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Species heterogeneity in food webs can reduce the potential for alternative stable states

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Abstract

Overexploitation can lead to a rapid collapse of consumers that is difficult to reverse if ecosystems exhibit alternative stable states. However, support for this phenomenon remains predominantly limited to simple models, whereas food webs might dissipate the feedback loops that create alternative stable states through species-specific demography and interactions. Here we develop a general model of consumer-resource interactions with two types of processes: either specialized feedbacks where individual resources become unpalatable at high abundance or aggregate feedbacks where overall resource abundance reduces consumer recruitment. We then quantify how the degree of interconnectedness and species differences in demography affect the potential for either feedback to produce consumer- or resource-dominated food web states. Our results highlight that such alternative stable states could be more likely to happen when aggregate feedbacks or lower species differences increase redundancy in species contributions to persistence of the consumer guild. Conversely, specialized palatability feedbacks with distinctive species roles in guild persistence reduce the potential for alternative states but increase the likelihood that losing vulnerable consumers cascades into a food web collapse at low stress levels, a fragility absent in few-species models. Altogether, we suggest that species heterogeneity has a greater impact on whether feedbacks prevent consumer recovery than on the presence of many-species collapses.

Key words: Critical transitions, food webs, cultivation-depensation, network dynamics, biodiversity-ecosystem function

Introduction

Many ecological systems exhibit distinct states characterized by the presence or collapse of consumer guilds. Whether these food web configurations represent alternatively stable states that can occur under the same environmental conditions determines whether ecosystems recover or shift into new ecological states after natural or anthropogenic disturbances cease (Scheffer et al. 2001). Alternative stable food web states can theoretically arise from strong feedback loops in many ecosystems, including 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). Most studies predicting the potential for alternative stable states, however, either consider 1-3 populations and omit all other taxa (De Roos and 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 dissipate feedback loops across different species (Neutel et al. 2002), or heterogeneity within guilds might lead to species-specific dynamics (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 species heterogeneity to weaken feedbacks brings the relevance of alternative stable states into question.

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One aspect of species heterogeneity that might reduce the relevance of alternative stable states is the degree to which feedbacks are species-specific ('specialized' hereafter). On one extreme, aggregate feedbacks might promote multispecies alternative stable states by allowing different species involved in the feedback to help each other persist. One example of such feedbacks is when corals shelter many different herbivore species, with all herbivores helping limit the total abundance of macroalgae that can outcompete corals (Mumby et al. 2007). At the other extreme where feedbacks affect specific, pairwise species interactions (Table 1), alternatively stable food web states may become less pronounced as different species collapse and recover at different disturbance levels rather than in unison. A multitude of stable states characterized by the presence or absence of single species can occur, for instance, in mutualistic networks where different pollinators facilitate different rather than shared plant hosts (Lever et al. 2014) and in models where strong interspecific competition is reciprocated within pairs of competitors (e.g., 7 stable states for 20 species, Levins 1966; Gilpin and Case 1976; van Nes and Scheffer 2004). Analogous feedback specialization might occur in food webs, where persistence of a consumer depends on the presence and palatability of only its primary resources. For instance, alternative stable states with gape-limited predators absent and many prey surviving to large body sizes or predators present and most prey small readily emerge in two-species models (De Roos and Persson 2002). In many-species systems, however, predators consuming different prey might collapse and recover at different predator mortality levels. The potential for specialization to diffuse feedbacks that in simple model drive alternative stable states motivates multispecies food web models that account for both direct and indirect interactions among distinct species.

The relevance of alternative stable states in food webs might additionally decrease because demographic heterogeneity among species can dissipate underlying feedbacks. Whereas dynamics in food webs with small differences among species might closely resemble simple models, different consumers can become increasingly interdependent as the frequency of species interactions ('connectance' hereafter) increases (Downing et al. 2012; Lever et al. 2014). For instance, overharvest of longer-lived predators with greater body and gape size could lead to a dominance of large-bodied prey inedible to more gape-limited predators. Loss of more vulnerable species might therefore weaken feedbacks maintaining the remaining consumer guild, reducing the overall potential for alternative stable states. Alternatively, connectance can synchronize feedback processes by allowing species to help each other persist (Downing et al. 2012; Lever et al. 2014). As with aggregate feedbacks, higher connectance might therefore translate to a greater potential for alternative stable states.

Here, we quantify how interactions among many species affect the potential for alternative stable food web states. For this we synthesize multiple existing models into two general models of aggregate and specialized feedbacks that, in the two-species case, exhibit alternative stable consumer- and resource-dominated states. We then examine how feedback specialization, species heterogeneity, 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) and alternative stable states might explain delays in consumer recovery when conservation reduces harvest (Gårdmark et al. 2015).

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Methods

2.1 Derivation of specialized and aggregate feedback models

To focus on the effect of feedback specialization and species heterogeneity we use general models of aggregate and specialized feedbacks of resources and their consumers (Fig. 1a), each derived from more mechanistic models using separation-of-time-scale assumptions. Here we summarize derivations of these simpler models, and provide mathematical derivations in Appendix A and extend our simulation results to more detailed models in Appendix B.

For specialized feedbacks we focus on the common pattern where abundant resources are more difficult to consume. One mechanism empirically resolved in both plant-herbivore (Briggs et al. 2018) and prey-predator systems (Persson et al. 2007) involves resource stage structure, with more abundant resource populations dominated by large adults that survive long enough to grow to a size refuge. A second common mechanism involves group defense, where grazing or attack rates analogously decline due to prey schooling (Freedman and Wolkowicz 1986) or dense stands of plants deterring herbivory (van de Koppel et al. 1996).

We simplify a size-dependent predation model to the case where juvenile resource abundance quickly reaches equilibrium on the time scale of adult resources and consumers by assuming that resources have high fecundity and can mature quickly. Given lower competitive ability of juveniles, juvenile abundance declines proportionally as adult abundance N_i approaches adult carrying capacity K_i, causing a decline in grazing/attack rates δ_k. Given a degree of gape limitation and/or group defense f_k and a Type I functional response, consumption of resource N_i by consumer C_k is then $\Phi(\delta_k N_i(1 - f_k N_i/K_i))$, where we ensure that total consumption is non-negative using $\Phi(x) = x\Theta(x)$, where the Heaviside function $\Theta(x) = 1$ for $x > 0$ and 0 otherwise. Consumers then convert consumption to production with efficiency b_k and experience mortality at a rate m, while adult resources grow logistically at a rate r_i. In a two-species model, strong feedbacks impacting palatability (i.e., high f_k) can produce alternative stable states dominated by either consumers or abundant, inedible resources over an intermediate range of consumer mortalities (Appendix A). In a food web, resources have specialized feedbacks because high density of any given resource allows that species to escape consumption, but it does not directly alter palatability of other resources (although indirect effects occur if consumer responses cascade through the food web).

For aggregate feedbacks, we focus on consumer recruitment success, which can decline with total resource abundance. This dynamic can arise when resources reduce survival of juvenile consumers via competition or predation: in pelagic systems, for instance, the larvae of different predators can all be eaten by a planktivorous prey species (Walters and Kitchell 2001). Resources can also reduce recruitment indirectly, for instance when macroalgae overgrow corals that shelter the larvae of different herbivores (Blackwood et al. 2012). In such systems, juvenile survival declines proportionally with resource abundance N_i by a factor f_k, where $\Phi(1 - f_k)$ is the baseline fraction of juveniles unaffected by resource densities. Given high consumer fecundity and fast maturation, juvenile consumer abundance quickly reaches equilibrium on the time scale of resources and adult consumers C_k. With this simplification,

