Prey body mass and richness underlie the persistence of a top predator

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Predators and prey often differ in body mass. The ratio of predator to prey body mass influences the predator’s functional response (how consumption varies with prey density), and therefore, the strength and stability of the predator–prey interaction. The persistence of food chains is maximized when prey species are neither too big nor too small relative to their predator. Nonetheless, we do not know if (i) food web persistence requires that all predator–prey body mass ratios are intermediate, nor (ii) if this constraint depends on prey diversity. We experimentally quantified the functional response for a single predator consuming prey species of different body masses. We used the resultant allometric functional response to parametrize a food web model. We found that predator persistence was maximized when the minimum prey size in the community was intermediate, but as prey diversity increased, the minimum body size could take a broader range of values. This last result occurs because of Jensen’s inequality: the average handling time for multiple prey of different sizes is higher than the handling time of the average sized prey. Our results demonstrate that prey diversity mediates how differences between predators and prey in body mass determine food web stability.

1. Introduction

Challenging the long-standing view that diversity promoted stability, Levins [1], Gardner & Ashby [2] and later May [3] concluded that diverse networks are more unstable than simple ones. Yet, most natural communities comprise complex, interconnected networks where species depend on other species for food and compete with other species for resources [4–6]. To address this discrepancy, researchers have focused on the non-randomness of food webs [7]. For example, compartmentalized food webs—where a subset of species interact more commonly among themselves—persist longer than randomly distributed food webs [8]. Similarly, a food web that contains more weak than strong interaction strengths is more stable than a food web with randomly distributed interaction strengths [9–11].

The distribution of interaction strengths in a food web determines the stability of the whole system [12–14]. In food webs, one weak interaction among multiple species interactions can stabilize other interactions. For example, when two prey species share a predator population, the prey with the weaker interaction with the predator can reduce the efficiency of the predator in attacking the other prey, stabilizing an otherwise strong and destabilizing interaction [10]. Similarly, omnivory can increase the stability of simple food chains [15], and increasing the prevalence of omnivory modules in a food web increases the web’s persistence [16]. Generally, food webs become stable when the distribution of interaction strengths is broad (i.e. contains both weak and strong interactions).

The stability and persistence of food webs therefore depends on the mechanisms that determine interaction strengths between species. One important determinant of interaction strengths, at least among animals, is the relative body masses of predators and prey [13,17]. For example, an empirical test
with crustacean predators showed that the predator–prey body mass ratio is correlated with the \textit{per capita} interaction strength [13]. The \textit{per capita} interaction strength between predators and prey depends on the predator’s functional response (the relationship between predation rate and prey density). How the predator’s functional response is modelled is in turn determined by two parameters that depend on the body mass of both the predator and the prey [17]: the attack rate (a measure of a predators hunting efficiency) and the handling time (the amount of time needed to kill, ingest and digest an individual prey) [18–21]. Similarly, the conversion efficiency from consumed prey into predator biomass also depends on the body mass of the predator and the prey [22,23]. This relationship between the ratio of predator and prey body masses and interaction strength has been integrated into population dynamic models, specifically by relating interaction strengths to the mean body masses of interacting species. Using these models, ecologists have found that species persistence is restricted to a narrow range of prey body mass relative to that of their predator—specifically predator–prey body mass ratios between 10 and 100 for both invertebrate and vertebrate predator–prey pairs [14,24,25]. Persistence is restricted to these intermediate body mass ratios because at high body mass ratios, population dynamics are unstable and at low body mass ratios, the predators do not consume enough energy to persist. This body of literature has allowed ecologists to understand when pairwise predator and prey interactions are unstable, and how the presence of other species’ populations may stabilize those interactions. Yet, we still do not know if predator and prey persistence requires that all the body mass ratios between the predator and its prey species are intermediate in value. Jensen’s inequality suggests that when relationships are not linear, such as the relationship between attack rate and handling time with body mass, then variation in body size within a prey population (or among prey species consumed by the predator) can alter the average interaction strength, thereby influencing the dynamics of the system [26]. Given Jensen’s inequality, it is not clear if the narrow range of intermediate body mass ratios that increase food chain persistence (food chains have one consumptive link between trophic levels) are also required to increase the persistence of large food webs (multiple consumptive links between trophic levels). We took a three-pronged approach to answering these questions. First, we empirically determined how body mass ratios between a generalist predator and various prey species of different size affect the functional response parameters of a natural food web: the aquatic invertebrates that inhabit bromeliads. Although previous studies have examined this question by pooling data between systems, the same pattern may not apply within a system—and it is at this scale that the allometric effects of body size on food web persistence are relevant [17]. We then used this empirically derived allometric functional response to simulate a food web with one predator and multiple prey, and confirmed that predator and prey persistence was maximized at intermediate prey body masses when the predator had only one prey. Finally, we tested (i) how differences between prey species in body mass affect the persistence of the entire food web or subcomponents and (ii) how the number of prey species affects the distribution of prey body masses required for persistence of the entire food web or subcomponents.

