equations to determine the effects of herbivores on plant diversity at equilibrium (Fig. A3–A4). To remain consistent with the main text, we limited our analysis to parameter combinations that resulted in stable coexistence at a point equilibrium both with and without herbivores. Stability was judged by calculating the dominant eigenvalue of the Jacobian matrix calculated at equilibrium (Eq. A2–A4, not shown). This model (like the well-known Rosenzweig–MacArthur model, of which this is the 2-resource extension) shows stable limit cycles for some parameter combinations; exploring this behavior further would be interesting but is beyond the scope of this paper.

Herbivores only increased plant diversity in the logistic-growth model in the presence of a defensive tradeoff. We illustrate some examples in Fig. A3 and A4 below. In all cases where herbivores increase plant diversity, the preferred plant species is always superior to the other in terms of growth rate or competitive ability. This stands in contrast to our findings with the regrowth model which show conditions in which herbivores may increase diversity while preferentially consuming the species that is inferior or equal to the other in all traits considered in the model. The implications of these differences are considered in the main text of our manuscript.

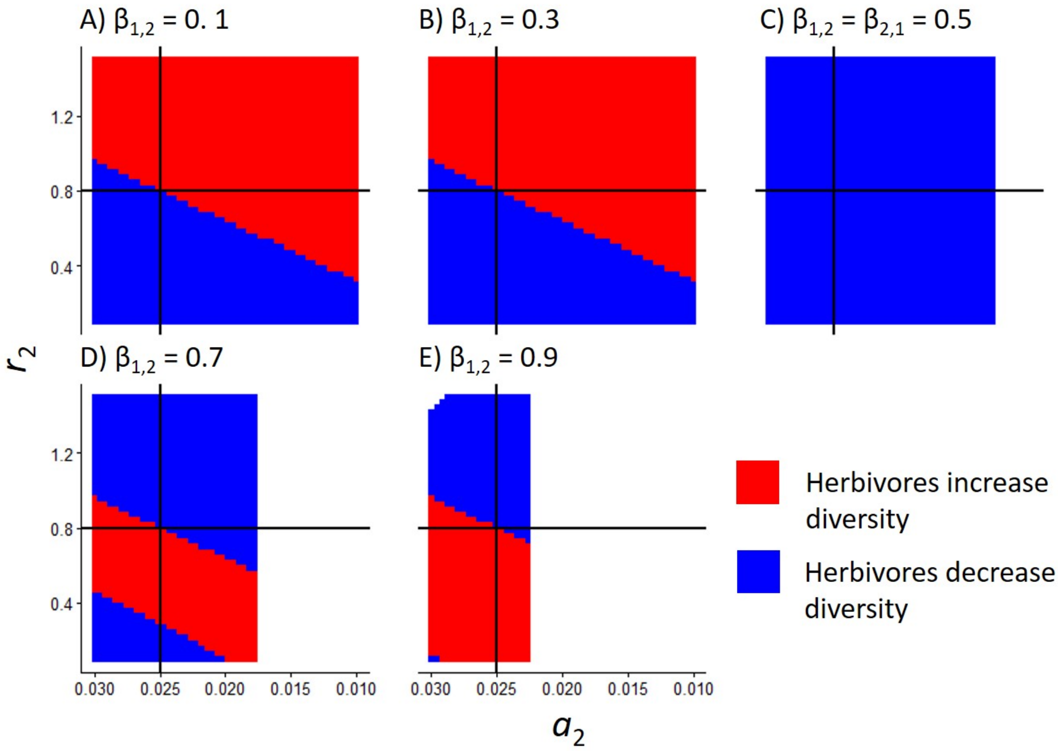

Figure A3. Growth rate–defense tradeoff effects on species diversity**.** For simplicity, the effect of herbivores is represented as a binary response of either increasing (red) or decreasing (blue) plant diversity when (A) $\beta_{1,2} = 0.1$, (B) $\beta_{1,2} = 0.3$, (C) $\beta_{1,2} = \beta_{2,1} = 0.5$, (D) $\beta_{1,2} = 0.7$, and (E) $\beta_{1,2} = 0.9$. Portions of the graphs without color represent parameter combinations without stable equilibria. Parameters for species 1 are represented by horizontal and vertical lines, dividing A–E into four portions with and without tradeoffs as described in the text. The a_2 axis is reversed to aid viewing such that plant defense increases from left to right. Unless otherwise stated, we used the following values to construct these graphs: $b = 0.6$; $c = 1.0$; $m = 1.0$; $r_1 = 0.8$; $a_1 = 0.025$; $\beta_{2,1} = 0.5$; $k_1 = k_2 = 100$.

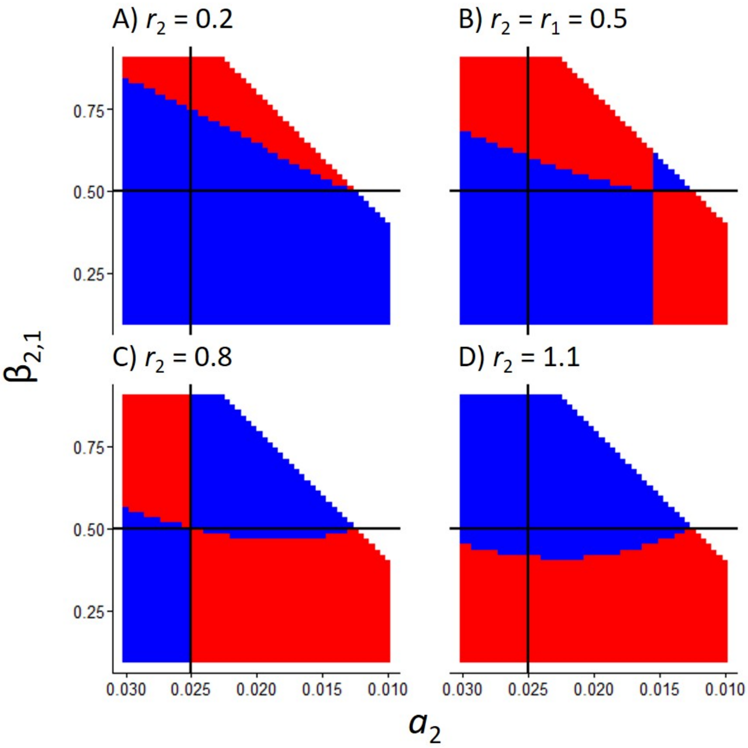

Figure A4. Competition–defense tradeoff effects on species diversity when (A) $r_1 = 0.2$, (B) $r_1 = r_2 = 0.5$, (C) $r_1 = 0.8$, and (D) $r_1 = 1.1$. Formatting and parameter values follow those provided for Fig. A3 except when otherwise shown.