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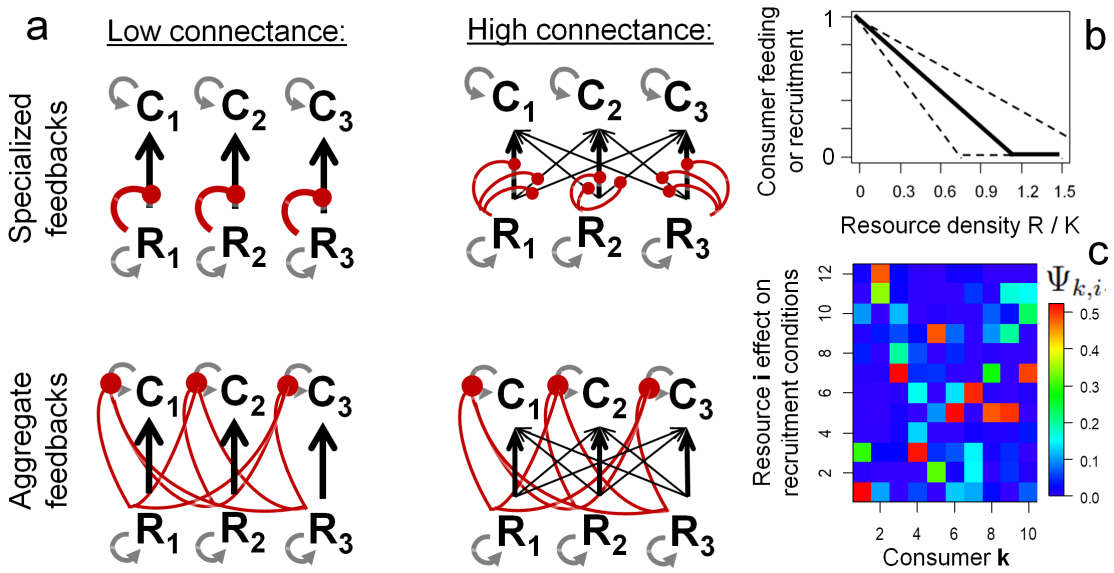
juvenile survival determines conversion efficiency from resources eaten to adult consumers b_k by the factor $\Phi(1 - f_k N_i/K_i)$. Combined with logistic resource growth and Type I consumption this feedback yields alternative stable states with adult consumers either present or extinct over a range of consumer mortality levels in two-species models (Appendix A).

Figure 1: (a) Model schematic of resources (R_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). (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 all consumers affected by the resource ($\Psi_{k,i} > 0$). Dashed lines indicate the maximum variation in this feedback among consumers at the highest heterogeneity levels considered. (c) Example of the matrix of weights $\Psi_{k,i}$ determining the impact of resource i on recruitment of consumer k.



2.2 Multispecies dynamics

We model guilds of consumers and resources, with competition between resources with interspecific competitive effect α, natural consumer mortality from intraspecific competition β_k, and diet specialization as the fraction of total consumption consumers k allot to each resource i, $\Omega_{k,i}$. We account for demographic heterogeneity using species-specific parameter values that account for variation in resource growth (r_i), carrying capacity (K_i, which implicitly models resource heterogeneity in competitive ability), consumer grazing rate δ_k, and consumer conversion efficiency b_k (which implicitly includes species variation in juvenile consumer survival). Additionally, we allow for heterogeneity in consumer sensitivity to feedbacks f_k that can arise, for instance, when larger species experience lower gape limitation.

The set of species-specific resource abundances $\vec{N}$ determines overall consumer-specific recruitment success $\mathbf{R}_k(\vec{N})$ and resource palatability $\mathbf{P}_{i,k}(\vec{N})$, where we constrain either

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$\mathbf{R}_k(\vec{N}) = 1$ to analyze specialized feedbacks only or $\mathbf{P}_{i,k}(\vec{N}) = 1$ to analyze aggregate feedbacks only. Following above derivations $\mathbf{P}_{i,k}(\vec{N}) = \Phi(1 - f_k N_i/K_i)$ for specialized feedbacks. In Appendix D we account for cases where juvenile resources nearing maturity do not predominantly compete with or stay close to adults of their own species by explicitly modeling juvenile-adult resource interactions using the matrix $\mathbf{\Gamma}$ in $\mathbf{P}_{i,k}(\vec{N}) = \Phi(1 - f_k \sum_j \Gamma_{i,j} N_j/K_j)$. For aggregate feedbacks, recruitment of a specific consumer might depend on only a subset of resources, for instance when larvae of some herbivores preferentially settle on exposed reef sections inhabited only by macroalgae tolerant to wave stress. Consequently, recruitment success of consumer k declines proportionally with the weighted average of resource abundance, with weights $\Psi_{k,i}$ varying among consumers to simulate species with shared but not identical recruitment requirements (Fig. 1c). Overall consumer-specific recruitment success is then $\mathbf{R}_k(\vec{N}) = \Phi(1 - f_k \sum_i \Psi_{k,i} N_i/K_i)$. This produces the full multi-species model

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} - \alpha K_i^{-1} \sum_{j \neq i} N_j\right) - N_i \sum_k \mathbf{P}_{i,k}(\vec{N})\, \Omega_{k,i} \delta_k C_k \tag{1}$$

$$\frac{dC_k}{dt} = C_k \mathbf{R}_k(\vec{N})\, b_k \delta_k \sum_i \mathbf{P}_{i,k}(\vec{N})\, \Omega_{k,i} N_i - \beta_k C_k^2 - m C_k. \tag{2}$$

2.3 Model implementation

We construct randomly generated food webs of 12 resource and 10 consumer species. We define food web connectance as the fraction of nonzero consumer-resource interactions. For each connectance level we assign interactions randomly but omit connectance matrices where any consumer has no resources assigned. Strengths of nonzero interactions then depend on (1) maximum consumer-specific grazing rate δ_k and (2) the fraction $\Omega_{k,i}$ of this rate a consumer k allots to each of its resources, as might occur when abiotic conditions constrain resources and consumers to similar habitats (i.e., higher $\Omega_{k,i}$). To ensure a constant net strength of consumer-resource interactions across all connectance levels, we randomly draw $\Omega_{k,i}$ for each consumer from a dirichlet distribution, with $\sum_i \Omega_{k,i} = 1$ and σ representing the standard deviation of $\Omega_{k,i}$. To implement recruitment dependence, we account for a moderate degree of specialization in the negative impacts of resources on juvenile consumers (e.g., due to spatial structure). For this we sample $\Psi_{k,i}$ from a dirichlet distribution, where weights $\sum_i \Psi_{k,i} = 1$ and the largest recruitment dependence of a consumer on any single resource is, on average, is 0.35.

To implement demographic heterogeneity, we sample each species' parameter values from a uniform distribution $\mathrm{U}(\mu(1-H), \mu(1+H))$, where upper and lower bounds differ from the average value μ by a proportion H, and H represents the degree of demographic heterogeneity. As large variations in demography did not always allow species coexistence, we omitted infeasible food webs where the abundance of any consumer fell below 0.25 at $m = 0.05$ starting from a consumer-dominated initial condition. Throughout, we use default (or average) parameter values $K = 1.5$, $r = 1$, $\delta = 1.2$, $b = 1$, $\alpha = 0.025$, $f = 1.1$, and $\sigma = 0.4$. We assume a low level of intraspecific consumer competition $\beta = 0.15$ to reduce occurrence of effectively few-species food webs dominated by a few consumers but in Appendix we show

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analogous results for $\beta = 0$. Using this process, we generate 40 replicate food webs to analyze dynamics at each level of heterogeneity, and generate a standard set of 40 food webs to analyze the effects of connectance only.

2.4 Model analysis

Throughout, we quantify the relevance of alternative stable states based on two metrics: the range of consumer mortality levels producing this phenomenon and the distinctiveness of consumer- and resource-dominated states. The range of alternative stable states reflects the likelihood that a disturbance of consumer-dominated food webs induces a change in overall ecosystem state, whereas distinctiveness reflects whether this change is likely to be ecologically meaningful and empirically detectable. 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. To resolve collapse points, we increase consumer mortality 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 years 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 simulated improving conditions by gradually reducing consumer mortality, again with step size 0.02. To resolve species recovery, 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. 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, whereas alternative stable states can be relevant when the range exceeds zero. 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 resolve how feedbacks depend on species-specific contributions, we quantify how the processes maintaining the consumer guild depend on consumer species richness. For this, we progressively randomly selected consumers from the food web at a low mortality level, moderate connectance, and moderate heterogeneity. After removing each consumer in this experiment, we simulate the food web for 200 time steps and then measure average palatability of all resources for specialized feedbacks and average survival probability of all consumer recruits for aggregate feedbacks. One way specialized feedbacks could lead to species-specific consumer contributions to guild persistence 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 dynamics of consumer collapse as consumer mortality exceeds the tipping point for each feedback under moderate connectance and heterogeneity.

