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The Potential for Alternative Stable States in Food Webs Depends on Feedback Mechanism and Trait Diversity

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ABSTRACT: Alternative stable ecosystem states are possible under the same environmental conditions in models of two or three interacting species and an array of feedback loops. However, multispecies food webs might weaken the feedbacks loops that can create alternative stable states. To test how this potential depends on food web properties, we develop a many-species model where consumer Allee effects emerge from consumer-resource interactions. We evaluate the interactive effects of food web connectance, interspecific trait diversity, and two classes of feedbacks: specialized feedbacks, where consumption of individual resources declines at high resource abundance (e.g., from schooling or reaching size refugia), and aggregate feedbacks, where overall resource abundance reduces consumer recruitment (e.g., from resources enhancing competition or mortality experienced by recruits). We find that aggregate feedbacks maintain, and specialized feedbacks reduce, the potential for alternative states. Interspecific trait diversity decreases the prevalence of alternative stable states more for specialized than for aggregate feedbacks. Increasing food web connectance increases the potential for alternative stable states for aggregated feedbacks but decreases it for specialized feedbacks, where losing vulnerable consumers can cascade into food web collapses. Altogether, multispecies food webs can limit the set of processes that create alternative stable states and impede consumer recovery from disturbance.

Keywords: critical transitions, food webs, emergent Allee effects, network dynamics, alternative stable states.

Introduction

Many ecological systems exhibit distinct states characterized by the presence or collapse of consumer guilds (Estes et al. 2011). Examples include pelagic food webs dominated by predators or prey (de Roos and Persson 2002; Persson et al. 2007), Caribbean tropical reefs dominated by grazing fish and corals or macroalgae (Bellwood et al. 2004; Mumby et al. 2007; Bruno et al. 2009), and salt marshes with abundant herbivores or dense vegetation (van de Koppel et al. 1996). These food web configurations might represent different states under different environmental conditions, or they might represent the possibility of multiple alternate stable states under the same conditions, where initial species densities determine which state occurs. Distinguishing between these two possibilities determines whether the target ecosystem state can recover from short-term natural or anthropogenic disturbances (Scheffer et al. 2001).

Alternative stable food web states can, theoretically, arise in many ecosystems from positive feedback loops (hereafter, "feedbacks"; Folke et al. 2004). While negative, dampening feedback loops act to maintain a state, positive, amplifying feedback loops lead to transitions between states (van Nes et al. 2016). Such phenomena can arise from a number of biological processes in consumer-resource interactions (table 1). For example, in many systems higher resource densities allow more effective group defense, such as fish schooling or mammals herding (Freedman and Wolkowicz 1986; Courchamp et al. 1999). In this case, if a decline in consumers increases resource densities, higher group defense reduces consumer feeding, and consumer declines feed back to further reduce consumer density. Through such feedbacks, consumer Allee effects "emerge" from consumer-resource interactions and can drive transitions from consumer- to resource-dominated food webs (de Roos and Persson 2013).

In investigations into the effect of focal feedbacks on community structure, most models predicting the potential for alternative stable states either consider one to three populations and omit all other taxa (de Roos and

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Table 1: Summary of processes underlying consumer collapse via specialized feedbacks involving resource consumption (top) and aggregate feedbacks involving consumer recruitment (bottom)

State 1	Feedback maintaining state 1	State 2	Feedback maintaining state 2	Example systems
Specialized feedbacks involving resource consumption				
Predators abundant, prey sparse	Prey vulnerable to predation	Prey dominant, predators rare	Prey group defense	Fish schools, mammal herds (Freedman and Wolkowicz 1986; Courchamp et al. 1999)
Herbivores abundant, plants sparse	Plants accessible or attract few predators	Plants dominant, herbivores rare	Plants block movement or attract predators	Temperate rocky reefs (Konar and Estes 2003), grasslands (Schneider and Kefi 2016), temperate forests (Laundré et al. 2001), salt marshes (van de Koppel et al. 1996); reviewed in Holt and Barfield (2013)
Predators abundant, prey sparse	Most prey small bodied and edible	Prey dominant, predators rare	Most prey survive to size refuge	Fish (Persson et al. 2007), kelp forests (Dunn et al. 2017), intertidal (Paine 1976)
Herbivores abundant, plants sparse	Most plants small and edible or nutritious	Plants dominant, herbivores rare	Most plants survive to large size and are unpalatable	Kelp forests (Ling et al. 2015), grasslands (Parsons et al. 1983), salt marshes (van de Koppel et al. 1996), coral reefs (Briggs et al. 2018)
Aggregate feedbacks involving consumer recruitment				
Predators abundant, prey sparse	High juvenile predator survival	Prey dominant, predators rare	Prey consume or outcompete juvenile predators	Lakes, pelagic fisheries; reviewed in Walters and Kitchell (2001), Gårdmark et al. (2015)
Predators and plants abundant, prey sparse	High juvenile predator survival	Prey dominant, predators and plants rare	Few plants to shelter juvenile predators	Kelp forests (Smith and Herrkind 1992; Ling et al. 2015)
Herbivores abundant, plants sparse	High juvenile herbivore recruitment	Plants dominant, herbivores rare	Plants outcompete species sheltering juvenile herbivores	Coral reefs (Blackwood et al. 2012), kelp forests (Baskett and Salomon 2010)

Persson 2002; Dunn et al. 2017) or aggregate species into larger guilds (Scheffer 1998; Mumby et al. 2007; May 2009). In reality, populations are embedded in larger food webs that can weaken feedback loops by distributing them across many species (Neutel et al. 2002) or across different species with differential response to, and recovery rates from, disturbance (Lever et al. 2014). Beyond ecosystems dominated by a few strongly interacting species, such as lakes, grasslands, and kelp forests (Schroder et al. 2005; Petraitis 2013), the potential for between-species differences in traits and feedbacks brings the relevance of alternative stable states into question (van Leeuwen et al. 2013).

One aspect of the distribution of feedbacks across species that might affect the relevance of alternative stable states is the degree to which feedbacks depend on the density of each species individually or on the aggregated density of all species in a guild (table 1). On one extreme, aggregate feedbacks might promote multispecies alternative stable states by allowing all individuals involved in the feedback, independent of species identity, to help each other persist. One example of such a feedback is when the overall habitat structure provided by corals enhances grazing on macroalgae by many herbivores (Williams et al. 2001; Hoey and Bellwood 2011), while high aggregate macroalgal cover can impede coral recruitment (McCook et al. 2001). Coral concentration of herbivore grazing on macroalgae, with macroalgae overgrowth of corals in the absence of herbivores, can then lead to alternative coral- and macroalgal-dominated states in a two-species model (Mumby et al. 2007). Aggregate feedbacks can also arise when resources reduce survival of juvenile consumers via competition or predation. In groundfish and forage fish interactions, for example, predator larvae can be eaten by their own planktivorous prey, termed “cultivation effects” because adult predators then “cultivate” a hospitable environment for their young by reducing prey densities (Walters and Kitchell 2001). These dynamics can lead to alternative stable predator- or prey-dominated states (Baskett et al. 2006). In all of these examples, the aggregate amount of resources, independent of species identity, can inhibit all consumers' early life stages, such that a set of resource species in a food web might act as a guild to drive alternative stable state dynamics, as occurs in models that represent guilds as a single population (e.g., Baskett et al. 2006; Mumby et al. 2007).

At the other extreme of specialized feedbacks, where feedbacks affect individual pairwise species interactions, alternative stable states become less pronounced and species-specific dynamics predominate in mutualistic and competitive networks (Levins 1966; Gilpin and Case 1976; van Nes and Scheffer 2004). One example of specialized feedbacks is the group defense dynamics mentioned above, where predators can experience emergent Allee effects when their prey form monospecific schools or herds (Freedman and Wolkowicz 1986). In addition, alternative stable states readily emerge in two-species models with gape-limited predation, where either (*a*) predators are absent and many prey survive to large body sizes that predators cannot consume or (*b*) predators are present and most prey are small and consumable (de Roos and Persson 2002). In multispecies food webs with either group defense or gape limitation, specialized feedbacks can cause the persistence of a consumer to depend on the ability to consume only its primary resource; subsequently, predators consuming different prey might collapse and recover at different predator mortality levels. However, because species persistence also depends on indirect interactions (Ives and Cardinale 2004), individual species collapses could still cascade to have community-wide effects.

Two additional food web properties might interact with feedback specialization to determine the prevalence of alternative stable states: the degree of trait diversity between species and food web connectance. As the frequency of species interactions (connectance) increases, different consumers can become increasingly interdependent. Interdependence can synchronize feedbacks across populations to increase alternative stable states in large dynamical systems (Downing et al. 2012; Lever et al. 2014), including, potentially, systems with specialized feedbacks. Interdependence can also lead to novel alternative stable state dynamics not possible in simpler models, as observed in spatially explicit dynamical systems (e.g., “domino effects”; van de Leemput et al. 2015). Conversely, as described above, trait diversity might erode the potential for alternative stable states under both specialized and aggregate feedbacks. For instance, interspecific diversity in longevity could increase variation in mortality or harvest thresholds at which different consumers collapse and recover given the greater effects of harvest in longer-lived, lower-natural-mortality species (Abesamis et al. 2014). A question is, then, when the potential for alternative stable states to increase with connectance and erode with diversity might be more likely and stronger: under aggregate or specialized feedbacks? With the greater expected prevalence of alternative stable states under aggregate feedbacks, we might expect a greater effect of connectance and diversity, but with the expected dampening effect of specialized feedbacks on alternative stable states, there might be more opportunity for synergistic interactions with connectance and diversity.

Here, we quantify how interactions between many species affect the potential for alternative stable food web states. In addition to testing and identifying mechanisms behind the above-described intuitive hypotheses for the effects of feedback type, trait diversity, and food web connectance, our modeling exercise allows us to explore how these factors compare and interact in their influence on the prevalence of alternative stable states. We focus on emergent consumer Allee effects (de Roos and Persson 2013), a broad group of mechanisms hypothesized to drive alternative stable states with consumers present or extinct (table 1). We first derive a generalized representation of two classes of emergent consumer Allee effect models: aggregate or specialized feedbacks. Two-species versions of these models both exhibit alternative stable consumer- and resource-dominated states. We then examine how feedback specialization, interspecific trait diversity, and connectance determine the presence and distinctiveness of alternative stable states in multispecies food webs. Throughout, we focus on mortality as the driver of consumer collapse because intensive human harvest of upper trophic levels impacts ecosystems globally (Estes et al. 2011), where a key question is whether alternative stable states can explain delays in consumer recovery after conservation reduces harvest (Gårdmark et al. 2015).

Methods

Our approach is to construct a broadly representative multispecies model that distinguishes the effects of feedback type, connectance, and trait diversity on the relevance of alternative stable states. Our model incorporates the potential for emergent Allee effects that arise from consumer-resource interactions (vs. within-population Allee effects), as these are the cases where food web properties such as connectance might play a role in feedback strength and the overall likelihood of alternative stable states. Below we first provide example derivations of specialized and aggregate feedbacks. We then describe the food web model structure, where either specialized or aggregated feedbacks mediate interactions between resources and consumers. Finally, we describe how we implement different levels of food web connectance and trait diversity and our analysis of how each factor (feedback class, connectance, and trait diversity) influences the prevalence of alternative stable states.