2. Methods

(a) Study system

Tank bromeliads accumulate water inside their leaf axils, providing habitat for communities of aquatic macroinvertebrates [27]. Inside each bromeliad, these aquatic macroinvertebrates interact to form a food web comprised detritivores, filter feeders, intermediate predators and top predators. All the species we used in our experiment were identified to species or morphospecies level. We distinguished the morphospecies-based multiple characteristics and not on body mass.

(b) Predator consumption rates

We quantified the consumption rate for one damselfly larvae predator and many of its prey. The top predator \textit{Leptagrion andromache} (Zygoptera: Odonata, dry mass = 3.31 mg, s.e. = 2.45, number of individuals measured = 29) was fed several densities of the most abundant prey in bromeliads, all of which are aquatic insect larvae (electronic supplementary material, table SA1). We chose \textit{Culex} sp. 1 (Culicidae: Diptera, density range = 1–50, mean dry mass = 0.17 mg, s.e. = 0.04, number of individuals measured = 25), \textit{Culex} sp. 2 (Culicidae: Diptera, 1–20, 0.09 mg, 0.02, 14), \textit{Fpsoriomycia} (Odonata: Dictyoptera: 1–60, 0.07 mg, 0.01, 5), \textit{Dero superterrenus} (Naididae: Haplotalaxida, 1–60, 0.12 mg, 0.01, 2), \textit{Psychodid} sp. (Psychodidae: 

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\frac{\text{per capita interaction rate}}{\text{per capita interaction rate}} = \frac{\text{per capita interaction rate}}{\text{per capita interaction rate}}
\end{equation}

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\text{per capita interaction rate}
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\text{per capita interaction rate}
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\text{per capita interaction rate}
\end{equation}
functional response, allowing a range of responses including type II ($q = 0$) and type III ($q = 1$). We initially fit a full model with all three parameters ($a$, $h$, and $q$). However, $q$ was not significantly different from zero, and we thus restricted $q = 0$ throughout our analyses (type II functional response). Because the prey were not replaced during the experiment, prey density dropped throughout the experiment as individuals were eaten. While the Roger’s random predator equation has been used to account for prey depletion in functional response experiments [31], we needed to fit a generalized functional response over multiple experiments. Therefore, we used numerical integration to calculate the true proportion of prey consumed [28,32]. This procedure has been made available by Bolker [33].

We calculated a single allometric functional response that allowed the attack rate and handling time to vary with the body mass of the prey and the predator. We fit two different cases. First, we fit simple power law functions (below equations) [34].

$$a = a_0 M_i^a M_p^b, \quad (2.2)$$

and

$$h = h_0 M_i^c M_p^d, \quad (2.3)$$

where $M_C$ is the mass of the consumer and $M_i$ is the mass of the resource. In all cases, $M_C = 3.3$. Second, since we used the same species of predator in all experiments, this allometric functional response need only consider variation in attack rate and handling time with respect to the mean prey body mass. Therefore, we fit these power law functions but simplified the predator term (below equations)

$$a = a_0 M_i^a, \quad (2.4)$$

and

$$h = h_0 M_p^d. \quad (2.5)$$

(e) Food web model

We built a food web model for a predator that consumes any number of prey with a type II functional response. If the model contained two or more prey, then the prey competed for resources.