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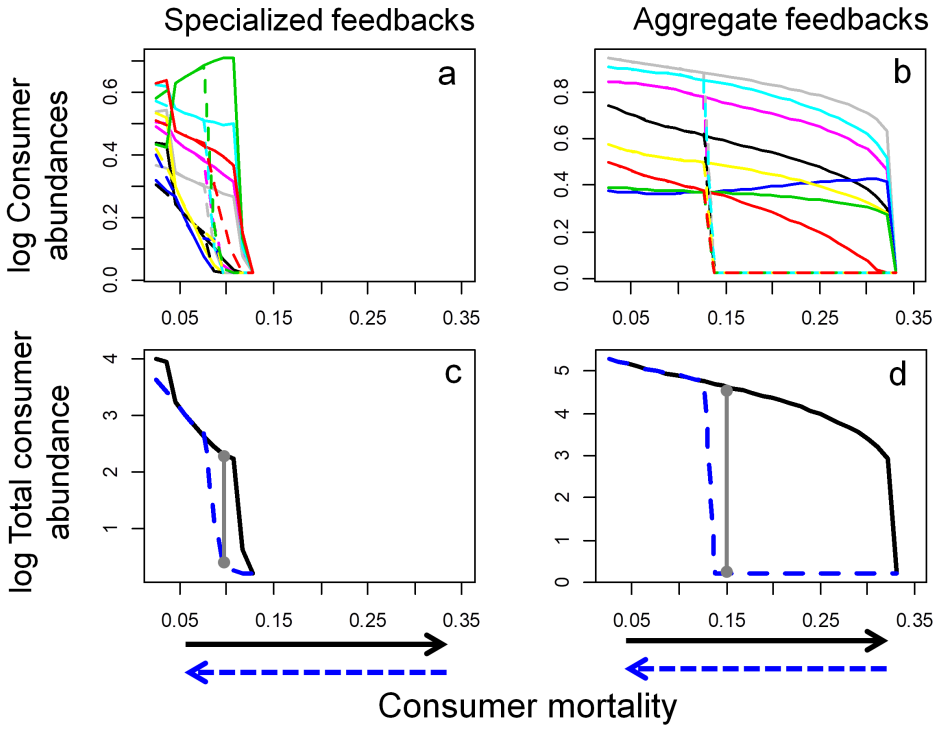
Figure 2: Alternative stable states are more distinct and occur over a wider range of mortality levels for aggregate (b, d) than specialized (a, c) feedbacks. Equilibrium consumer abundances as mortality sequentially increases (solid lines) and then decreases (dashed lines), shown for individual species (a, b) and total consumer abundance (c, d). Here we set connectance at 0.7 and heterogeneity at 0.25. Vertical gray lines in (c, d) show the abundance-based metric of state distinctiveness used throughout.



Results

Under moderate connectance and heterogeneity distinctive alternative stable states can arise from both feedback types, but are more prevalent in the model with aggregate feedbacks based on a number of metrics (Fig. 2). First, consumer collapse and recovery each occur at the same mortality values for nearly all consumers under aggregate feedbacks (Fig. 2b) but a variety of values under specialized feedbacks (Fig. 2a). Second, as a result, a greater distinctiveness between states under aggregate (Fig. 2d) than specialized (Fig. 2c) feedbacks occurs throughout the range of alternative stable states and a range of values for connectance (Fig. 3c,d) and demographic heterogeneity (Fig. 4c,d). Greater synchrony and distinctiveness with aggregate than with specialized feedbacks arise because all consumers experience the same persistence bottleneck, namely that overall resource densities remain low. In contrast, with specialized feedbacks consumers experience multiple persistence bottlenecks as each of their primary resources must remain edible (i.e., limited to low densities), where the bottlenecks differ among consumers with different diets.

Alternative stable states additionally occur over a wider range of mortality values under aggregate (Fig. 2d) than under specialized (Fig. 2c) feedbacks. At high connectance with specialized feedbacks, the collapse threshold of the entire consumer guild converges

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on the threshold of the most vulnerable consumers, namely, the species that at low connectance collapse at the lowest mortality levels (Fig. 3a). This arises because consumers divide their consumption among many different resources and cannot singlehandedly 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 energy uptake for other consumers and, potentially, a multi-species collapse that gradually cascades across species (Fig. 5b,c). Accordingly, average resource palatability and the strength of specialized feedbacks maintaining the consumer guild both decline proportionally with the number of consumer species present (Fig. 5a). Aggregate feedbacks produce alternative stable states over a larger mortality range because favorable recruitment conditions require control of only the overall resource abundance; this redundancy in consumer contributions to recruitment translates to (i) a weaker effect of species loss on aggregate compared to specialized feedbacks at high diversity (Fig. 5a) and (ii) a more synchronized loss of all consumers at the collapse point (Fig. 5b). Taken together, alternative stable states are more prevalent under aggregate feedbacks that both synchronize consumer collapse and remain strong when vulnerable species decline.

3.1 The effect of connectance

Connectance can increase the potential for alternative stable states with aggregate feedbacks but decreases the potential for alternative stable states with specialized (Fig. 3). For specialized feedbacks, connectance 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 species (as described above). For aggregate feedbacks, connectance increases both the distinctiveness and the range of alternative stable states across consumer mortality levels (Fig. 3b, c). 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. 3d). Greater feedback strength also allows consumers to persist at higher mortality levels but has no effect on recovery from the consumer-extinct state with poor recruitment conditions, leading to an overall increase in the range of alternative stable states (Fig. 3b).

3.2 The effect of demographic heterogeneity

Given moderate connectance (0.7), heterogeneity in species demography reduces the distinctiveness and range of alternative stable states, with greater sensitivity to heterogeneity under specialized than under aggregate feedbacks (Fig. 4). Greater heterogeneity 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 heterogeneity, where more dominant consumer species (e.g., those with greater δ_k and b_k) can singlehandedly maintain favorable resource edibility or recruitment conditions. Such species also help other consumers recover, increasing the median recovery threshold.

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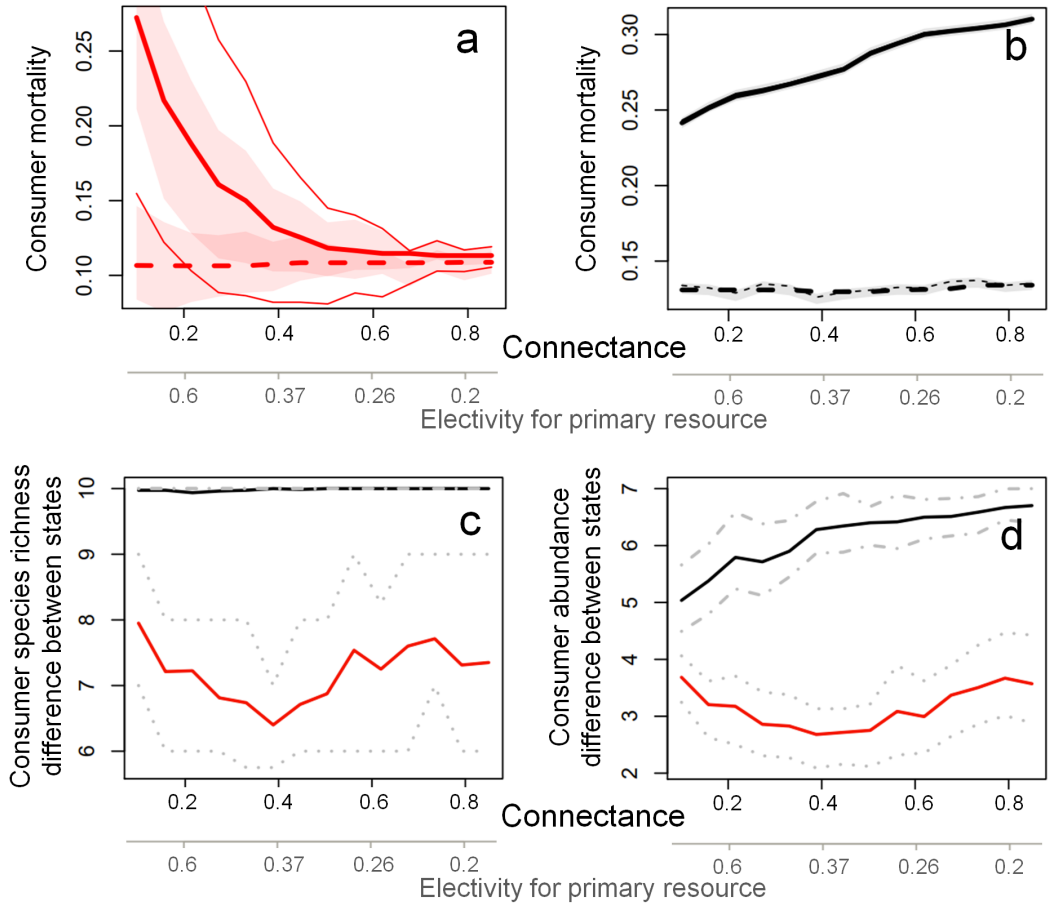
Figure 3: The potential for alternative stable states decreases with connectance for specialized feedbacks but increases with connectance for aggregate feedbacks. (a, b) Median thresholds at which consumer species collapse (solid lines) and recover (dashed lines) for specialized feedbacks (a, red colors) and aggregate feedbacks (b, black colors), with alternative stable states present between these thresholds. As a more intuitive population-level metric, the secondary x-axis denotes the fraction of diet comprised by each consumer's primary resource when resources are equally abundant, averaged across all consumers (i.e., Ivlev electivity, $= 10^{-1} \sum_k \max_i(\Sigma_{i,k})$). Shaded regions in (a, b) denote the interquartile range of each threshold, 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 gray lines denoting interquartile ranges. All panels show results over 100 simulated food webs at each connectance level.