Deriving Feedback Modeling Frameworks

We derive phenomenological models of aggregate or specialized feedbacks from two widespread, more mechanistic models using separation-of-timescale assumptions. We use a consumer-resource model where resource density feeds back to affect consumer dynamics through either (*a*) specialized feedbacks, where consumption of individual resources declines at high abundance of each resource, or (*b*) aggregate feedbacks, where recruitment of early consumer life history stages declines at higher levels of the total resource density (fig. 1). These derivations highlight how population stage structure can lead to a decline in consumer density at high resource densities, a key component of emergent consumer Allee effects (Freedman and Wolkowicz 1986) in models of type IV functional responses, cultivation effects, and resource escape (table 1). We present these as one possible approach to deriving our representation of specialized and aggregate feedback mechanisms of emergent consumer Allee effects generally. In appendix A, we show how similar functional forms can be derived from other mechanistic models, expand these derivations to the case of many consumers and resources, and analytically demonstrate the potential for alternative stable states in the two-species models derived here (as our question is whether, and under what conditions, multispecies interactions might erode alternative stable states in few-species models). We also extend our food web analyses to the more mechanistic stage-structured models in appendix B.

Specialized Feedbacks. For specialized feedbacks, we focus on the common dynamic that abundant resources are more difficult to consume in both plant-herbivore and

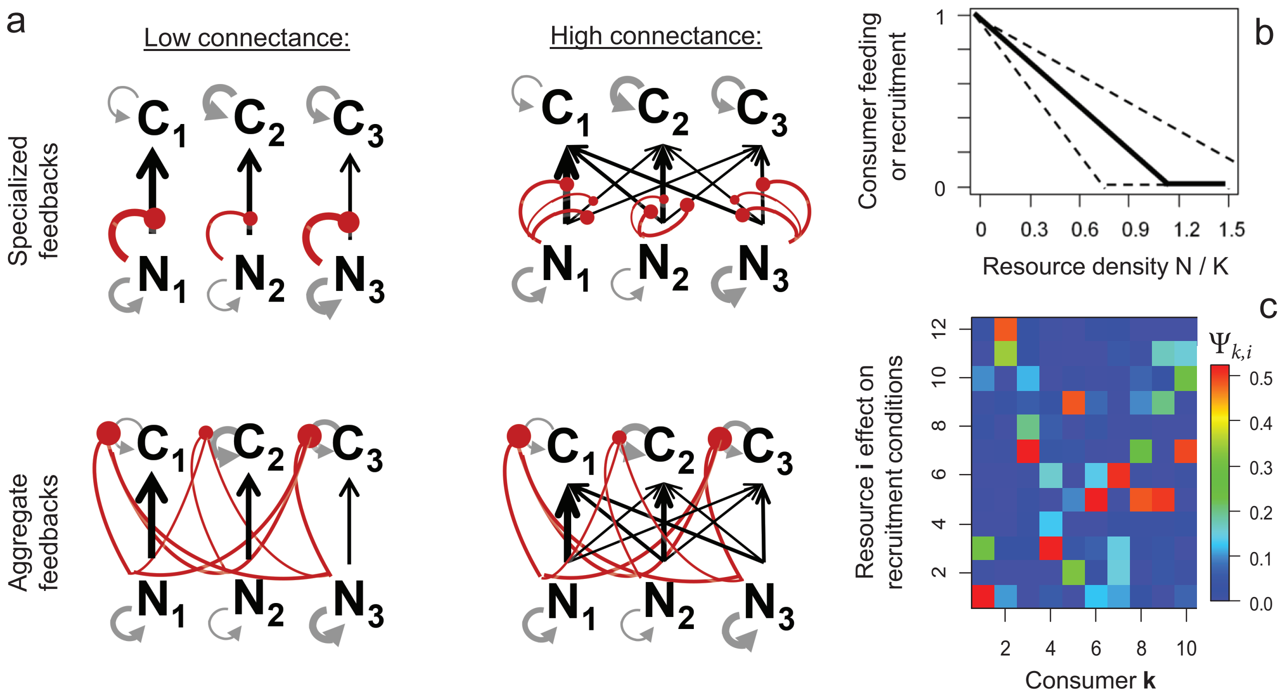

Figure 1: *a*, Model schematic of resources (N_i) and consumers (C_k) showing consumption (black arrows), self-recruitment (gray arrows), and feedbacks where resources inhibit consumption in specialized feedbacks or consumer recruitment in aggregate feedbacks (red lines) for low and high levels of trophic connectance. Variable arrow thickness exemplifies trait diversity, which can arise as species have different growth rates, conversion efficiency, competitive ability (thicker self-recruitment arrows), grazing rates (thicker consumption arrows), and sensitivity to resource abundance (e.g., lower gape limitation or lower reliance on corals, represented by thinner feedback lines). *b*, Functional form of the feedback describing how the density of a resource, relative to carrying capacity, reduces either the resource's vulnerability to consumption in specialized feedbacks or recruitment of all consumers affected by the resource ($\Psi_{i,k} > 0$). Dashed lines indicate the maximum diversity in this feedback between consumers at the highest trait diversity ranges considered. *c*, Example of the matrix of weights $\Psi_{i,k}$ determining the impact of resource *i* on recruitment of consumer *k*.

prey-predator systems (table 1). As described above, one mechanism for this feedback is size refuge from predation: more abundant resource populations become dominated by large adults that survive long enough to grow to the refuge size. To derive the consumer-resource model of specialized feedbacks, we start with a model tracking abundances of a consumer C and a resource with juvenile N_{J} and adult N_{A} stages. Juvenile resources mature to adults at a constant rate γ. Adult resources produce juveniles at rate r with density-dependent recruitment given a carrying capacity K for the adult population (assuming that fellow juveniles are smaller and less competitive such that they cause minimal intraspecific competition relative to that from adults). Consumers eat juveniles at rate δ' and larger-sized adults at rate $g\delta' < \delta'$, where $0 < g < 1$ to reflect slower consumption of adults. Consumers then convert that consumption into production with efficiency b and experience mortality at rate m, giving the dynamics

$$\begin{aligned}
\frac{dN_{\mathrm{J}}}{dt} &= rN_{\mathrm{A}}\left(1-\frac{N_{\mathrm{A}}}{K}\right) - \delta' C N_{\mathrm{J}} - N_{\mathrm{J}}\gamma,\\
\frac{dN_{\mathrm{A}}}{dt} &= N_{\mathrm{J}}\gamma - g\delta' C N_{\mathrm{A}},\\
\frac{dC}{dt} &= b\delta' C(N_{\mathrm{J}} + gN_{\mathrm{A}}) - mC.
\end{aligned} \tag{1}$$

We simplify this model by assuming that resources have high fecundity and mature quickly, that is, $r, \gamma \gg \delta'$; in appendix B, we verify that this assumption does not qualitatively alter our results. This leads to a timescale separation where juvenile resource abundance quickly reaches equilibrium $\bar{N}_{\mathrm{J}}(N_{\mathrm{A}}, C)$ on the timescales of adult resource and adult consumer dynamics and follows

$$\begin{aligned}
\bar{N}_{\mathrm{J}}(N_{\mathrm{A}}, C) &= \frac{rN_{\mathrm{A}}(1-N_{\mathrm{A}}/K)}{\gamma + \delta' C}\\
&\approx \frac{rN_{\mathrm{A}}(1-N_{\mathrm{A}}/K)}{\gamma}\left(1-\frac{\delta' C}{\gamma}\right),
\end{aligned} \tag{2}$$

where the approximation simplifies the model by linearizing $\bar{N}_{\mathrm{J}}(N_{\mathrm{A}}, C)$ with respect to C around $C = 0$. This simplification approximates dynamics involving consumer collapse and recovery at low to moderate abundance levels. Substituting $\bar{N}_{\mathrm{J}}(N_{\mathrm{A}}, C)$ for N_{J} into adult dynamics and rearranging yields

$$\begin{aligned}
\frac{dN_{\mathrm{A}}}{dt} &\approx rN_{\mathrm{A}}\left(1-\frac{N_{\mathrm{A}}}{K}\right) - \delta' C N_{\mathrm{A}}\left(\frac{r}{\gamma}\left(1-\frac{N_{\mathrm{A}}}{K}\right) + g\right),\\
\frac{dC}{dt} &\approx b\delta' C N_{\mathrm{A}}\left(r\left(\frac{1}{\gamma} - \frac{\delta' C}{\gamma^2}\right)\left(1-\frac{N_{\mathrm{A}}}{K}\right) + g\right) - mC.
\end{aligned} \tag{3}$$

Reflecting our timescale separation assumption where $\gamma \gg \delta'$, we omit the higher-order γ^{-2} term as $\delta'/\gamma^2 \approx 0$. Defining $\delta = \delta'(g + r/\gamma)$, the proportion $f^P = r/(r + g\gamma)$, and rearranging lets us express the per capita consumption (functional response) as $\delta N_{\mathrm{A}}(1 - f^P N_{\mathrm{A}}/K)$. This formula highlights how consumption depends on edibility according to the function $P(N_{\mathrm{A}}) = 1 - f^P N_{\mathrm{A}}/K$, which reflects the decline in edible juvenile resource abundance as inedible adult resource abundance approaches carrying capacity (eq. [2]). With these substitutions, equation [1] becomes

$$\begin{aligned}
\frac{dN_{\mathrm{A}}}{dt} &= rN_{\mathrm{A}}\left(1-\frac{N_{\mathrm{A}}}{K}\right) - \delta C N_{\mathrm{A}} P(N_{\mathrm{A}}),\\
\frac{dC}{dt} &= b\delta C N_{\mathrm{A}} P(N_{\mathrm{A}}) - mC.
\end{aligned} \tag{4}$$

In the two-species model (eq. [4]), strong feedbacks impacting edibility (i.e., high f^P) can produce alternative stable states dominated by either consumers or abundant inedible resources over an intermediate range of consumer mortalities (app. A). In a food web, resources have specialized feedbacks because a high density of any given resource allows that species to escape consumption, but it does not directly alter edibility of other resources (although indirect effects occur if consumer responses cascade through the food web). For simplicity, in the main analysis we assume that juveniles compete with or form groups with only conspecific adults. In appendix C, we explore the case where juvenile resources additionally interact with adults of other species.

Aggregate Feedbacks. For aggregate feedbacks, we focus on consumer recruitment success that declines with total resource abundance, as occurs in both the recruitment inhibition and cultivation effect dynamics described above (table 1). We derive the model of aggregate feedbacks from the cultivation effects model by Baskett et al. (2006), where resources N (as a single stage) directly outcompete or consume juvenile consumers C_{J}, given a competitive or consumptive effect of resources on juvenile consumers f^R. As with the specialized feedbacks model, resources have density-dependent population growth with growth rate r and carrying capacity K, and adult consumers C_{A} predate on resources with rate δ and convert that predation into reproduction with conversion factor b. Juvenile consumers mature to adults at rate γ', and adult consumers experience density-independent mortality at rate m, giving the dynamics

$$\begin{aligned}
\frac{dN}{dt} &= rN\left(1-\frac{N}{K}\right) - \delta C_{\mathrm{A}} N,\\
\frac{dC_{\mathrm{J}}}{dt} &= b\delta C_{\mathrm{A}} N\left(1-\frac{f^R N}{K}\right) - \gamma' C_{\mathrm{J}},\\
\frac{dC_{\mathrm{A}}}{dt} &= \gamma' C_{\mathrm{J}} - mC_{\mathrm{A}}.
\end{aligned} \tag{5}$$

We assume that juveniles can quickly mature to become adults ($\gamma' \gg 0$) and a high adult reproductive potential ($b \gg 0$). This leads to a separation of timescales where juvenile consumer abundance reaches steady state $\bar{C}_\mathrm{J}(C_\mathrm{A}, N)$ quickly on the timescales of adult dynamics, yielding

$$\bar{C}_\mathrm{J}(C_\mathrm{A}, N) = \frac{b\delta}{\gamma'} C_\mathrm{A} N \left(1 - \frac{f^R N}{K}\right). \tag{6}$$

Substituting $\bar{C}_\mathrm{J}(C_\mathrm{A}, N)$ for C_J into adult consumer dynamics and defining adult consumer recruitment success as $R(N) = 1 - f^R N/K$ (declining with resource abundance), equation (5) becomes

$$\begin{aligned} \frac{dN}{dt} &= rN\left(1 - \frac{N}{K}\right) - \delta C_\mathrm{A} N, \\ \frac{dC_\mathrm{A}}{dt} &= b\delta C_\mathrm{A} N R(N) - m C_\mathrm{A}. \end{aligned} \tag{7}$$

Note that aggregate feedbacks assume that only the numerical consumer responses are unimodal functions of resource density, while specialized feedbacks assume that both functional and numerical responses are unimodal functions of resource density.