The abundance of prey is given by

$$N_i(t + 1) = N_i(t) + r(M_i) N_i(t) \left(1 - \frac{N_i(t) + \sum_j N_j(t)}{K(M_i)} \alpha_i N_i(t) \right) - \frac{a(M_i) N_i(t) P(t)}{1 + \sum_j a(M_j) h(M_j) N_j(t)}. \quad (2.6)$$

In the above equation, $N_i(t)$ is the abundance of prey $i$ at time $t$ and $r(M_i)$ is the intrinsic growth rate of prey (equation (2.7)). $P(t)$ is the abundance of the predator at time $t$. The prey experiences logistic growth where its carrying capacity $K(M_i)$ is determined by its body mass $M_i$ (equation (2.8))

$$r = r_0 M_i^a, \quad (2.7)$$

and

$$K = K_0 M_i^c. \quad (2.8)$$

We explicitly added a term, $\alpha_i$, which signified the intensity of competition between prey $i$ and $j$, to our equation, as otherwise nonlinear functional responses can transform apparent competition into apparent mutualism [35]. The attack rate, $a(M_i)$, as well as the handling time, $h(M_i)$, are determined by the body mass $M_i$ of prey $i$ as given by equations (2.4) and (2.5).

The intensity of competition $\alpha_i$ was dependent on the amount of niche overlap, which was given by the body mass of the prey

$$\alpha_{ij} = \frac{(M_{ij} - M_{ij}^0)^2}{2a_i^2}, \quad (2.9)$$

where $M_{ij}$ is the body mass of species $i$ and $M_{ij}$ is the body mass of species $j$, $a_i$ represents the niche width. The competition coefficient is based on a decaying function between the body masses of species $i$ and $j$ [36]. This equation assumes that competition is symmetrical. Evidence suggests that larger organisms outcompete smaller ones, and that competition is often asymmetrical [37].

We evaluate this scenario in electronic supplementary material, appendix S2 using the following equation

$$a_i = \left(1 + \left(M_i - M_j + \beta)/(2a_i^2)\right) \left(1 + \beta^2/2a_i^2\right), \quad (2.10)$$

where $\beta$ determines the asymmetry of the competition coefficients [38]. When $\beta = 0$, competition is symmetric [36], on the other hand, when $\beta > 0$, the competition is asymmetric, where larger individuals outcompete smaller individuals.

The growth of the predator results from the sum of the consumption all prey species, determined by their individual attack and handling time [39]. The abundance of the predator is therefore given by

$$P(t + 1) = P(t) + \frac{P(t) \sum_i B_i a(M_i) N_i(t) - CP(t)}{1 + \sum_i a(M_i) h(M_i) N_i(t)} \quad (2.11)$$

where $P(t)$ is the abundance of the predator at time $t$. The per capita mortality rate of the predator is $C$, $B$ is the standard conversion efficiency, which converts prey biomass into predator biomass. This conversion efficiency varies as a function of prey and predator body mass

$$B = GGE \frac{M_p}{M_i}. \quad (2.12)$$

where $GGE$ is the gross growth efficiency [23]. Since the mass of the predator was constant throughout the model, we simplified this equation to

$$B = GGE \frac{M_i}{M_i}. \quad (2.13)$$

(f) Simulations based on all possible combinations

We ran the simulation for prey body masses starting at 0.05 mg and increasing at 0.01 mg intervals until reaching 1 mg.

For the one and two prey scenarios, we ran every combination of prey body masses. The starting abundances were 10 individuals for each prey and seven individuals for the predator. All simulations were run for 500 time steps. As previously mentioned, the attack rate, handling time, intrinsic growth rate of the prey, the carrying capacity and the conversion efficiency were all determined by the body mass of the prey (table 1; electronic supplementary material, figure S1).