Discussion

We have shown that alternative stable states can occur in interconnected food webs of many different species, especially with aggregate feedbacks (Fig. 2) 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 parallels work modeling more nested mutualistic networks where multiple species pollinate a shared host (Lever et al.

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2014) and community resistance to invasion by a shared competitor (Scheffer and van Nes 2006) 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 conditions in the same way, for instance 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 conditions (Fig. 5a), 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. 3b). This leads to a potential resistance-resilience tradeoff (Downing et al. 2012): communities with greater functional redundancy and resistance to stress (here, collapse at higher consumer mortality) may also exhibit a greater potential for alternative stable states (i.e., lower ecological resilience) and, when they collapse, require a larger reduction in stress in order to recover.

Our results emphasize that the potential for alternative stable states declines with specialized palatability feedbacks where a resource species can become inedible to multiple consumers at high abundance (Fig. 2; Table 1). This contrasts 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. 5a), for instance by preventing its primary resource from surviving to large body sizes and becoming inedible to other species (De Roos and Persson 2002; de Roos and Persson 2013). Loss of vulnerable species at low mortality levels therefore can reduce ecosystem functions maintaining the consumer guild (here, resource palatability) and cascade into a many-species collapse (Fig. 3a, 5). Thus, with palatability feedbacks connectivity can impart the vulnerability of a few species onto the rest of the food web. Given the similar potential for palatability and recruitment feedbacks to drive alternative stable states in few-species models (Gårdmark et al. 2015; van de Leemput et al. 2016, Appendix A), our many-species simulations also highlight how species heterogeneity narrows but does not eliminate the set of processes most likely to create alternative stable states and impede food web recovery from disturbance.

Despite reducing the potential for alternative stable states, we find that specialized feedbacks can still drive many-species collapses following small increases in mortality (Fig 2). This result parallels spatial regime shifts where heterogeneity favors a more resilient (here, resource-dominated) state, which propagates across space from more to less vulnerable patches in a domino effect (van Nes and Scheffer 2005). Therefore, alternative stable states present in well-mixed systems are greatly reduced when matter or organisms move slowly and affect feedbacks only in nearby locations. In our model, food web connectance is analogous to dispersal and specialized feedbacks parallel localized, within-patch feedbacks. This suggests an opportunity for future research, using models developed here as a starting point, to expand food web resilience theory based on insights from the better-developed literature on spatial regime shifts and early-warning signals (van Nes and Scheffer 2005; van de Leemput et al. 2016; Dakos et al. 2011).

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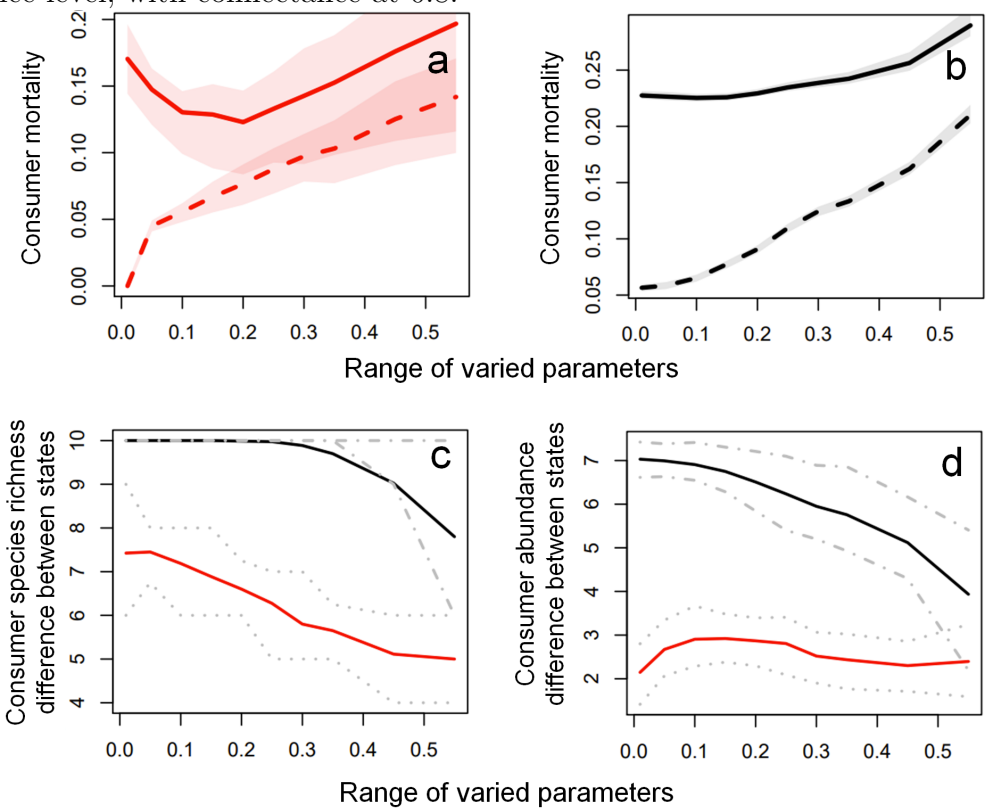
Figure 4: Demographic heterogeneity decreases hysteresis and the distinctiveness of alternative stable states. (a, b) Median thresholds at which consumer species collapse (solid lines) and recover (dashed lines) for specialized feedbacks (a, red colors) and aggregate feedbacks (b, black colors), with alternative stable states present between these thresholds. Interquartile ranges of thresholds not visible in (b) because collapses and recoveries each happen synchronously across species. (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, with connectance at 0.8.



4.1 Drivers of feedback specialization

The reduced potential for alternative stable states and reduced resistance of species guilds to mortality found here for specialized feedbacks extends beyond processes in our base models. The distinction between specialized palatability and aggregate recruitment feedbacks prevails even when palatability of each resource depends on the abundance of many but not all resource species, for instance in multi-species fish schools or plant stands, and when consumers eat the same resources that outcompete or consume their young in cases of high spatial structure (i.e., $\mathbf{\Psi} = \mathbf{\Omega}$; Appendix D). Beyond food webs, co-occurring species can facilitate each other in unique ways by providing different limiting nutrients, protection against attack by different consumers, ameliorating different disturbances, or a combination of these. Such facilitation may occur indirectly, for instance when multiple pollinators benefit a shared, mutualist plant. Reviewing existing case studies, (Afkhami et al. 2014) found