In a two-species model, this feedback yields alternative stable states with adult consumers either present or extinct over a range of consumer mortality levels (app. A). In a food web, resources have aggregated feedbacks because they similarly impact the juveniles of multiple consumers, for instance by overgrowing a habitat-forming foundation species; for this reason, consumers collapse and resources become dominant only when aggregate resource density exceeds a threshold.

Food Web Modeling Framework

To combine our specialized-feedback and aggregated-feedback two-species models and extend the combined model to multiple species within each of the resource and consumer guilds, we follow consumer densities C_k for each species k and resource densities N_i for each species i. As before, resources have logistic growth with species-specific population growth rate r_i and carrying capacity K_i. Given multiple resources, we add interspecific competition with strength α relative to intraspecific competition (identical for all resources).

Consumers then consume resources at a rate $\Phi_{i,k}$ specific to each consumer (k)–resource (i) pair (with the $\Phi_{i,k}$ values determining the food web connectance and diet specialization, as described in the next subsection below). For specialized feedbacks, consumption further depends on the edibility of resource i $P_i(N_i)$. Analogous to the two-species model, the factor f_i^P scales the decline in edibility with resource i density, expressed relative to is maximum. To determine this maximum, we account for the effect of interspecific competition constraining resources below their carrying capacity, on average, by a factor $1 - \alpha(\max(i) - 1)$, where $\max(i)$ is the total number of resource species. Therefore, in our multispecies model, $P_i(N_i) = 1 - f_i^P N_i/(K_i(1 - \alpha(\max(i) - 1)))$.

Consumers convert consumption to reproduction with species-specific conversion factors b_k. For aggregate feedbacks, consumer recruitment further depends on resource density with the function $R_k(\vec{N})$. Because the adults of one resource species can impact the juveniles of multiple consumer species, we denote each pairwise resource i–consumer juvenile k interaction as $\Psi_{i,k}$. Given f_i^R as the factor scaling the decline in consumer recruitment with resource i density relative to its maximum (given the effect of interspecific competition constraining resource densities noted above), $R_k(\vec{N}) = 1 - \sum_i f_i^R \Psi_{i,k} N_i/(K_i(1 - \alpha(\max(i) - 1)))$. To focus our analysis on the effect of changing consumer mortality rate, we assume that all consumers have the same density-independent mortality rate m. With multiple consumers, we also incorporate consumer mortality due to intraspecific competition at a (low) density-dependent rate β_k. This allows a greater number of consumer species to coexist at high levels of food web connectance and therefore helps us better resolve the effect of many interacting species on emergent Allee effects.

Combining these dynamics, the full multispecies model is

$$\begin{aligned} \frac{dN_i}{dt} &= r_i N_i \left(1 - \frac{N_i}{K_i} - \frac{\alpha \sum_{j \neq i} N_j}{K_i}\right) - N_i \sum_k P_i(N_i)\, \Phi_{i,k} C_k, \\ \frac{dC_k}{dt} &= C_k R_k(\vec{N})\, b_k \sum_i P_i(N_i)\, \Phi_{i,k} N_i - \beta_k C_k^2 - m C_k. \end{aligned} \tag{8}$$

We constrain either $f_i^R = 0$ (such that $R_k(\vec{N}) = 1$) for specialized feedbacks present and aggregate feedbacks absent or $f_i^P = 0$ (such that $P_{i,k}(N_i) = 1$) for aggregate feedbacks present and specialized feedbacks absent. In the appendixes, we relax two of the key assumptions of this model and analyze models where (*a*) there is no timescale separation between juveniles and adults (app. B) and (*b*) there is no consumer density dependence (app. D).

Manipulating Connectance and Trait Diversity

For each influencing factor (feedback type, degree of connectance, degree of species trait diversity), we construct a series of randomly generated food webs of 12 resource and 10 consumer species. We define food web connectance as the proportion of nonzero consumer-resource interactions out of the total 120 possible interactions. For each connectance level we assign interactions randomly but omit connectance matrices where any consumer has no resources assigned. Nonzero interactions may vary in strength, for instance as abiotic conditions constrain resources and consumers to different habitats. To ensure a constant net strength of consumer-resource interactions across all connectance levels, for each consumer k we randomly draw $\Phi_{i,k}$ from a Dirichlet distribution, with $\sum_i \Phi_{i,k} = \delta_k$, given species-specific total grazing rate δ_k and standard deviation σ. As an additional, population-level metric, for each connectance level we quantify the proportion of diet comprised by each consumer's primary resource when resources are equally abundant, averaged across all consumers (i.e., Ivlev electivity; $= \max(k)^{-1} \sum_k \max_i(\Phi_{i,k}/\delta_k)$).

We account for diversity in a range of species "traits," as it leads to species differences in population-level growth, competition, consumption, and life stage interactions. Among resources, we consider diversity in (1) population growth r_i, which can arise from differences in fecundity and individual growth, and (2) carrying capacity K_i, which arise from differences in resource utilization efficiency. Among consumers, we consider diversity in intraspecific competition β_k, total grazing rate δ_k, and conversion constant b_k, which reflects a combination of energetic efficiency, fecundity, and juvenile survival. While all of these species characteristics emerge from an array of phenotypes or individual traits (e.g., body size, maturation timing), we use the term "traits" to describe them, as these are how phenotypic differences affect species differences in our model. To evaluate varying degrees of trait diversity, we draw each species' parameter values from a uniform distribution with bounds defined by H, the range of trait diversity. Specifically, we draw each parameter j with average value $\bar{j}$ from $\mathrm{U}(\bar{j}(1 - H), \bar{j}(1 + H))$ (see table 2 for a list of parameters).

We also model random diversity across species in the impact of resources on consumer feeding and recruitment. For specialized feedbacks, diversity in overall edibility f_i^P can arise, as resources differ in the rates of population growth r, maturation γ, and adult edibility g given the definition of $f^P = r/(r + g\gamma)$ in the two-species model. For aggregated feedbacks, the source of diversity in resource impact on consumer recruitment f_i^R depends on the feedback mechanism. For example, if the mechanism is cultivation effects, planktivorous prey species may consume predator larvae to a greater extent than benthivorous prey. In addition, for aggregate feedbacks, the juveniles of different consumers may be affected by different resource species. To standardize our comparison between the two feedback types, we use the same range of diversity for both feedbacks. To ensure $f_i^P, f_i^R \leq 1$, we drew these values from a range $\mathrm{U}(\bar{f}^n(1 - H/3), \bar{f}^n(1 + H/3))$. We then assign pairwise resource-consumer juvenile interactions $\Psi_{i,k}$ from a Dirichlet distribution, where weights $\sum_i \Psi_{i,k} = 1$ and the parameter ψ is the largest recruitment dependence of a consumer on any single resource (averaged across all consumers). Here, $\psi = 1$ if the juveniles of each consumer interact with only a single resource and $\psi = 1/12$ if juveniles interact equally with all resources; throughout, we use $\psi = 0.35$.

As randomly drawn parameterizations did not always allow species coexistence, we omitted food webs that could not support all consumer species, that is, where the abundance of any consumer fell below 0.1 at the lowest mortality level $m = 0.025$ given with low initial resource and consumer densities. Using this process, we

Table 2: Descriptions and mean values of parameters used in the base many-species model

Parameter	Description	Mean value
r_i	Resource i growth rate	1
K_i	Resource i carrying capacity	1.35
α	Interspecific resource competition strength	.025
δ_k	Consumer k total grazing or consumption rate	1.1
b_k	Conversion constant of resources to consumer k recruits	1
f_i^P	Decline in edibility with adult density for resource i	.87
f_i^R	Decline in consumer recruitment with adult density of resource i	.87
σ	Standard deviation of trophic interaction strengths in $p_{i,k}$	.5
$\Phi_{i,k}$	Grazing rate of consumer k on resource i, with $\sum_i \Phi_{i,k} = \delta_k$ for consumer k's total grazing rate	Varied
$\Psi_{i,k}$	Strength of recruitment interaction between resource i and consumer k	
β_k	Density-dependent consumer mortality	.15
m	Density-independent consumer mortality	Varied

Note: Parameters without subscripts do not vary among species.

generate 120 replicate food webs to analyze dynamics at each level of trait diversity, and we generate a standard set of 120 food webs to analyze the effects of connectance.

Analysis of the Prevalence of Alternative Stable States

We quantify the prevalence of alternative stable states on the basis of two metrics: the distinctiveness of consumer- and resource-dominated states and the range of consumer mortality levels producing this phenomenon. Whereas distinctiveness reflects whether these different states are likely to be ecologically meaningful and empirically detectable, the range of alternative stable states reflects the likelihood that initial species densities (or a short-term disturbance) affect the overall ecosystem state. Within this continuum, whether or not this range is zero indicates the presence of alternative stable states.

We quantify the range of alternative stable states using a hysteresis (path dependency) analysis to find the difference between the median mortality level at which consumer species decline to extinction (abundance < 0.025) and the median mortality level at which consumers recover (abundance > 0.025). To resolve collapse points, we increase consumer mortality m stepwise from 0.05 by increments of 0.02. For each step, we start at the equilibrium of the preceding mortality level and numerically simulate the model for 500 time steps to reach steady state using a Runge-Kutta method, additionally checking the final 50 time points for any cyclic dynamics. After reaching the point with all consumers extinct, we simulate improving environmental conditions by gradually reducing consumer mortality, again with step size 0.02. To quantify recovery points, for each step we set the initial abundance of all extinct species to 0.025 to start near, but not exactly at, the equilibrium value of zero (and we start all extant species at the equilibrium of the previous mortality level). If the median mortality values for collapse and recovery are identical (range $= 0$), then hysteresis does not occur on the community level and alternative stable food web states are not relevant. We then quantify the distinctiveness of states as the maximum difference in steady-state total consumer abundance and consumer species richness between the forward (increasing mortality) and backward (decreasing mortality) simulations across mortality values within the range of alternative stable states.

To understand how species collapses, when they occur, cascade through communities, we explore how each consumer species contributes to the persistence of the overall consumer guild. We quantify this by measuring how mean resource edibility (for specialized feedbacks) or mean consumer recruitment (for aggregate feedbacks) depend on consumer species richness. Here, more saturated relations indicate more redundant species contributions, wherein the loss of one consumer is compensated by a corresponding release from competition and increase in abundance of another consumer to maintain a consumer-dominated state. To manipulate species richness, we simulate high connectance (0.8) and high trait diversity ($H = 0.35$) at low mortality ($m = 0.05$) and progressively remove randomly selected consumers from the food web. After removing each consumer, we simulate the food web for 200 time steps and then measure average edibility of all resources for specialized feedbacks and average survival probability of all consumer recruits for aggregate feedbacks. We repeat this process 10 times for each food web to control for the sequence of randomly chosen extinctions and then repeat the analysis for each of the 120 replicate food webs (i.e., 1,200 total simulations for each level of species richness). One way species-specific consumer contributions to guild persistence can arise is if the extinction of one species causes secondary extinctions in a domino effect. To measure the degree to which consumers collapse in such a gradual cascade versus in unison, we additionally examine the duration of consumer guild collapse after consumer mortality exceeds the tipping point for each feedback under moderate connectance and trait diversity.