(g) Simulations based on sampled parameter space

Scenarios with three or more prey are computationally difficult, as the potential combinations of prey body masses increase exponentially with the number of prey. Fortunately, a recently proposed Monte Carlo strategy for sampling parameter space helps to make this tractable [41]. In this sampling process, we begin by defining a binary outcome of interest as $R$ specific. This sampling process allows us to estimate the conditional probability of a set of parameter values, given that the predator persisted (see details in electronic supplementary material, appendix S1). The outcomes $R$ that we required were that (i) all species survived, (ii) only prey survived, and (iii) at least one prey and the predator survived.

We ran the sampling process for 10 000 steps for one and two prey and for 20 000 steps for three or more prey. For the first 10 000 steps, we used a variance for the step size of 0.3, and then increased this to 0.5 for the next 10 000 steps. Parameter space was well sampled with the Monte Carlo sampling strategy (electronic supplementary material, figure S2).
To examine the impact of Jensen’s inequality on food web dynamics, we compared parameters of the functional response calculated as the mean for all species versus based on the mean mass of the species. Specifically, for every run where all the prey species and the predator persisted, we calculated the attack rate and the handling time for each prey species and averaged these values over species to obtain $a(m)$ and $h(m)$. Then we averaged the body mass of all prey species before calculating the attack rate and the handling time to obtain $a(M)$ and $h(M)$. Owing to the nonlinearity and the upward curvature of the attack rate and the handling time with body mass (electronic supplementary material, figure SA1), we would expect that $a(m) = a(M)$ and $h(m) = h(M)$ only when prey diversity is one. We refer to diversity as the number of prey species. As diversity increases, we expect that $a(m) > a(M)$ and $h(m) > h(M)$ (electronic supplementary material, figure SA5).

All analyses were performed using R [42] and the bbmle package [43].

3. Results

(a) Allometric feeding rates

We compared two models that describe the relationship between feeding rate and prey body mass: (i) a power law function and (ii) a power law function with the predator terms simplified (figure 1). Of these two cases, the model with the lowest BIC was the power law function with the predator terms simplified ((i) $D\Phi = 6$, $BIC = 720.3538$; (ii) $D\Phi = 4$, $BIC = 664.7065$).

(b) Simulation

We found that one predator–one prey food chains could not persist when the prey species was very small. In this case, the attack rate of predators on prey is so high that the predator

![Figure 1](https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2019.0622)

**Figure 1.** (a–c) Fitted type II functional response for all prey species (different colours represent different species) separated in the three panels into small, medium and large prey species. Prey body mass is calculated on a per species basis as the mean of all individuals of that species in the experiment.

**Table 1.** The parameter values used for the simulations of the food web and their relationship with the body mass of the prey. Assigning $k = -1$ implies that $K_0m$ is constant. GGE was obtained from previous experiments that estimated the assimilation efficiency of damselflies [40]. For all the parameters in the attack rate and handling time, $p < 0.001$.

<table>
<thead>
<tr>
<th>parameter</th>
<th>description</th>
<th>body mass scaling</th>
<th>estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>attack efficiency of the predator</td>
<td>$a = a_0M^{a_0}$</td>
<td>$a_0 = 0.014$, $a_0 = -1.33$</td>
</tr>
<tr>
<td>$h$</td>
<td>handling time of the predator</td>
<td>$h = h_0M^{h_0}$</td>
<td>$h_0 = 23.36$, $h_0 = 2.40$</td>
</tr>
<tr>
<td>$K$</td>
<td>carrying capacity of the prey</td>
<td>$K = k_0M^k$</td>
<td>$k_0 = 6$, $k = -1$</td>
</tr>
<tr>
<td>$r$</td>
<td>maximum population growth rate of the prey</td>
<td>$r = r_0M^r$</td>
<td>$r_0 = 0.05$, $r_0 = -0.2$</td>
</tr>
<tr>
<td>$B$</td>
<td>conversion efficiency</td>
<td>$B = GGE \times M$</td>
<td>$GGE = 0.8$</td>
</tr>
<tr>
<td>$C$</td>
<td>predator death rate</td>
<td>constant</td>
<td>0.4</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>niche width</td>
<td>constant</td>
<td>0.025</td>
</tr>
<tr>
<td>$\beta$</td>
<td>degree of asymmetry in competition function</td>
<td>constant</td>
<td>0 (0.5 in electronic supplementary material, appendix S2)</td>
</tr>
</tbody>
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consumed the prey quickly, driving the prey species extinct, which consequently led to the collapse of the predator population (figure 2a). On the other hand, when the one prey was large, the handling time was so long that the predator could not meet its energetic demands (figure 2c). Only at intermediate body masses of the prey were both prey and predator able to persist through time.