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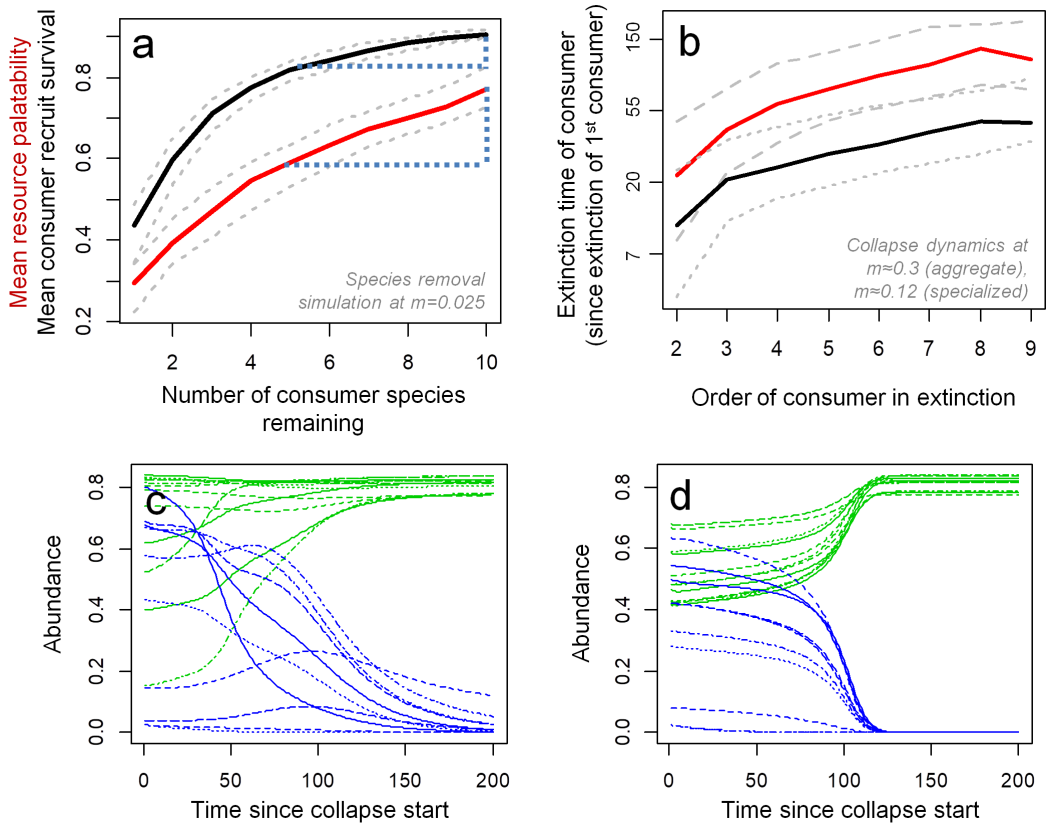
that the presence of multiple mutualist partners in most cases synergistically promoted the central host species, indicating that the mechanisms by which species indirectly facilitate each other in many systems may be limited. Where species removal experiments (e.g., Fig. 5a) are not feasible, however, quantifying feedback specialization at large scales relevant to ecosystem processes directly through measurements or experiments may be difficult, particularly because facilitation often becomes prominent only under stressful conditions (Bruno et al. 2003), which in the presence of feedback mechanisms also translate to a high risk of sudden community collapse (Lever et al. 2014).

Figure 5: More species-specific contributions to guild persistence arise with specialized feedbacks due to a greater propensity for cascades of multiple secondary extinctions following the loss of the most vulnerable consumer species compared with more synchronous extinctions under aggregate feedbacks. (a) Effects of progressively removing randomly selected consumer species (left to right along x-axis) on mean resource palatability (specialized feedbacks, red line) and mean consumer recruit survival (aggregate feedbacks, black line); blue dotted lines denote effects of removing 5 consumers. (b) Distribution of consumer extinction times, in time steps from first extinction, in simulations where mortality crosses the threshold leading to the collapse of all remaining consumers, with greater values reflecting a greater frequency of cascading, delayed extinctions. (c,d) Example time series of consumer collapse (blue lines) and resource growth (green lines) over the course of consumer extinction for specialized (c) and aggregate (d) feedbacks. Lines in (a,b) denote medians (red and black) and interquartile ranges (gray lines) across 100 simulations. Heterogeneity is 0.15 and connectance is 0.7.



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More generally, feedback specialization may increase with the number of processes involved. Our analysis focuses on feedback loops comprised of 2-3 processes, such as when greater herbivore abundance leads to (1) reduced macroalgae, (2) increased coral cover, and (3) increased herbivore recruitment. Given that each process increases the potential for feedback specialization, such as when different macroalgae outcompete different coral species, "longer" feedbacks involving more processes are more likely to be specialized. Many different processes can also regulate consumer persistence when several short feedbacks involve different types of species or physical features. For instance, reduced abundance of predatory fish may translate to (1) reduced palatability of prey (following Table 1) and (2) increased mortality as fisheries respond to reduced catch with increased fishing effort, particularly on more valuable species. Ultimately, quantifying the cumulative degree of specialization across multiple feedbacks in well-studied systems might best be achieved using emerging metrics of modularity in (multi-layer) networks that account for multiple types of interactions.

4.2 Results robustness

For tractability, we omitted several factors that might affect the potential for alternative stable states in multispecies food webs. Our approach might 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 down-regulate 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 potential for heterogeneity to reduce the potential for alternative stable states emphasized here underscores the importance of future system-specific studies that model observed species heterogeneity and its underlying life history trade-offs. Our generalized, simple 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 conditions over which this phenomenon occurs (e.g., Guttal and Jayaprakash 2007). Finally, whilst we base our analyses on 800 randomly constructed food webs, the effects of feedback specialization, connectance, and demographic heterogeneity in any particular food web may differ from the overall patterns.

Several additional factors can increase the potential for alternative stable states with palatability feedbacks from our main analysis. First, palatability feedbacks may be less specialized than modeled here, for instance when juvenile resources compete with adults of many species and fish form many-species schools (Gil et al. 2018). In these cases distinctive alternative stable states might occur over a larger range of conditions. Second, consumers may adjust their diet composition to concentrate feeding only on resources which remain palatable. Further modeling work is needed to determine whether alternative stable states become more likely as this process strengthens consumer-resource interactions or less likely

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as converging diets increase competitive exclusion among consumers. We also note that in reality diets may be constrained by seasonality, spatial structure, or nutrient requirements by the consumer.

4.3 Detecting alternative stable states in food webs

Anticipating the sudden collapse and difficult recovery of target ecosystem states may require model-based approaches in diverse systems. Increased complexity that is associated with diversity can increase the potential for transient dynamics, which can reduce the distinctiveness of both different ecological states and transitions among them. For instance, when herbivore recruitment decreases at low coral cover, long-lived herbivores might decline gradually over decades and obscure the abrupt underlying change in ecosystem steady states. Longer-lived species also may not exhibit variance-based early warning signals before the onset of food web collapse. An alternate approach to anticipating alternative stable states couples dynamical models with empirical data (Mumby et al. 2013). In multispecies systems, such models typically focus on aggregate species groups, thereby omitting connectance, heterogeneity, and feedback specialization. Compared with our many-species simulations simplified aggregative models conservatively over-predict hysteresis by omitting heterogeneity, and by omitting connectance under-predict collapse thresholds for aggregate feedbacks. However, we find that simple models can also over-predict collapse thresholds (Fig. 3), and therefore overall resilience, by overlooking key species that uniquely facilitate multiple species and are sensitive to stress. Taken together, our findings emphasize the importance of detecting specialized feedbacks and, where such feedbacks are absent, the efficacy of aggregative, simple models in conservatively predicting ecosystem resilience.