Results

Effect of Feedback Type

Under moderate connectance and diversity, alternative stable states can arise from both feedback types but are more prevalent and distinct in the model with aggregate feedbacks (fig. 2). Different consumers can collapse or recover at different mortality values for specialized feedbacks (figs. 2*a*, 3*a*), but those values are simultaneous across species (with different collapse and recovery points for the full community) for aggregate feedbacks (fig. 2*b*). As a result, a greater distinctiveness between states under aggregate (fig. 2*d*) than specialized (fig. 2*c*) feedbacks occurs throughout the range of alternative stable states. This greater distinctiveness for aggregate feedbacks holds over a range of values for connectance (fig. 3*c*, 3*d*) and trait diversity (fig. 4*c*, 4*d*). Greater distinctiveness with aggregate than with specialized feedbacks arises because all consumers experience the same persistence bottleneck—namely, that overall resource densities remain low—in the case of aggregate feedbacks. In contrast, with specialized feedbacks each consumer can have a unique persistence bottleneck based on the edibility of its primary resource, such that each consumer can collapse at a different point depending on its unique diet.

Alternative stable states can also occur over a wider range of mortality values under aggregate (fig. 2*d*) than under specialized (fig. 2*c*) feedbacks. At low connectance,

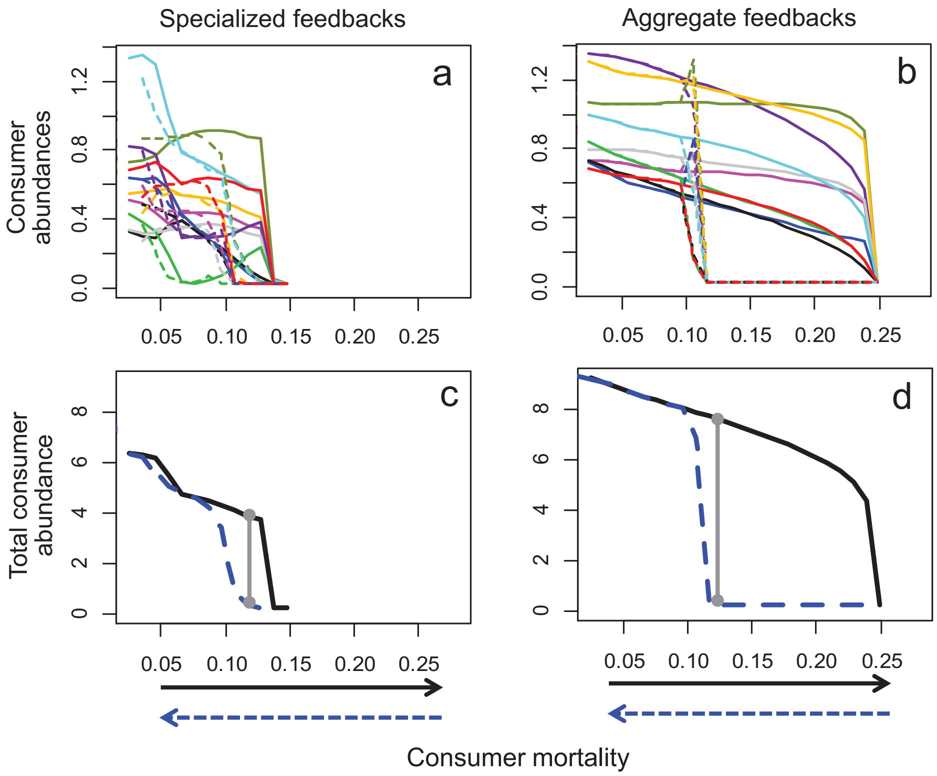

Figure 2: Alternative stable states are more distinct and occur over a wider range of mortality levels for aggregate (*b*, *d*) than specialized (*a*, *c*) feedbacks. Equilibrium consumer abundances as mortality sequentially increases (solid lines) and then decreases (dashed lines), shown for individual species (*a*, *b*) and total consumer abundance (*c*, *d*). Here, we set connectance at 0.7, with a trait diversity range of 0.15. Vertical gray lines in *c* and *d* show the metrics of state distinctiveness used throughout.

lower prevalence of alternative stable states occurs with specialized feedbacks because consumer-resource pairs exhibit separate dynamics. At moderate to high connectance, the escape of one resource from consumption reduces resource uptake for all species that consume the resource. This causes a decline in abundance for multiple consumers, allowing the next resource to escape consumption and repeating this feedback. In other words, the entire consumer guild can experience multiple persistence bottlenecks as most resource species must be edible for consumers to persist. We therefore find that above low connectance, the collapse threshold of the entire consumer guild converges on the threshold of the most vulnerable consumers, namely, the species that collapse at the lowest mortality levels (fig. 3*a*). This arises because consumers divide their consumption between many different resources and cannot single-handedly maintain all consumed resources in edible, low-density states. Loss of vulnerable consumers at low mortality levels and escape of their primary resources to high abundance therefore translates to reduced resource uptake for other consumers and, potentially, a multispecies cascading series of consumer collapses (fig. 5*b*, 5*c*). Accordingly, average resource edibility and the strength of specialized feedbacks maintaining the consumer guild both decline proportionally with the number of consumer species present (fig. 5*a*). Aggregate feedbacks produce alternative stable states over a larger mortality range because favorable recruitment levels require control of only the overall resource abundance. This redundancy in consumer contributions to recruitment is reflected in a weaker effect of species loss on aggregate compared with specialized feedbacks at high diversity (fig. 5*a*) and causes a more synchronized loss of all consumers at the collapse point (fig. 5*b*, 5*d*). In summary, alternative stable states are more prevalent under aggregate than specialized feedbacks because aggregate feedbacks both synchronize consumer collapse and remain strong when vulnerable consumer species decline.

The Effect of Connectance

Connectance can increase the potential for alternative stable states with aggregate feedbacks but decrease the potential for alternative stable states with specialized feedbacks (fig. 3). For specialized feedbacks, connectance

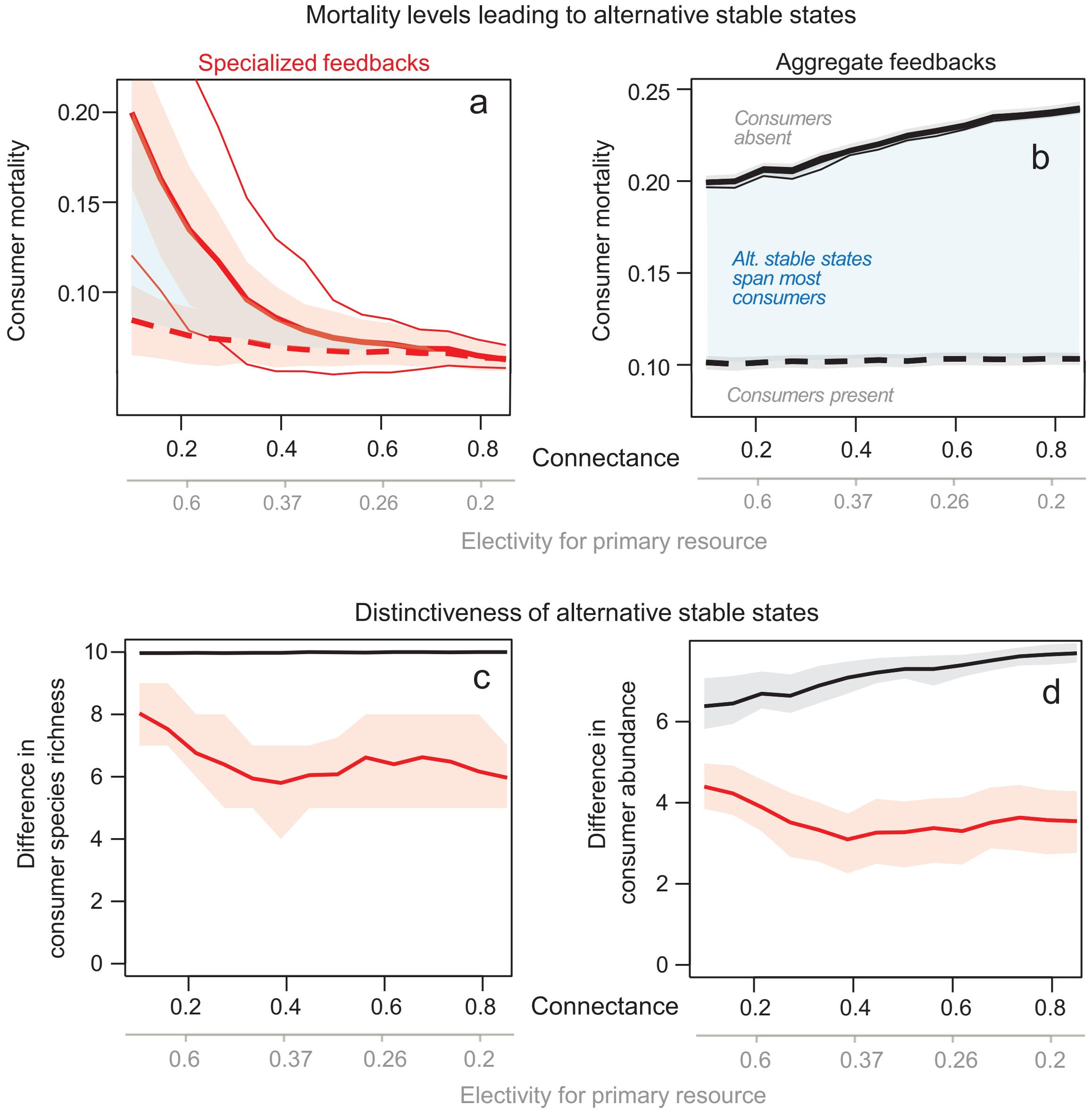

Figure 3: The potential for alternative stable states decreases with connectance for specialized feedbacks but increases with connectance for aggregate feedbacks. *a*, *b*, Median thresholds at which consumer species collapse (solid lines) and recover (dashed lines) for specialized feedbacks (*a*; red) and aggregate feedbacks (*b*; black), with alternative stable states present between these thresholds (blue-shaded regions in *a* and *b*). Red and gray regions in *a* and *b* denote the interquartile range of each threshold across species, and thin lines denote thresholds at which the first and last consumers collapse as mortality gradually increases (variation not visible for aggregate feedbacks). *c*, *d*, Distinctiveness of consumer- and resource-dominated states, measured in species richness (*c*) and in total consumer abundance (*d*), with shaded regions denoting interquartile ranges across replicate food webs. Results at each connectance level span 120 simulated food webs, with trait diversity range of 0.15.

decreases the range of mortality levels leading to alternative stable states by making persistence of the consumer guild increasingly reliant on the presence of the most vulnerable consumer species (as described above). For aggregate feedbacks, connectance increases both the distinctiveness and the range of alternative stable states across consumer mortality levels (fig. 3*b*, 3*c*). This greater range with connectance arises because more dominant consumers (e.g., those with higher grazing rates or conversion efficiency) consume a larger fraction of resources, thereby strengthening the feedback loop maintaining consumer-dominated states (fig. 3*d*). Greater feedback