Similarly, when two prey species were present, the predator required at least one prey to have an intermediate body mass in order for the predator to persist (figure 3a). Surprisingly, the body mass of the second prey could be almost any mass except for very small, including a prey body mass that was so large that, on its own, the prey could not sustain the predator. When the body mass of the second prey was small, only the predator and the larger of the two prey persisted, as the smallest prey was driven to extinction due to the high attack rate of the predator (figure 3c). By contrast, when both prey species were very small, the whole community went extinct, and when both prey species were very large, the prey persisted, but the predator went extinct (figure 3b).

Figure 2. Time series for the abundance of the predator and one prey at three different prey body masses. Predator and prey persistence is maximized at intermediate prey body masses. (a) When the prey is small (0.25), the attack rate of the predator is very high and the predator consumes all the prey, driving the prey and itself extinct. (b) When the prey has intermediate body mass (0.40), both predator and prey can persist. (c) When the prey has high body mass (0.90), the handling time is too long and the predator is limited by the amount of energy it can obtain.

Figure 3. Predator persistence is constrained only by the body mass of one prey, where one prey must have an intermediate body mass, but the second prey can be of any mass. On the x-axis is the body mass of prey 1, and on the y-axis is the body mass of prey 2. (a–c) The combinations parameter space with a certain outcome, where yellow represents that the outcome of interest is present and purple is absent. The outcome of interest is whether: (a) both prey species and the predator persist; (b) the predator goes extinct and only the two prey persist; (c) one prey and the predator persist and one prey goes extinct (in every case, the smaller prey). These scenarios are detailed in the food web modules: the grey circles represent species that go extinct and the black circles represent species that persist.
We only observed competitive exclusion in the presence of the predator. When the predator went extinct, competition between prey only generated differences in their abundances (electronic supplementary material, figures SA3 and SA4).

In food webs with more than two prey species, predator persistence shows a unimodal relationship with prey diversity, increasing with modest numbers of prey species but decreasing with larger numbers of prey species (figure 4a). Within this overall effect of prey diversity, different effects of prey body mass can be discerned. At low prey diversity, predator persistence requires the prey communities have neither small nor large species (figure 4b,c). At high prey diversity, predator persistence increases when large prey are added to the community (figure 4c). Regardless of prey diversity, predator persistence decreased as the proportion of the community with small prey increased (figure 4b). By contrast, the proportion of prey species that strongly competed had only modest effects on predator persistence (electronic supplementary material, figure SA6). Although these results pertain to the initial prey diversity, the patterns are unchanged even when we use the final prey diversity as the determinant (electronic supplementary material, figure SA7).

For a given diversity of prey, we found that food web persistence requires a minimum body mass for at least one prey species. As prey diversity increases, this minimum body mass first takes a wider range of values, but at high prey diversity again is constrained to a narrow range of values (figure 5a). The broadening of the minimum body mass that allows all species to persist is due to the increasing importance of Jensen’s inequality as we increase prey diversity. When we plotted $\hat{a}(m)$ against $\hat{a}(m)$ and $\hat{b}(m)$ against $\hat{b}(m)$ (figure 5b,c), we find that for both parameters, the effective attack rate or handling time initially increases with diversity and then decreases. All scenarios, when prey diversity is greater than one, fall above the 1 : 1 line. Therefore, initially, as prey diversity increases, the attack rate and the handling time increase allowing the predator to persist at larger body masses (figure 5c). As diversity continues to increase, the effective attack rate decreases more than the effective handling time, reducing the body masses of the prey where the predator can persist.