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

State 1	**Feedback maintaining state 1**	**State 2**	**Feedback maintaining state 2**	**Example systems**
Predators abundant, prey sparse	Prey vulnerable to predation	Prey dominant, predators rare	Prey group defense	Fish schools; mammal herds (Freedman and Wolkowicz 1986)
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)
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); marine invertebrates
Herbivores abundant, plants sparse	Most plants small and edible or nutritious	Plants dominant, herbivores rare	Most plants survive to large size and unpalatable	Kelp forests (Ling et al. 2015), grasslands, coral reefs (Briggs et al. 2018)
Predators abundant, prey sparse	High juvenile predator survival	Prey dominant, predators rare	Prey consume or outcompete juvenile predators	Cultivation effects (Walters and Kitchell 2001); intraguild predation (Polis et al. 1989)
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 (Dixson et al. 2014), kelp forests (Baskett and Salomon 2010)

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Appendix A: Model derivations

1.1 Specialized feedback model

To derive the consumer-resource model of specialized feedbacks (eqns. 1-2), we start with a general model tracking abundance of consumers C and a resource with juvenile J and adult A stages. Throughout, we assume juveniles as being competitively inferior to adults, for instance seedlings and small plant stages that only grow on free space, and rescale abundance by carrying capacity of the resource K. Thus, adults A produce offspring at rate r, and a fraction $1-A$ of offspring successfully recruit to the juvenile stage; note that adults may cause juvenile mortality when adults exceed carrying capacity (e.g., trees shading out seedlings). Juveniles then mature at a rate $\gamma(A)$ that may depend on available resources, and therefore $\gamma(A)$ declines with adult abundance. Additionally, both juveniles and adults loss to consumption at a rate δ. Resource loss to consumption may differ between juvenile and adult resources by a factor g, with $g < 1$ indicating lower consumption of adults, as might arise from consumer gape limitation. Finally, consumers have a conversion efficiency b and mortality rate m, giving the full dynamics:

$$\frac{dJ}{dt} = rA(1-A) - \delta CJ - J\gamma(A) \tag{S1}$$

$$\frac{dA}{dt} = J\gamma(A) - g\delta CA \tag{S2}$$

$$\frac{dC}{dt} = b\delta C(J + gA) - mC. \tag{S3}$$

We simplify these dynamics first by assuming that juvenile resource stages are relatively brief on the time scale of adults and consumers, that is, $r, \gamma(A) >> \delta$, which yeilds

$$\bar{J}(A, C) = \frac{rA(1-A)}{\gamma(A) + \delta C}.$$

Second, we simplify the consumption term $(\gamma(A)+\delta C)^{-1}$ using the first two terms of a Taylor approximation expanded with respect to C around $C = 0$ to arrive at a consumer-resource interaction form where juvenile abundance declines linearly rather than geometrically with consumer abundance. Juvenile abundance is then approximately

$$\bar{J}(A, C) \approx \frac{rA(1-A)}{\gamma(A)} \Phi\left(1 - \frac{\delta C}{\gamma(A)}\right), \tag{S4}$$

where as in the main text, $\Phi(x)$ ensures that total consumption is non-negative. Whilst differing qualitatively at high consumer densities, this simplification can approximate dynamics involving collapse of consumers from low-moderate abundance levels. Substituting this term

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for J in adult and consumer dynamics yields

$$\begin{aligned}\frac{dA}{dt} \approx & rA(1-A)\Phi\left(1-\frac{\delta C}{\gamma(A)}\right) - g\delta AC \\ = & rA(1-A) - \delta CA\Phi\left(\frac{r(1-A)}{\gamma(A)} + g\right) \qquad \text{(S5)} \\ \frac{dC}{dt} = & b\delta C(J+gA) - mC \\ \approx & b\delta C\left(\frac{rA(1-A)}{\gamma(A)}\Phi\left(1-\frac{\delta C}{\gamma(A)}\right) + gA\right) - mC \\ = & b\delta CA\Phi\left(\frac{r(1-A)}{\gamma(A)} + g\right) - mC, \qquad \text{(S6)}\end{aligned}$$

where the final simplification reflects the time scale separation $\gamma(A) >> \delta$, such that $\delta/\gamma(A) \approx 0$.

In the case of density-independent maturation rates (i.e., $\gamma(A) = \gamma_0$), renaming $N{=}A$ and defining $\delta' = \delta(g + r/\gamma_0)$ and $f = r/(r + g\gamma_0) \leq 1$, simplifies eqns. S5-S6 into eqns. 1-2:

$$\begin{aligned}\frac{dN}{dt} = & rN(1-N) - CN\delta'\Phi(1-fN) \\ \frac{dC}{dt} = & bCN\delta'\Phi(1-fN) - mC,\end{aligned}$$

where the fraction of edible resources $\Phi(1-fN)$, hereafter defined as $\xi(N)$, declines with abundance. Here, note that greater palatability of adults g translates to a lesser decline in $\xi(N)$ with N (i.e., lower f), weakening the feedback that drives alternative stable states.

To explore the case where juveniles mature slower when adults deplete resources, we consider resource palatability in eqn. S5-S6 for a simple case where $g = 0$ and $\gamma(A) = \gamma_0(1 - zA)$, where the fraction $z < 1$ reflects maturing juveniles being less vulnerable to competition from adults than newly recruiting juveniles. In this case resource palatability is convex and predominantly declines at high adult abundance (Fig. S1a). This reflects the case where slower maturation due to resource depletion by adults translates to a greater period of resource individuals being vulnerable to predation. Analogous patterns 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 among adults and juveniles (Fig. S1b). Here, the fraction of total resource biomass comprised by smaller juveniles more vulnerable to consumption similarly declines in populations that experience lower juvenile mortality and reach greater total biomass. Finally, we note that in conventional models of group defense ('Type IV' functional forms, Freedman and Wolkowicz 1986; Bate and Hilker 2014) resource palatability can decline in a concave fashion (Fig. S1a).

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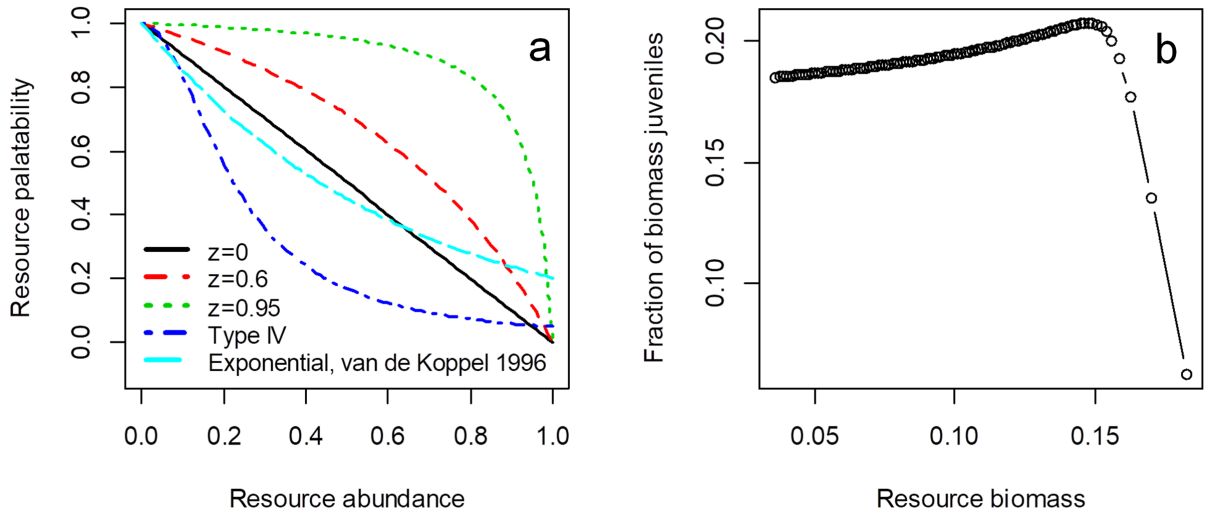
Figure S1: (a) Comparison of declines in resource palatability with abundance across levels of maturation sensitivity to competition (z in $(1-A)(1-zA)^{-1}$), Type IV group defense functional response ($(1+\eta N^2)^{-1}$), and exponential declines in grazing as abundant vegetation impedes movement ($\exp(-\eta N)$, $\eta = 1.65$ in van de Koppel et al. 1996). (b) Fraction of total equilibrium resource biomass represented by smaller (i.e., more palatable) 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 generated by increasing juvenile mortality to simulate different densities of a gape-limited consumer.



1.2 Aggregate feedback model

Here, we derive the general model of aggregate feedbacks (eqns. 3-4) from models where resources inhibit consumer recruitment directly or indirectly.