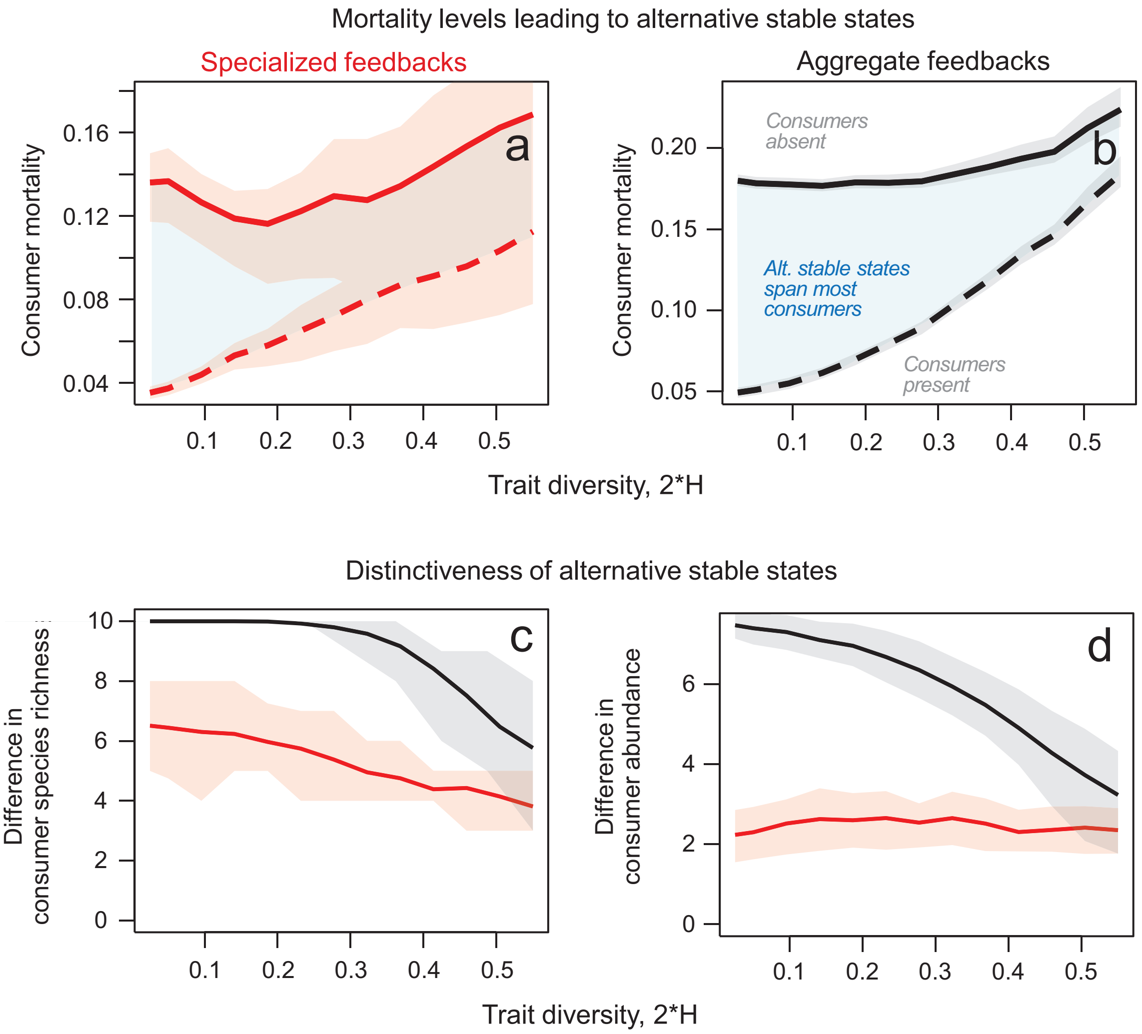

Figure 4: Interspecific trait diversity decreases hysteresis and the distinctiveness of alternative stable states. *a*, *b*, Median thresholds at which consumer species collapse (solid lines) and recover (dashed lines) for specialized feedbacks (*a*; red colors) and aggregate feedbacks (*b*; black colors), with alternative stable states present between these thresholds (blue-shaded regions in *a* and *b*). *c*, *d*, Distinctiveness of consumer- and resource-dominated states, measured in species richness (*c*) and in total consumer abundance (*d*). Results at each trait diversity level span 120 simulated food webs, with connectance at 0.25. Shaded areas denote interquartile ranges, as described in the figure 3 legend.

strength also allows consumers to persist at higher mortality levels but has no effect on consumer recovery from the resource-dominated state with poor consumer recruitment levels, leading to an overall increase in the range of alternative stable states (fig. 3*b*).

The Effect of Trait Diversity

Given moderate connectance (0.25), trait diversity reduces the distinctiveness and range of alternative stable states, with greater sensitivity to diversity under specialized than under aggregate feedbacks (fig. 4). Greater trait diversity translates to the most vulnerable consumers being more vulnerable, which, following our preceding results, disproportionally weakens specialized feedbacks. In addition, alternative stable states driven by both feedbacks decline at high diversity, where more dominant consumer species (e.g., with a greater conversion efficiency b_k) can single-handedly maintain favorable levels of resource edibility or recruitment. Such species also help other consumers recover, increasing the median recovery threshold.

Discussion

We have shown that alternative stable states can occur in interconnected food webs of many different species,

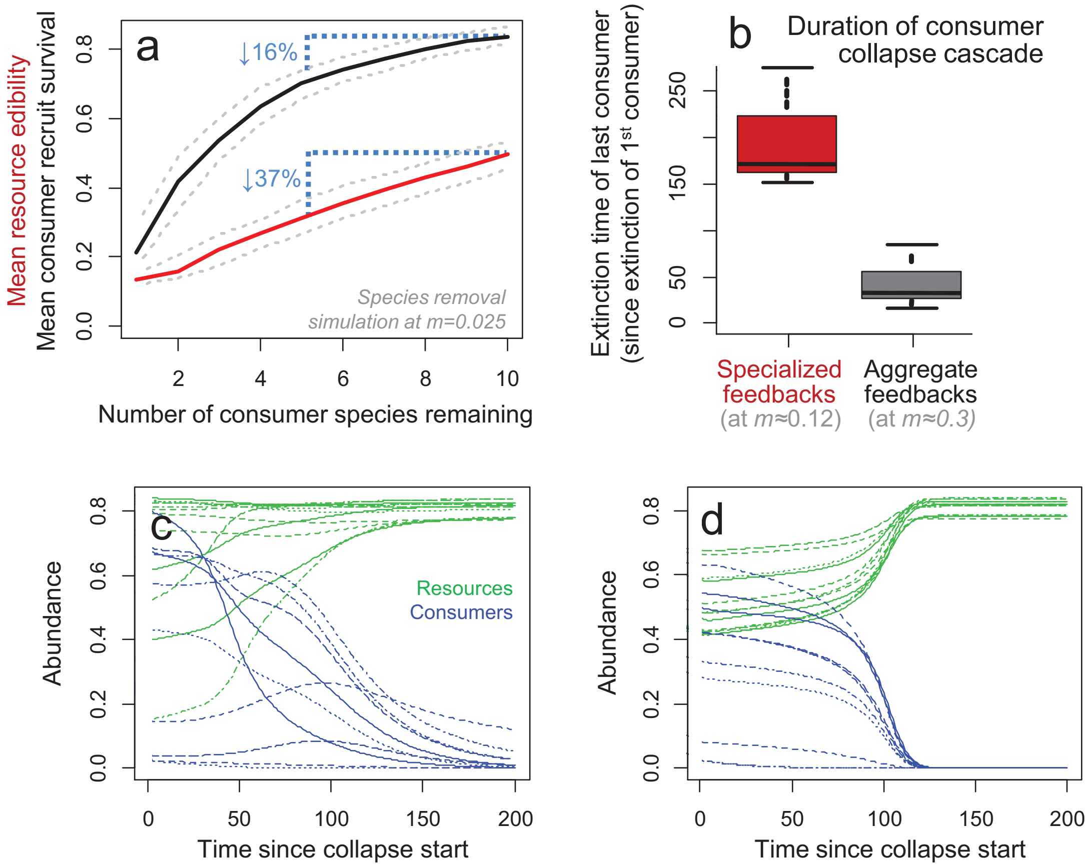

Figure 5: Compared with aggregate feedbacks, specialized feedbacks lead to species-specific consumer contributions to guild persistence and prolonged cascades of secondary extinctions following the loss of vulnerable consumers. *a*, Effects of consumer species richness at low mortality ($m = 0.025$) on the average edibility of resources (specialized feedbacks; red) and the average survival of consumer recruits (aggregate feedbacks; black), with increasing numbers of species removed from right to left along the *x*-axis; blue dotted lines denote how removing five consumers reduces edibility much more than recruitment. *b*, Duration of consumer collapse cascades in simulations where mortality just crosses the threshold leading to the collapse of all remaining consumers. *c*, *d*, Example time series from *b* of consumer collapse (blue lines; C_k) and resource growth (green lines; N_i/K_i) for specialized (*c*) and aggregate (*d*) feedbacks. *a* and *b* show medians (red and black) and interquartile ranges (gray lines in *a*, boxes in *b*) across 120 food webs. In *b*–*d*, trait diversity is 0.15 and connectance is 0.7.

especially with aggregate feedbacks (figs. 2, 6), which can arise from a wide range of ecological processes affecting consumer recruitment (table 1). A greater potential for alternative stable states through aggregate feedbacks than through specialized feedbacks parallels results from models of mutualistic networks where multiple pollinators additively benefit a shared host (i.e., higher nestedness; Lever et al. 2014) and community resistance to invasion by a shared competitor (Case 1990) or predator (Downing et al. 2012). In all cases, multispecies alternative stable states arise despite species differences because species help each other persist by improving ecological conditions in the same way (e.g., herbivores promoting habitat-forming corals by limiting total macroalgal cover). We find that such aggregate feedbacks translate to a greater redundancy in species contributions to maintaining favorable recruitment levels (fig. 5*a*), a result analogous to saturating relationships between biodiversity and ecosystem functioning (Schwartz et al. 2000). This functional redundancy makes the overall consumer guild resistant to the decline of sensitive consumer species that comes with increased mortality, but it does not affect recovery after the entire guild collapses (fig. 3*b*). This leads to a potential resistance-resilience trade-off (Downing et al. 2012): a community with greater functional redundancy and resistance to stress (here, collapsing at higher mortality) may also exhibit a greater potential for alternative stable states where, when it collapses, the community requires a larger reduction in stress in order to recover (i.e., lower ecological resilience sensu Holling 1973).

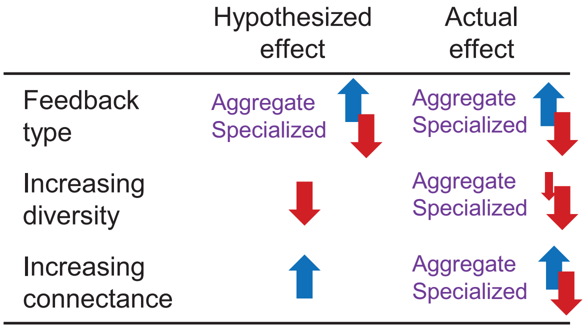

Figure 6: Hypothesized versus actual effects of feedback type, species trait diversity, and food web connectance. Up arrows indicate an increase, and down arrows indicate a decrease, in the potential for alternative stable states, with different arrow sizes reflecting the different magnitude of outcomes for the effect of increasing diversity under different feedback types.

While the greater potential for alternative stable states with aggregated feedbacks than specialized feedbacks is intuitive, our model allows us to further explore how the feedback type influences the relative effects of, and interacts with, interspecific trait diversity and food web connectance. First, while greater trait diversity reduced the potential for alternative stable states as expected, this had a larger influence on the distinctiveness of these states for specialized than aggregate feedbacks (fig. 4). Second, while greater connectance increased the potential for alternative stable states in the presence of aggregated feedbacks, as expected, the opposite occurred for specialized feedbacks (fig. 3). Our model dynamics elucidate the mechanism driving both outcomes for specialized feedbacks: through a "weakest-link" phenomenon. In comparison to aggregate recruitment feedbacks, where resource species can only reach high abundance in unison once most consumers decline, under specialized feedbacks each consumer species uniquely benefits the larger guild (fig. 5*a*). For example, each consumer could prevent its primary resource from surviving to large body sizes and becoming inedible to other species (de Roos and Persson 2002, 2013). Loss of vulnerable consumer species at low mortality levels can therefore reduce ecosystem functions maintaining the consumer guild (here, resource edibility) and cascade into a many-species collapse (figs. 3*a*, 5). Thus, with specialized feedbacks, food web connectivity imparts the vulnerability of a few species (the weakest links) onto the rest of the food web. In few-species models, specialized and aggregate feedbacks have a similar potential to drive alternative stable states (Gårdmark et al. 2015; van de Leemput et al. 2016; app. A). Our multispecies simulations therefore highlight how species diversity narrows but does not eliminate the set of processes that could create alternative stable states and impede food web recovery from disturbance.