4. Discussion

In this study, we tested: (i) how differences in body mass between prey species affect the persistence of an apex predator and its various prey in the bromeliad food webs, and (ii) how the diversity of prey determines the distribution of prey body masses needed for an apex predator persistence. We found that when the predator had one prey, predator persistence required the prey to be of intermediate body mass. As prey diversity increased, the range of prey body masses that allowed for predator persistence became first broader and then narrower. We also found that prey diversity had a unimodal relationship with predator persistence. At low prey diversity, increasing diversity increased predator persistence, whereas, at high prey diversity, increasing diversity decreased predator persistence. Furthermore, the effects of prey body mass on predator persistence reversed between low and high prey diversity conditions. We now consider each of these main results.

We found that the effect of prey body mass on the functional response of damselfly larvae in bromeliads largely conformed to previously estimated forms of the allometric functional response (e.g. [17,44]). While this points to a qualitative generality in the effect of body mass on functional responses, we caution against any quantitative extension of
Inequality has a greater impact on handling time, as the mean handling time, deviation from the 1:1 line is particularly pronounced at low prey diversity, and approaching the 1:1 line at high diversity. These studies found that intermediate predator–prey body mass, but with a narrow range of body masses [14]. Our results also are consistent with previous observations that weak interactions can stabilize a system with strong interactions [10].

Figure 5. Food web persistence depends on the number of prey and the body mass of the smallest prey species. Circles of different colours represent food webs that successfully persisted. (a) Some combinations of prey number and smallest body mass did not lead to food web persistence, due either to extinction of at least one prey (shaded red area) or predator extinction (shaded blue area). The food web modules illustrate these scenarios of food web persistence and extinction; the dashed circles represent species that may, but do not necessarily go extinct, the grey circles represent species that go extinct and the black circles represent species that persist. (b) Jensen’s inequality is demonstrated by the mean attack rate, \( a(m) \), being higher than the attack rate on a species with mean mass \( a(m) \), but this effect is strong at low diversity and weak at high diversity, given the deviation from the black 1:1 line. As diversity increases, both \( a(m) \) and \( a(m) \) decrease. (c) Jensen’s inequality has a greater impact on handling time, as the mean handling time, \( h(m) \), is higher than the handling time on a species with mean mass, \( h(m) \). The deviation from the 1:1 line is particularly pronounced at low prey diversity, and approaching the 1:1 line at high diversity.

Our first main result from the model was that predator persistence increased when its sole prey had an intermediate body mass. As in other studies [14,25], this occurred because of the opposing effects of body mass on two parameters of the predator’s functional response. If the prey had a very small body mass, then the predator had a high attack rate and consumed all prey individuals, driving the prey and itself extinct. If the prey had a large body mass, then the predator had a long handling time and it could not offset its mortality via reproduction and went extinct. Even when the food web contained multiple prey, only the body mass of the smallest prey constrained predator persistence; the body mass of the other prey species could be either large, intermediate or small. This result is consistent with the case of asymmetrical competition between the prey, as long as the prey can coexist (electronic supplementary material, appendix S2). These results extend previous studies of the effects of prey body mass on food web stability, which either considered only a single prey species [25] or multiple prey species but with a narrow range of body masses [14]. These studies found that intermediate predator–prey body mass ratios maximize food web persistence, similar to our single prey results. Our novel result is that with a wide range of prey body masses, persistence depends on the smallest prey being of intermediate body size.