1.2.1 Cultivation effects

For cultivation effects where prey C directly outcompete or consume juvenile predators J and are consumed by adult predators P, we start with the model of Baskett et al. 2006 (eqns. A1-A3). This model follows a standard Lotka-Volterra competition and predation formulation, with intrinsic juvenile growth given by total predator consumption. Modifying the original model to have a carrying capacity term K shared among juveniles and prey ($K_J = K/\alpha_{JJ}$, $K_C = K/\alpha_{CC}$), the original model reads

$$\frac{dC}{dt} = rC(1 - \alpha_{CC}CK^{-1} - \alpha_{JC}JK^{-1}) - \delta_C PC \tag{S7}$$

$$\frac{dJ}{dt} = P(\beta_J\delta_J J + \beta_C\delta_C C)(1 - \alpha_{JJ}JK^{-1} - \alpha_{CJ}CK^{-1}) - (\delta_J P + \gamma)J \tag{S8}$$

$$\frac{dP}{dt} = \gamma J - mP. \tag{S9}$$

We first simplify the model by assuming negligible predator cannibalism ($\delta_J = 0$), that juveniles have no competitive effect on prey ($\alpha_{JC} = 0$), and negligible competition among

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juveniles ($\alpha_{JJ} = 0$). This assumption reflects the case where juvenile body size (and consequently resource consumption) is smaller than that of prey, and may be biologically inaccurate in pristine systems with very high juvenile predator abundance. Second, we assume that juveniles can quickly mature to become adults ($\gamma >> 0$) and a high adult reproductive potential ($\beta_i >> 0$) such that juvenile abundance reaches steady state faster than prey or predator abundance. With these simplifications, steady state juvenile abundance is

$$\bar{J}(P, C) = \gamma^{-1}\beta_C\delta_C PC(1 - \alpha_{CJ}CK^{-1}). \tag{S10}$$

Substituting this expression into predator dynamics yeilds the final set of equations

$$\frac{dC}{dt} = rC(1 - \alpha_{CC}CK^{-1}) - \delta_C PC \tag{S11}$$

$$\frac{dP}{dt} = \beta_C\delta_C PC(1 - \alpha_{CJ}CK^{-1}) - mP. \tag{S12}$$

These dynamics reflect the form of eqns. 3-4 in our main analysis, where larger f corresponds to stronger competitive effect of prey on juveniles.

1.2.2 Consumer habitat loss effects

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 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 yeilds:

$$\frac{dA}{dt} = r_A A(1 - AK_A^{-1}) - \delta_A AU \tag{S13}$$

$$\frac{dU}{dt} = a\delta_A AU - \delta_U UP \tag{S14}$$

$$\frac{dP}{dt} = b\delta_U UP(1 - f_c + f_c AK^{-1}) - mP. \tag{S15}$$

We simplify these dynamics to reflect the fact that urchins can overgraze kelp forests within weeks ($\delta_A >> 0$), while at low urchin densities kelp grow rapidly and reach carrying capacity within several months ($r_A >> 0$). 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

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this term into urchin and predator dynamics yeilds

$$\frac{dU}{dt} = a\delta_A K_A(1 - U\delta_A/r_A)U - \delta_U UP \tag{S16}$$

$$\frac{dP}{dt} = b\delta_U UP(1 - f_c U\delta_A/r_A) - mP. \tag{S17}$$

Which gives eqns. 3-4 with $K = r_A/\delta_A$ and $r = a\delta_A K_A$.

1.3 2-species bifurcation analysis

In the case of a single consumer feeding on a single resource, both the specialized (palatability) and the aggregate (recruitment) feedbacks simplify to the same dynamics characterized by a strong consumer Allee effect. We first focus on the consumer mortality level at which the consumer-dominated equilibrium disappears in a saddle-node bifurcation. For simplicity, we assume $\beta = 0$. Solving the equation of the consumer dynamics at equilibrium ($\dot{C} = 0$) for the equilibrium resource abundance $\bar{N}$ when both species are present gives

$$\bar{N} = \frac{b\delta \pm \sqrt{b^2\delta^2 - 4b\delta f K^{-1} m}}{2b\delta f K^{-1}}. \tag{S18}$$

This shows there can be two positive coexistence equilibria, with the lower unstable and the higher stable. The exception happens when the two equilibria meet at $b^2\delta^2 - 4b\delta f K^{-1} m = 0$, producing the bifurcation. Solving for m gives the mortality level above which consumers collapse $m_{collapse} = b\delta K/4f$. Consumers recover (and the resource-only state becomes unstable) at a level of mortality below $m_{recover}$ for which they can invade the system with resources initially at their consumer-free equilibrium $\bar{N} = K$. Solving for the point where the consumer growth rate becomes positive, $0 = b\delta\bar{N}\Phi(1 - f\bar{N}K^{-1}) - m$, gives $m_{recover} = b\delta K\Phi(1 - f)$. Thus, the size D and center L of the bistability region with respect to mortality are:

$$D = m_{collapse} - m_{recover} = b\delta K\left(\frac{1}{4f} - \Phi(1 - f)\right) \tag{S19}$$

$$L = \frac{m_{collapse} + m_{recover}}{2} = \frac{1}{2}b\delta K\left(\frac{1}{4f} + \Phi(1 - f)\right). \tag{S20}$$

Critically, in the two-species case the above analysis gives identical locations L and ranges D of mortality leading to alternative stable states for the palatability and the recruitment feedbacks because they share the same consumer dynamics. 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 D. This reflects that stronger interactions promote bistability by reinforcing feedback loops. The change in location and extent of the hysteresis range with consumer grazing here also underscores the importance of holding total consumption constant as we evaluate the effect of increased food web connectance on alternative stable states in our main analysis.

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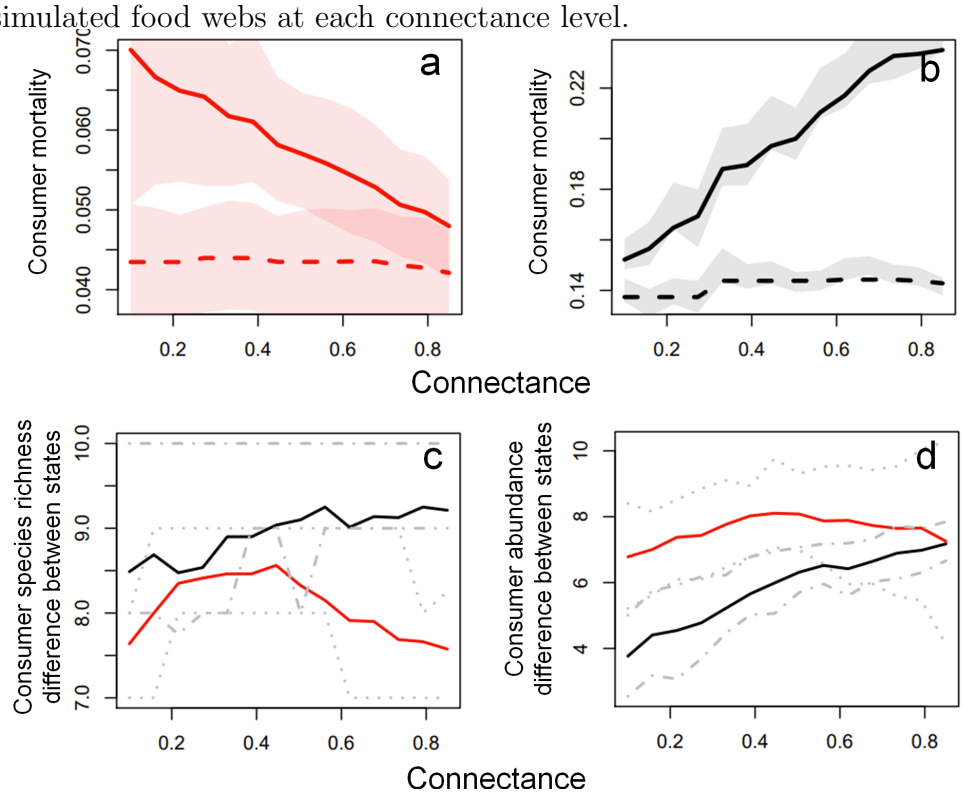
Appendix B: Dynamics with explicit stage structure

Here, we verify that the greater potential for aggregate feedbacks to produce alternative stable states remains in more complex models explicitly accounting for resource or consumer stage structure. For specialized feedbacks, we implement eqns. S7-S9 with mean parameter values $r = 1$, $\delta = 1.2$, $b = 1$, $g = 0.02$, and $\gamma = 0.5$. For aggregate feedbacks, we implement eqns. S7-S9 with the simplifications $\delta_J = 0$, $\alpha_{JC} = 0$, and $\alpha_{JJ} = 0$ which retain stage structure and the key cultivation-depensation feedback. We set the mean values of the remaining parameters to $r = 1$, $K = 1.1$, $\delta_C = 1.1$, $\beta_C = b = 1$, $\alpha_{CJ} = f = 1.5$, and $\gamma = 0.3$. Following the main text, we also incorporate the matrix of consumer-juvenile interactions $\mathbf{\Psi}$ here denotes how much each consumer affects each predator juvenile. Finally, following our multi-species analyses in the main text, for both models we incorporate density-dependent predator mortality $\beta_P = 0.075$, among-resource competition $\alpha = 0.025$, and the matrix of trophic connectance $\mathbf{\Omega}$. With these parameters and a species heterogeneity 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.