Despite reducing the potential for alternative stable states, our approach also reveals that specialized feedbacks can still drive a multispecies collapse of consumer guilds following small increases in mortality (figs. 2, 5*c*). This resembles a "Maxwell point" dynamic observed in spatial regime shifts, wherein a more resilient (here, resource-dominated) state propagates across space from more vulnerable to less vulnerable patches in a domino effect (van Nes and Scheffer 2005). In van de Leemput et al. (2016), alternative stable states present in well-mixed systems are greatly reduced, but a domino effect remains, when matter or organisms move slowly and affect feedbacks only in nearby locations. Localized spatial feedbacks parallel specialized feedbacks in our model, where consumption of a resource depends on intraspecific interactions (competition or group defense) and affects only the resource's consumers, such that consumer collapse cascades gradually throughout the food web. This suggests an opportunity for future research, using models developed here as a starting point, to expand food web resilience theory on the basis of insights from the better-developed literature on spatial regime shifts (van Nes and Scheffer 2005; van de Leemput et al. 2016) and spatial early-warning signals (Dakos et al. 2011).

Drivers of Feedback Specialization

The reduced potential for alternative stable states and reduced resistance of species guilds to mortality found here for specialized feedbacks can apply to a wide range of feedbacks and systems. These include trophic interactions in coastal and pelagic marine systems, lakes, and forests (table 1). We point out that our results are also robust to more complex food web interactions (app. C), such as when the juveniles of one resource face competition from adults of multiple resource species (i.e., intraguild predation between prey or priority effects between plants) and when prey form multispecies herds or schools (Gil et al. 2018). Beyond food webs, co-occurring species can also facilitate each other in competition-dominated systems: animal species richness promotes habitat-forming foundation species when animals experience strong intraspecific competition (invertebrates cleaning sediments off corals [Stier et al. 2012], fish protecting anemones [Schmitt and Holbrook 2003]) or when animal species prevent different taxa from fouling a foundation species (Stachowicz and Whitlatch 2005). In mutualistic systems, multiple pollinators often benefit a shared host plant (Lever et al. 2014). Reviewing existing case studies, Afkhami et al. (2014) found that the presence of multiple mutualist partners in most cases synergistically promoted the central host species, indicating that the mechanisms by which species indirectly facilitate each other in many systems may be species specific.

Model Assumptions and Results Robustness

For tractability and to focus on the role of different feedback types, we omitted several factors that might affect the potential for alternative stable states in multispecies food webs. Our separation-of-timescale assumptions of high fecundity and fast maturation do not qualitatively alter our findings (app. B); however, explicit stage structure may reduce the potential for alternative states compared with stage-implicit models by destabilizing consumer-dominated states. Our approach might also overestimate this potential by assuming that feedbacks strongly affect most species. In reality, species less affected by feedback processes might reduce the potential for alternative stable states: for instance, larger predators that more readily consume large prey might prevent a prey-dominated state in which more gape-limited predators are extinct (van Leeuwen et al. 2013). Alternatively, our randomized parameter selection may underestimate the presence of alternative stable states by omitting trade-offs in species life histories. For example, on tropical reefs larger-bodied herbivores with less gape limitation (Briggs et al. 2018) or less sensitive juvenile stages might also have lower fecundity, here modeled implicitly as a lower conversion efficiency. For such species, a more limited effect of low coral cover might trade off with greater sensitivity to mortality. The capacity for interspecific trait diversity to reduce the potential for alternative stable states emphasized here underscores the importance of future system-specific studies that model observed species diversity and its underlying life history trade-offs. Our models also omit spatial structure, more complicated functional responses (e.g., type II or III), and stochasticity, all of which could further obscure alternative stable states or reduce the range of environmental conditions over which this phenomenon occurs (e.g., Guttal and Jayaprakash 2007). Finally, while we base our analyses on 120 randomly constructed food webs, the effects of feedback specialization, connectance, and trait diversity in any particular food web may differ from the aggregate patterns.

Additional factors could also increase the potential for alternative stable states with specialized feedbacks from our main analysis. In particular, consumers might adjust their diet composition to concentrate feeding only on resources that remain edible. Further modeling work is needed to determine whether alternative stable states become more likely as this process strengthens consumer-resource interactions or less likely as converging diets increase competitive exclusion between consumers. However, we note that diet flexibility may be limited by seasonality, spatial structure, or nutrient requirements by the consumer.

Anticipating Alternative Stable States in Food Webs

Our results suggest that the potential for simple models to predict alternative stable states in diverse food webs depends on the relative strength of aggregate versus specialized feedbacks. Establishing the presence of and environmental conditions leading to alternative stable states based on field data alone is rarely feasible because of the need for long-term data on each state at large spatial scales under identical environmental conditions (Petraitis and Dudgeon 2004; Petraitis 2013). Simple data-driven mechanistic models therefore represent a common approach to quantifying the potential for alternative stable states to explain observed patterns in diverse ecosystems (Mumby et al. 2007, 2013; Ives et al. 2008; Karatayev et al. 2021). Our results show that the results of such simple models might be robust to food web complexity with aggregate feedbacks. In the presence of specialized feedbacks and trait diversity, however, accounting for additional diversity alter expectations for anticipating community collapse and alternative stable states.

In reality, many food webs have both specialized and aggregated feedbacks. On coral reefs, for example, abundant macroalgae can simultaneously (i) become less edible in dense plant stands (Briggs et al. 2018) and (ii) overgrow corals that facilitate recruitment of herbivores (Blackwood et al. 2012). This raises two avenues for future study. First, more empirical studies might quantify the strength of specialized versus aggregate feedbacks, with alternative stable states being more likely in systems where aggregate feedbacks predominate. Second, future theory might resolve the dynamics of systems where specialized and aggregate feedbacks co-occur.

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Statement of Authorship

V.A.K. took the lead on conceiving the study, model development, and writing, with substantial input at all stages from M.L.B. and E.H.v.N.

Data and Code Availability

Code to reproduce all simulations is available in Zenodo (https://doi.org/10.5281/zenodo.7586681; Karatayev 2023).

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The potential for alternative stable states in food webs depends on feedback mechanism and trait diversity,

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S1 Appendix A: Model derivations and analyses

S1.1 A.1 Alternative formulations of the aggregate feedback model

In addition to directly inhibiting consumer recruitment, resource species can inhibit recruitment indirectly by negatively affecting species on which consumers rely. We examine one such case where herbivores consume plants that promote survival of juvenile predators (Karatayev and Baskett 2020). Such dynamics occur, for instance, on rocky temperate reefs in California where urchins U consume kelp (algae) A, while kelp provide shelter to juvenile predators P, sheephead and spiny lobsters. Intense fishing of predators frequently leads to high urchin densities that overgraze kelp, causing predator collapse and producing persistent urchin barrens with few predators. Predator recruitment therefore depends on the amount of urchins consumed and increases proportionally with kelp abundance by a factor f_c, where $1 - f_c$ is the baseline predator recruitment success without kelp. Accounting for kelp density dependence, Type I grazing rates on algae δ_A and urchins δ_U, conversion constants a, b, and predator mortality m yields:

$$\frac{dA}{dt} = r_A A \left(1 - \frac{A}{K_A}\right) - \delta_A A U \tag{S1}$$

$$\frac{dU}{dt} = a\delta_A A U - \delta_U U P \tag{S2}$$

$$\frac{dP}{dt} = b\delta_U U P \left(1 - f_c + f_c \frac{A}{K_A}\right) - mP. \tag{S3}$$

We simplify these dynamics to reflect the fact that urchins can overgraze kelp forests within weeks ($\delta_A >> \delta_U$), while at low urchin densities kelp grow rapidly and reach carrying capacity within several months ($r_A >> \delta_U$). As a result, kelp rapidly reach steady state abundance $\bar{A}(U) = K_A(1 - U\delta_A/r_A)$ on the time scales of urchins and predators. Plugging this term into urchin and predator dynamics yields

$$\frac{dU}{dt} = a\delta_A K_A (1 - U\delta_A/r_A)U - \delta_U U P$$

$$\frac{dP}{dt} = b\delta_U U P (1 - f_c U \delta_A / r_A) - mP.$$

Substituting $K = r_A/\delta_A$, $r = a\delta_A K_A$, $f^R = f_c$, and $\delta = \delta_U$ gives eqn. 7 :

$$\frac{dU}{dt} = rU\left(1 - \frac{U}{K}\right)U - \delta U P \tag{S4}$$

$$\frac{dP}{dt} = b\delta U P \left(1 - \frac{f^R U}{K}\right) - mP. \tag{S5}$$

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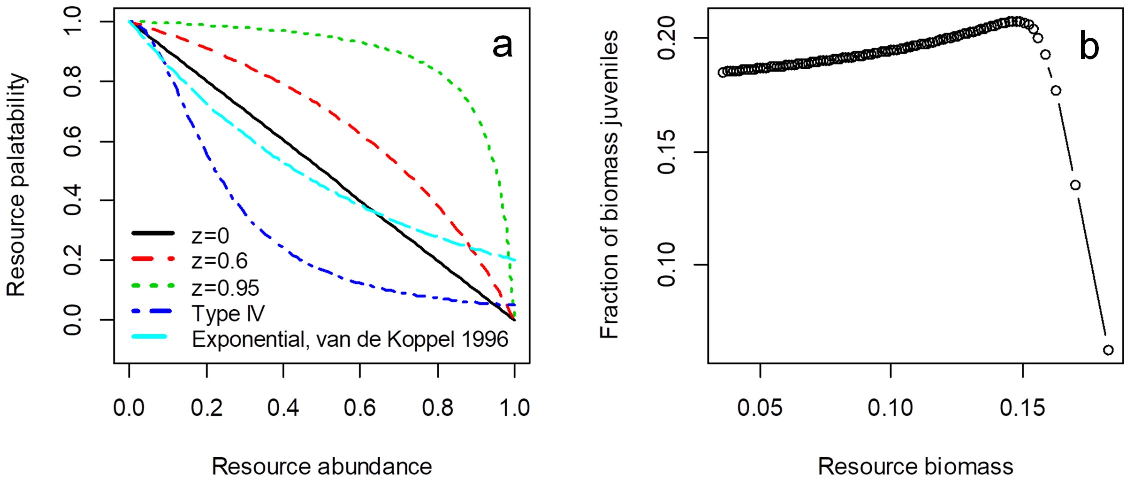
S1.2 A.2 Alternative formulations of the specialized feedback model

Here we visualize how the specialized feedback model qualitatively captures the dynamics in a range of more complex consumer-resource models in Table 1. We first explore a version of the 2-species specialized feedback model where juvenile resource maturation rate is not constant and declines from a baseline level γ_0 as adult resource density increases, $\gamma(N_A) = \gamma_0(1 - zN_A/K)$. With $z > 0$, maturation slows as adult resources deplete the energy needed for juvenile growth, causing resource individuals to ve vulnerable to predation for a longer period of their lives. In this case, resource edibility in eqn. 4 becomes $P(N_A) = (1 - f^P N_A/K)/(1 - zN_A/K)$ and predominantly declines at high resource density (Fig. S1a). Analogous patterns in edibility arise at steady state in more detailed, biomass-based models (e.g., de Roos and Persson 2013, Chapter 3, eqn. 24) that explicitly model juvenile dynamics, energy uptake, and competition between adults and juveniles (Fig. S1b). In conventional models of group defense in animals (‘Type IV’ functional forms, Freedman and Wolkowicz 1986; Bate and Hilker 2014, Fig. 1a blue line) and plants (van de Koppel 1996, Fig. 1a cyan line), resource edibility declines in a concave fashion with resource density.