Even though the body mass of only one prey species constrained predator persistence, this optimal body mass—that is, the body mass that maximizes predator persistence—may still change with increasing diversity. Indeed, we found that increasing prey diversity broadens and then narrows the range of body masses that promote predator persistence. Prey with body masses too large to allow predator persistence on their own, could, as part of a diverse prey community, now allow the predator to persist. The mechanism here relates to Jensen’s inequality: since the attack rate and the handling time are nonlinear with respect to prey body mass, variation around the mean body mass (i.e. when diversity increases) increases the effective attack rate and handling time. Therefore, the predator experiences a much higher attack rate and handling time than expected from the mean body mass of all prey, allowing the predator to persist when otherwise it would not [26]. Intermediate prey diversity effectively relaxes the bottom-up energetic constraint imposed by having only one prey, allowing the attack rate and the handling time to be higher and resulting in an overall high total intake for the predator. Gibert & DeLong [49] found a similar pattern, where the predator’s total intake is maximized at low diversity when prey is optimally matched in phenotype (e.g. body mass) to the predator and maximized at higher diversity when the prey is poorly matched in phenotype to the predator.
between predators and prey determined interaction strength: prey species with a small body mass had strong interactions with the predator, whereas prey species with a large body mass had weak interactions with the predator. When a predator had a strong interaction with one prey, leading to the extinction of both the predator and the prey, adding a large prey species would often allow the predator to persist. We found, consistent with McCann et al. [10], that adding a large prey would stabilize many strong interactions between a predator and a small prey. This was not true for very small prey, which could not be stabilized even in diverse communities (e.g. figure 3).

So far, we have shown that predator persistence is constrained by the presence of at least one prey of intermediate body mass. This result helps explain why, at low prey diversity, adding more prey species can increase persistence of the predator: increasing diversity increased the probability that at least one prey has the optimal body mass. This sampling mechanism is consistent with models that show only intermediate body mass ratios between predators and prey can result in a positive relationship between food web stability and prey diversity [14]. However, our analysis not only allows us to confirm this result, but also to test the interaction between body mass ratios and diversity. We discovered that prey diversity had a unimodal relationship with predator persistence, which is mediated by the body mass distribution of the prey. The increasing portion of this relationship, at low prey diversity, reflects sampling of an optimal body mass prey. At high prey diversity, adding prey species generally decreased predator persistence, but this depends on the body mass distribution of added prey. Specifically, adding large prey species increased predator persistence, whereas adding intermediate and small prey species decreased predator persistence. As before, the mechanism here is a weakening in interaction strength as prey body size increases relative to that of their predator, allowing for stabilization of the whole food web [10]. Consequently, we found that the food webs with the highest prey diversity at the end of the simulation comprised many large prey species. This result, however, is different when prey compete asymmetrically. In this scenario, higher diversity only reduces predator persistence. Adding small prey species has the same effect as in the symmetrical competition scenario, but adding large prey species now decreases predator persistence since large species drive intermediate species extinct due to competition (electronic supplementary material, appendix S2). The implication of the symmetrical competition results is that we would expect the largest food webs in nature to have large-sized prey relative to their predators. Some food webs have shown a pattern where slow energy channels, which have weaker interactions, are more diverse than fast energy channels [50]. An explanation of this pattern is that habitat complexity promotes both diversity and weaker interactions. Another explanation can be that slow channels with weaker interactions are more stable. Our results would support the latter explanation.

Taken together, these results suggest that: (i) only a few prey species, not all, constrained predator persistence; (ii) increased prey diversity can lead to increased predator stability if the additional prey contain at least one species of optimal body mass (low prey diversity) or enough large prey to weaken interactions with the predator (high diversity). That is, not all diversity is equal in terms of food web stability: the body mass of those gained or lost species has major consequences for the stability of food webs. This conclusion buttresses earlier findings that food web stability is more influenced by variation in the body mass ratios of predators and prey than by prey diversity alone [14]; (iii) the food webs we see in nature are only the observed surviving configurations. We expect that larger food webs will be skewed towards having larger prey species per predator when competition between prey is symmetrical.


Competing interests. We declare we have no competing interests.

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