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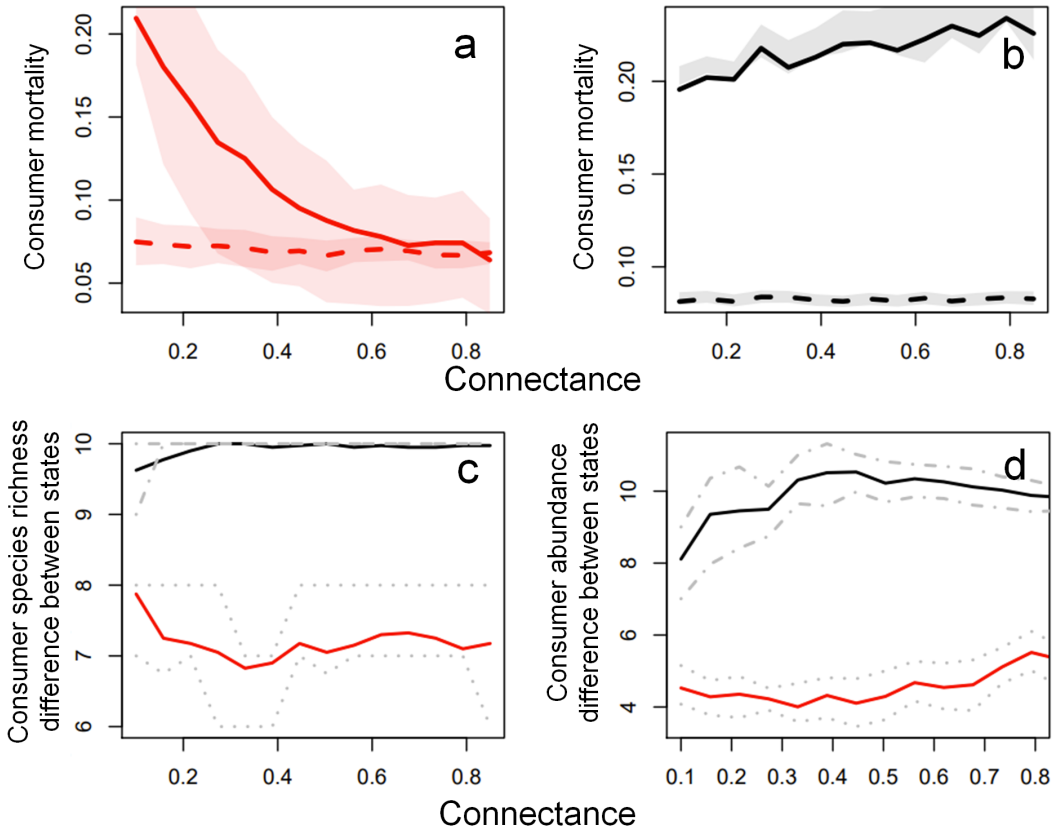
Appendix C: Dynamics without consumer density dependence

Here, we verify that the greater potential for aggregate feedbacks to produce alternative stable states remains without consumer density dependence, i.e., $\beta = 0$. To reduce among-consumer competition we change mean parameters slightly to $\delta = 1.15$ and $K = 1.1$, model lower species heterogeneity of 0.1 (vs. 0.15 in the main text), and omit two consumer species (i.e., modeling 12 resources and 8 consumers).

Figure S3: 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.



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Appendix D: Effects of specialization in recruitment and palatability interactions

Here, we expand our main analysis to consider how the potential for alternative stable states depends on both connectivity consumer diet $\mathbf{\Omega}$ as well as specialization in palatability interactions $\mathbf{\Gamma}$ and in recruitment interactions $\mathbf{\Psi}$. Biologically, our analyses explore four scenarios. First, palatability feedbacks involving size-dependent consumption may be less specialized than in our main analysis (where we assume $\mathbf{\Gamma}$ is an identity matrix) 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. Second, palatability feedbacks involving group defense may likewise be less specialized when resource species form multi-species herds, schools, or plant stands to deter consumption. Third, for recruitment feedbacks, we consider higher degrees of specialization, where close temporal or spatial overlap cause the survival of a consumer's juveniles to depend predominantly on the abundance of only a few resource species. Finally, we consider recruitment feedbacks where strong spatial structure (or, equivalently, relatively immobile adult consumers) where consumers eat the same resources that affect their young (i.e., $\mathbf{\Psi} = \mathbf{\Omega}$).

Throughout, we define specialization S in interactions as the mean maximum weight of palatability dependence of one resource i on any other resource j ($= 12^{-1} \sum_i \max_j(\Gamma_{j,k})$) and, equivalently, the mean maximum weight of recruitment dependence of one consumer k on any resource i ($= 10^{-1} \sum_k \max_i(\Psi_{i,k})$). This metric is analogous to consumer electivity for its primary resource (Fig. 3). For both $\mathbf{\Psi}$ and $\mathbf{\Gamma}$, we draw entries 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 than with palatability feedbacks over all levels of connectance and feedback specialization (Fig. S4). 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 palatability 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 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 where leads to $\mathbf{\Psi} = \mathbf{\Omega}$.

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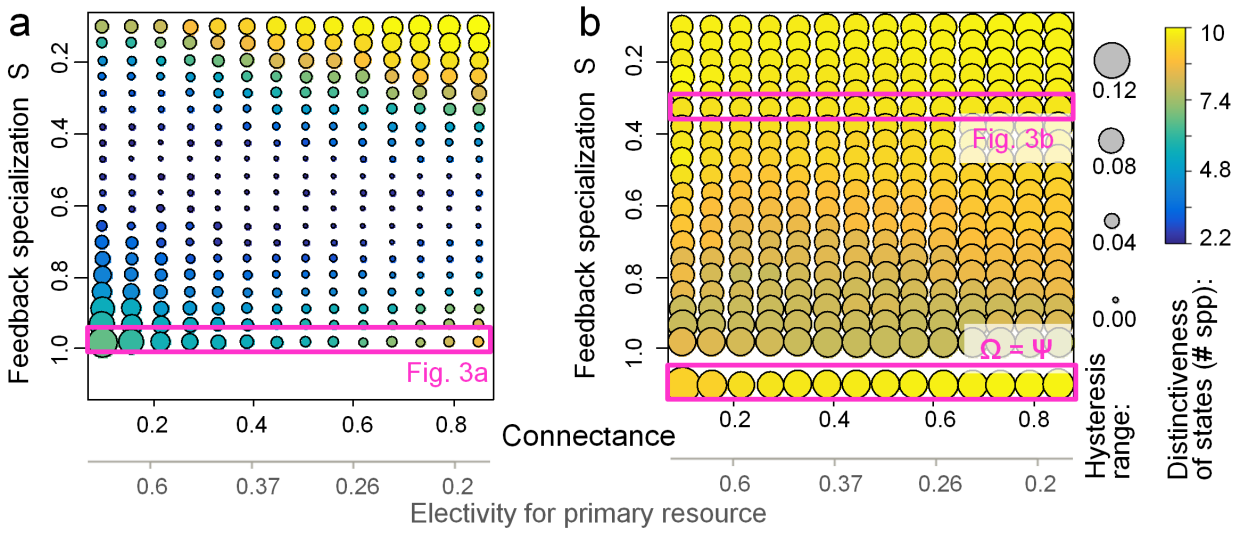
Figure S4: Palatability feedbacks (a) decrease the potential for alternative stable states compared with recruitment feedbacks (b) over all levels of connectance and feedback specialization S. Points at each connectance and specialization level denote the distinctiveness of alternative stable states (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 80 simulated food webs. The secondary x-axis denotes the fraction of diet comprised by each consumer's primary resource when resources are equally abundant, averaged across all consumers (i.e., Ivlev electivity, $= 10^{-1} \sum_k \max_i(\Sigma_{i,k})$), and is analogous to feedback specialization.



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