Figure S1: (a) Comparison of declines in resource edibility with resource abundance across consumer-resource models of specialized feedbacks. Curves exemplify different levels of maturation sensitivity to competition z, Type IV group defense functional response $(1/(1+\eta N^2))$, and exponential declines in grazing as abundant vegetation impedes movement $(\exp(-\eta N)$, $\eta = 1.65$ in van de Koppel et al. 1996). Resource abundance measured in units of carrying capacity. (b) Proportion of total equilibrium resource biomass represented by smaller (i.e., more edible) juveniles across total equilibrium resource biomass in the model and parameterization of de Roos and Persson 2013 (Chapter 3, eqn. 24). Ranges of equilibrium biomass in (b) generated by increasing juvenile mortality to simulate different densities of a gape-limited consumer.



S1.3 A.3 2-species bifurcation analysis

In the case of a single consumer feeding on a single resource, both the specialized (edibility-dependent) and the aggregate (recruitment-dependent) feedbacks simplify to the same dynamics characterized by an emergent consumer Allee effect. In this case our model (eqn. 8) exhibits three equilibria: one with consumers extinct and resources at carrying capacity ($\bar{N} = K$, $\bar{C} = 0$) and two coexistence equilibria with $\bar{N} < K$ and $\bar{C} > 0$. For simplicity, we assume $\beta = 0$. With both species present, solving the equation of the consumer dynamics at $dC/dt = 0$, $\bar{C} > 0$ for the equilibrium resource abundance $\bar{N}$ can give two positive coexistence equilibria

$$\bar{N} = \frac{b\delta \pm \sqrt{b^2\delta^2 - 4bm\delta f^n/K}}{2b\delta f^n/K}, \tag{S6}$$

where $f^n = f^P > 0$ for specialized feedbacks and $f^n = f^R > 0$ for aggregate feedbacks.

In our 2-dimensional system, the resource-only equilibrium has the Jacobian

$$J|_{\bar{N}=K,\bar{C}=0} = \begin{bmatrix} -r & 0 \\ -\delta K(1-f^P) & b\delta K(1-f^P)(1-f^R) - m \end{bmatrix}$$

with eigenvalues $\lambda_1 = -r$ and $\lambda_2 = b\delta K(1-f^P)(1-f^R) - m$. Given $r > 0$, $\lambda_1 < 0$, and the equilibrium is locally stable if $\lambda_2 < 0$ and unstable otherwise. In both the specialized feedback model ($f^P > 0$, $f^R = 0$) and the aggregate feedback model ($f^P = 0$, $f^R > 0$), stability of the resource-only equilibrium then requires

$$m > b\delta K(1-f^n). \tag{S7}$$

Existence of the coexistence equilibrium requires $1 - f^n\bar{N}/K > 0$, which is guaranteed as f^n are proportions. At the coexistence equilibrium the model-specific Jacobians are

$$J|_{\bar{N}>0,\bar{C}>0} = \begin{bmatrix} -(\bar{N}/K)(r - f^P\delta\bar{C}) & \bar{C}b\delta(1 - 2f^P\bar{N}/K) \\ -\bar{N}\delta(1 - f^P\bar{N}/K) & 0 \end{bmatrix}$$

for specialized feedbacks and

$$J|_{\bar{N}>0,\bar{C}>0} = \begin{bmatrix} -r\bar{N}/K & \bar{C}b\delta(1 - 2f^R\bar{N}/K) \\ -\bar{N}\delta & 0 \end{bmatrix}$$

for aggregate feedbacks. Here we use the Routh-Hurwitz criteria (negative trace and positive determinant) for stability. A negative trace in $J|_{\bar{N}>0,\bar{C}>0}$ always occurs for aggregate feedbacks and for specialized feedbacks requires $r > f^P\delta\bar{C}$. Solving $dN/dt = 0$ for $\bar{C}$ and substituting gives $r > \ f^P\delta\frac{r(1-\bar{N}/K)}{\delta(1-f^P\bar{N}/K)}$, which simplifies to $f^P < 1$; in multi-species models interspecific competition between resources ensures $\bar{N}_i < K_i$, allowing coexistence equilibria with $f^P > 1$. In $J|_{\bar{N}>0,\bar{C}>0}$ the bottom-left entries are always negative, such that for both feedbacks a positive determinant requires only $0 < 1 - 2f^n\bar{N}/K$. Substituting the lower $\bar{N}$ equilibrium from eqn. S6, stability of the coexistence equilibrium requires

$$\begin{aligned} 0 &< 1 - \frac{2f^n}{K}\left(\frac{1}{2f^n/K} - \frac{\sqrt{b^2\delta^2 - 4bm\delta f^n/K}}{2b\delta f^n/K}\right) \\ 0 &< b^2\delta^2 - 4bm\delta f^n/K \\ m &< b\delta K/(4f^n), \end{aligned} \tag{S8}$$

whereas $m_2 = b\delta K/4f^n$ yields a zero determinant and, by definition, a saddle-node bifurcation point at which the coexistence equilibrium disappears. At lower mortality values, a transcritical bifurcation at $m_1 = b\delta K(1 - f^n) < m_2$ (eqn. S7) leaves coexistence as the only stable equilibrium for $m < m_1$ Therefore, the range of mortality values leading to two stable states $D = m_2 - m_1$ is positive for $f > 1/2$ and given by

$$D = b\delta K\left(\frac{1}{4f^n} - 1 + f^n\right). \tag{S9}$$

Note that we do not predict limit cycles in our model because those would require purely imaginary eigenvalues, and therefore a zero trace and positive determinant, for the Jacobian at the coexistence equilibrium, while the coexistence Jacobian here always has a negative trace ($-r\bar{N}/K$).

Critically, in the two-species case the range D of mortality levels leading to alternative stable states is identical for the specialized and aggregate feedbacks because they share the same consumer dynamics. We expect stability conditions to differ in the multispecies formulations of these models, and therefore in the main text we rely on simulations to analyze hysteresis. This analysis also highlights that consumer conversion efficiency (or the energetic value of resources), consumer grazing rate, and resource carrying capacity all increase the size of the bistability region. This reflects that stronger interactions promote bistability by reinforcing feedback loops. The change in hysteresis range with consumer grazing also underscores the importance of holding total consumption constant as we evaluate the effect of increased connectance on alternative stable states in our main analysis.

S1.4 A.4 Derivation of unstructured food web models

Throughout, we assume maturation rates γ and adult resource susceptibility g (for specialized feedbacks) vary across species. For clarity, we define $H_i(\vec{N}) = N_i + \alpha\sum_{j\neq i} N_j$ to refer to the net competitive pressure exerted on resource i. For aggregate feedbacks, we start with a multi-species version of eqn. 5,

$$\begin{aligned}
\frac{dN_i}{dt} =& r_i N_i (1 - H_i(\vec{N})/K_i) - N_i \mathbf{\Phi}_{i,\cdot} \cdot \vec{C_A} \\
\frac{dC_{J,k}}{dt} =& b_k C_{A,k} (\vec{N} \cdot \mathbf{\Phi}_{\cdot,k}) \left(1 - \mathbf{\Psi}_{\cdot,k} \cdot \frac{\vec{f^R} \vec{H}(\vec{N})}{\vec{K}} \right) - \gamma_k C_{J,k} \\
\frac{dC_{A,k}}{dt} =& \gamma_k C_{J,k} - m C_{A,k} - \beta C_{A,k}^2 .
\end{aligned} \tag{S10}$$

where $\mathbf{\Phi}_{i,\cdot}$ refers to the i^{th} row of $\mathbf{\Phi}$ and $\cdot$ is the vector dot product. Following eqn. 6, solving for the steady-state consumer juvenile abundance yields

$$\bar{C_{J,k}}(\vec{N}, C_{A,k}) = \gamma_k^{-1} b_k C_{A,k} (\vec{N} \cdot \mathbf{\Phi}_{\cdot,k}) \left(1 - \mathbf{\Psi}_{\cdot,k} \cdot \frac{\vec{f^R} \vec{H}(\vec{N})}{\vec{K}} \right) .$$

As in the main text we assume time scale separation and substitute steady state juvenile consumer abundance $\bar{C_{J,k}}(\vec{N}, C_{A,k})$ into adult consumer dynamics, yielding

$$\frac{dC_{A,k}}{dt} = b_k C_{A,k} (\vec{N} \cdot \mathbf{\Phi}_{\cdot,k}) \left(1 - \mathbf{\Psi}_{\cdot,k} \cdot \frac{\vec{f^R} \vec{H}(\vec{N})}{\vec{K}} \right) - m C_{A,k} - \beta_k C_{A,k}^2 . \tag{S11}$$

For specialized feedbacks, we assume that the vulnerability of adult resources to consumption g depends predominantly on adult resource traits (e.g., adult body size) rather than adult consumer traits. Using $H_i(\vec{N_A}) = N_{A,i} + \alpha \sum_{j \neq i} N_{A,j}$, this yields the multispecies dynamics

$$\begin{aligned}
\frac{dN_{J,i}}{dt} =& r_i N_{A,i} (1 - H_i(\vec{N_A})/K_i) - N_{J,i} \mathbf{\Phi}_{i,\cdot} \cdot \vec{C} - N_{J,i} \gamma_i \\
\frac{dN_{A,i}}{dt} =& \gamma_i N_{J,i} - N_{A,i} g_i \mathbf{\Phi}_{i,\cdot} \cdot \vec{C} \\
\frac{dC_k}{dt} =& b_k C_k \mathbf{\Phi}_{\cdot,k} \cdot (\vec{N_J} + \vec{g} \vec{N_A}) - m C_k - \beta_k C_k^2 ,
\end{aligned} \tag{S12}$$

As in the main text (eqn. 3) we assume time scale separation to solve for near-steady state juvenile resource abundance as a function of adult resource and consumer abundances $\bar{N_{J,i}}(\vec{N_A}, \vec{C})$

$$\bar{N_{J,i}}(\vec{N_A}, \vec{C}) = \frac{r_i N_{A,i} (1 - H_i(\vec{N_A})/K_i)}{\gamma_i + \mathbf{\Phi}_{i,\cdot} \cdot \vec{C}} \approx \frac{r_i N_{A,i} (1 - H_i(\vec{N_A})/K_i)}{\gamma_i} \left(1 - \frac{\mathbf{\Phi}_{i,\cdot} \cdot \vec{C}}{\gamma_i} \right) . \tag{S13}$$

Substituting this expression into adult resource dynamics and re-arranging yields

$$\frac{dN_{A,i}}{dt} = r_i N_{A,i} (1 - H_i(\vec{N_A})/K_i) - N_{A,i} \mathbf{\Phi}_{i,\cdot} \cdot \vec{C} \left(\frac{r_i}{\gamma_i} (1 - H_i(\vec{N_A})/K_i) + g_i \right) .$$

We simplify this expression by defining (1) a matrix of consumer grazing rates $\boldsymbol{\Delta}_{i,k} = \boldsymbol{\Phi}_{i,k}(g_i + r_i\gamma_i^{-1})$ and (2) adult resource density - edibility relations $\vec{f} = \vec{r}/(\vec{r} + \vec{g}\vec{\gamma})$, yielding

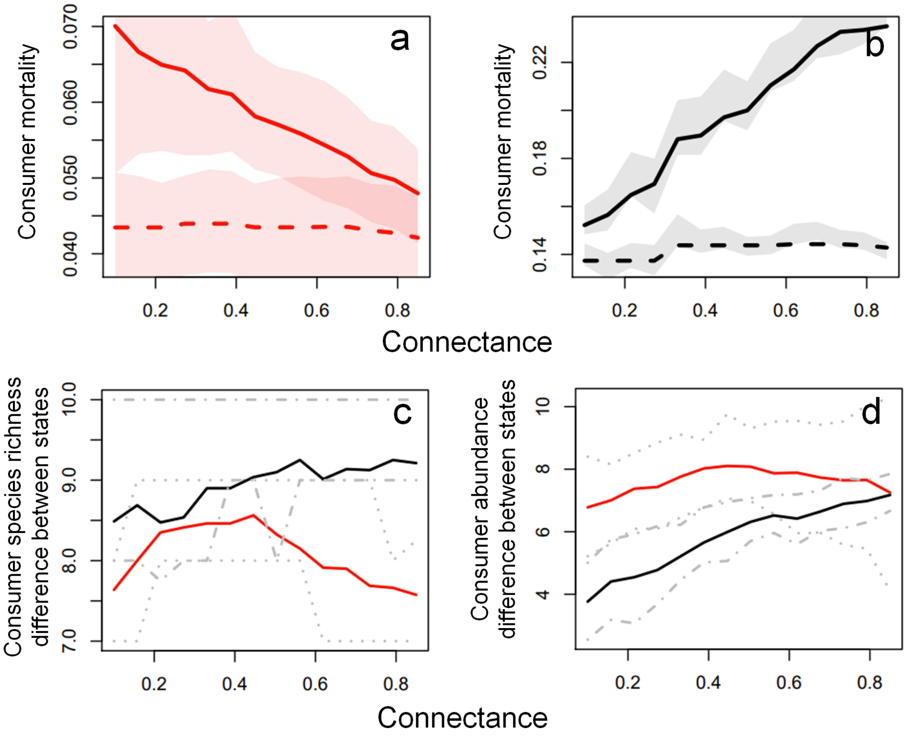
$$\begin{aligned}\frac{dN_{A,i}}{dt} =& r_i N_{A,i}\left(1 - \frac{H_i(\vec{N_A})}{K_i}\right) - N_{A,i}\boldsymbol{\Delta}_{i,\cdot} \cdot \vec{C}\left(1 - f_i^P \frac{H_i(\vec{N_A})}{K_i}\right)\\ \frac{dC_k}{dt} =& b_k C_k \boldsymbol{\Delta}_{\cdot,k} \cdot \vec{N_A}\left(1 - \vec{f}^P \frac{\vec{H}(\vec{N_A})}{\vec{K}}\right) - mC_k - \beta_k C_k^2. \end{aligned} \tag{S14}$$

Note that these models (eqns. S11, S14) differ from our main analysis, where we assume that the edibility or impact on recruitment of a resource depends only on the abundance of that species, and model resource competition implicitly by scaling resource carrying capacity K by a proportion $1 - \alpha(\max(i) - 1)$. In Appendix C we show that differences between specialized and aggregate feedbacks in our main analysis persist when we explicitly model interspecific juvenile resource i - adult resource j interactions across a range of assumptions.

S2 Appendix B: Dynamics with explicit stage structure

Here, we verify that the greater potential for aggregate feedbacks to produce alternative stable states remains in more complex models that explicitly account for resource or consumer stage structure. We model food webs of 12 resource species, 8 consumer species, and either 12 resource juveniles (for specialized feedbacks) or 8 consumer juveniles (for aggregate feedbacks). For specialized feedbacks, we implement eqn. S12 with mean parameter values $\bar{\delta} = 1.2$, $\bar{g} = 0.02$, and $\bar{\gamma} = 0.5$. For aggregate feedbacks, we implement eqn. S10 with $\bar{\delta} = 1.15$, $\bar{f^R} = 1.05$, and $\bar{\gamma} = 0.3$. As in the main text, for aggregate feedbacks we also incorporate the effects of each resource i on each consumer juvenile j, $\Psi_{i,j}$, with $\psi = 0.35$. Finally for both models we incorporate density-dependent consumer mortality $\bar{\beta} = 0.075$, $\bar{K} = 1.5$, and set remaining parameters to their default mean values in Table 2. With these parameters and a trait diversity range of 0.4, we find qualitatively similar effects of connectance on the potential for alternative stable states in each model (Fig. S2).

Figure S2: The potential for alternative stable states decreases with connectance for specialized feedbacks but increases with connectance for aggregate feedbacks in models with explicit stage structure. (a, b) Median thresholds at which consumer species collapse (solid lines) and recover (dashed lines) for specialized feedbacks (a, red colors) and aggregate feedbacks (b, black colors), with alternative stable states present between these thresholds. Shaded regions in (a, b) denote the interquartile range of each threshold. (c, d) Distinctiveness of consumer- and resource-dominated states, measured in species richness (c) and in total consumer abundance (d), with gray lines denoting interquartile ranges. All panels show results over 100 simulated food webs at each connectance level.



S3 Appendix C: Effects of specialization in recruitment and edibility interactions

Here, we expand our main analysis to consider how the potential for alternative stable states depends on both connectivity consumer diet as well as the degree of specialization in both classes of feedbacks. For feedbacks involving consumer recruitment, greater degrees of specialization compared to those in our main analysis can arise when the survival of a consumer's juveniles predominantly depends on the abundance of only a few resource species. With strong spatial sorting (or, equivalently, with relatively immobile adult consumers), specialization in recruitment-dependent feedbacks may also follow specialization in trophic interactions (i.e., $\Psi_{i,k} = \Phi_{i,k}/\delta_k \ \forall i, k$). For feedbacks involving resource edibility, our main analysis assumes that the edibility of one resource species depends only on that species' density (i.e., high specialization). Here we relax this assumption by introducing juvenile resource i - adult resource j interactions $\Gamma_{j,i}$ and modify $P_i(N_i)$ to $P_i(\vec{N}) = 1 - f_i^P \sum_j \Gamma_{j,i} N_j/(K_j(1 - \alpha(\max(i) - 1)))$. Feedbacks involving size-dependent consumption may be less specialized when the proportion of vulnerable juveniles in a resource population depends on several resource species, as might occur when juvenile resources are outcompeted by the adults of multiple resource species rather than only by conspecific adults. Analogously, feedbacks involving group defense may be less specialized when resource species form multi-species herds, schools, or plant stands to deter consumption.

Throughout, we define specialization S in interactions as the mean maximum weight of edibility dependence of one resource i on any other resource j $(= \max(i) \sum_i \max_j(\Gamma_{j,i}))$ and, equivalently, the mean maximum weight of recruitment dependence of one consumer k on any resource i $(= \max(k) \sum_k \max_i(\Psi_{i,k}))$. This metric is analogous to consumer electivity for its primary resource (Fig. 3). For both $\Psi_{i,k}$ and $\Gamma_{j,i}$, we draw interaction weights from a dirchlet distribution parameterized such that the largest entries in each column are, on average, S. For each model, we then measure (1) the hysteresis range of consumer mortality levels between the median points of consumer collapse and recovery and (2) state distinctiveness, measured as the maximum difference in consumer species richness between resource- and consumer-dominated food web states.

Our expanded analysis reiterates the greater distinctiveness and hysteresis range of alternative stable states with recruitment-dependent than with edibility-dependent feedbacks over all levels of connectance and feedback specialization (Fig. S3). In general, specialization tends to decrease the distinctiveness of alternative states for both feedbacks. We also find that high connectance and a very high low of specialization (S <0.2) can produce distinctive alternative stable states over a large range of mortality levels for edibility-dependent feedbacks. We consider this case uncommon, however, as juvenile resources nearing maturity are likely to have a stronger niche overlap with conspecific than with heterospecific adults. Finally, we find that recruitment-dependent feedbacks produce distinctive alternative stable states over a large range of mortality levels over all levels of connectance and feedback specialization, including scenarios where strong spatial structure leads to $\Psi_{i,k} = \Phi_{i,k}/\delta_k \ \forall \ i, k$.

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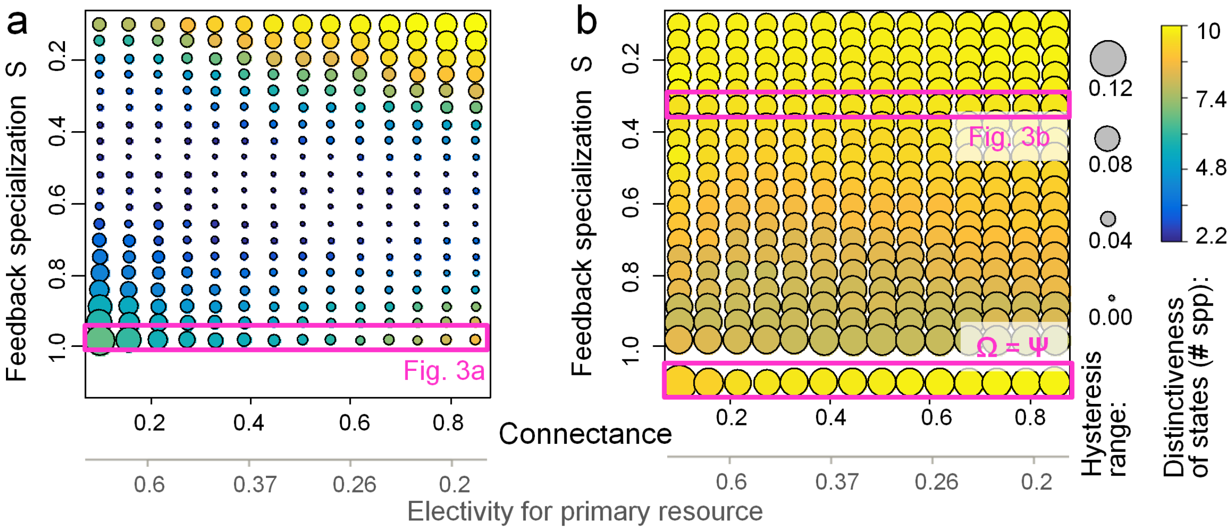
Figure S3: edibility-dependent feedbacks (a) decrease the potential for alternative stable states compared with recruitment-dependent feedbacks (b) over all levels of connectance and feedback specialization S. Points at each connectance and specialization level denote the distinctiveness of alternative stable states (difference in consumer species richness between resource-and consumer-dominate states, point color) and the difference between the median mortality level of consumer collapse and the median mortality level of consumer recovery (point size), averaged over 120 simulated food webs. The secondary x-axis denotes the proportion of diet comprised by each consumer's primary resource when resources are equally abundant (Ivlev electivity), and is analogous to feedback specialization.



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S4 Appendix D: Dynamics without consumer density dependence

Here we verify that the greater potential for aggregate feedbacks to produce alternative stable states remains without consumer density dependence, i.e., $\beta_k = 0 \ \forall \ k$. To reduce between-consumer competition we model lower interspecific trait diversity range of 0.1 (vs. 0.15 in the main text) and omit two consumer species (i.e., modeling 12 resources and 8 consumers). We find that the effects of connectance on the prevalence of alternative stable states for both feedbacks (Fig. S4) are analogous to the case with consumer density dependence (Fig. 3).

Figure S4: The potential for alternative stable states decreases with connectance for specialized feedbacks but increases with connectance for aggregate feedbacks in models without consumer density dependence. (a, b) Median thresholds at which consumer species collapse (solid lines) and recover (dashed lines) for specialized feedbacks (a, red colors) and aggregate feedbacks (b, black colors), with alternative stable states present between these thresholds. Shaded regions in (a, b) denote the interquartile range of each threshold. (c, d) Distinctiveness of consumer- and resource-dominated states, measured in species richness (c) and in total consumer abundance (d), with gray lines denoting interquartile ranges. All panels show results over 100 simulated food webs at each connectance level.