

Research

Prey diversity constrains the adaptive potential of predator foraging traits

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Predators are generally under selective pressure to get better at foraging, leading to steeper functional responses and stronger predator–prey interactions. Yet strong interactions can de-stabilize food webs, and most interactions across ecological communities are thought to be weak. This conflict between evolutionary and community expectations for the strength of predator–prey interactions represents a fundamental gap in our understanding of how the evolution of foraging plays out in food webs. Here we help to resolve the conflict by showing analytically that the expectation for the evolution of steeper functional responses is relaxed in communities with diverse prey types. We simulate communities with varying prey richness and show that increasing prey richness can indeed constrain the adaptive potential of predator foraging traits, but that at low prey richness predators can evolve to have a stronger interaction with prey that have high net energy yields. Our results also indicate that handling time plays a role in determining whether predators may evolve to have a stronger interaction with abundant prey, suggesting that the evolution of keystone predator modules in food webs is most likely when handling times are negligible. Our results also provide a new mechanism predicting more diffuse interactions in diverse tropical communities relative to more species-poor communities at higher latitudes.

Keywords: eco-evolutionary dynamics, food web stability, functional response, GEM, keystone predator

Introduction

The structure and function of ecological communities is highly dependent on consumer–resource interactions. Which interactions are present and their strength determine the flow of energy through food webs, the dynamics of interacting populations and the aggregate fluxes of nutrients in ecosystems (Lindeman 1942, Carpenter et al. 1985, Cohen et al. 1993, McCann 2011, Moore and de Ruiter 2012). How interaction strengths are set, then, is fundamental to understanding biological processes across multiple levels of organization (Novak 2010, Gilbert et al. 2014).

Community and evolutionary ecology perspectives lead to differing views on the forces driving variation in interaction strengths. At the level of individuals, predator

fitness depends on the ability to consume prey. Natural selection therefore generally should favor traits that confer improvements in the ability of predators to find, detect and successfully capture prey (Abrams 2000, DeLong 2021). In contrast, food webs become less stable when a large proportion of interaction strengths are high, suggesting that interactions should be weak overall because some level of species persistence is required to even have an ecological community (May 1972, McCann et al. 1998, Borrelli et al. 2015). These two views suggest that we lack a clear mechanism for evolution to not destabilize consumer–resource based systems by strengthening predator–prey interactions. Although there are mechanisms that might stabilize systems given that a strong interaction exists, such as interference competition (Arditi et al. 2004), prey-switching (Oaten and Murdoch 1975) and specific body-size scaling patterns (Brose et al. 2006), these mechanisms do not diminish the expectation that natural selection may increase the strength of interactions generally. As it is not clear whether stabilizing mechanisms are sufficient to generate observed patterns of stability in ecological systems, an alternative hypothesis is that those interaction strengths are not generally that strong to begin with.

Part of the conceptual divide is that the evolutionary expectations emerge from considering pairwise, or only a few, consumer–resource interactions (Abrams 2000, Peacor and Werner 2004). Many predators, however, have very broad diets (Hector 1985), indicating a need to understand selection on traits that influence interaction strengths in the presence of multiple prey types. Here, we directly evaluate the effect of the number of prey types on the evolution of predator–prey interactions. Using both an analytical and simulations-based approach, we show that increasing the number of prey types available reduces the expectation that natural selection would generally tend to increase interaction strengths. This result helps to resolve the conflict between community and evolutionary ecology expectations and generates new ideas about the role and effect of prey diversity on predator evolution in food webs.

Selection on the functional response

Interaction strengths can be written in a variety of ways, but all interaction strength metrics are some quantity that reflects the relative importance of predation to the abundance and/or fitness of the interacting species (Wootton and Emmerson 2005, Novak 2010, Gilbert et al. 2014). A key component of the interaction strength for predator and prey is the functional response, which is the relationship between the per capita foraging rate f_{pc} of the predator and prey abundance R (Solomon 1949, Holling 1959):

$$f_{pc} = \frac{a_1 R_1}{1 + a_1 h_1 R_1} \quad (1)$$

where a is the space clearance rate (the rate at which a predator clears space of its prey), and h is the handling time (the reduction in time available for searching due to the capture of prey), here referring specifically to prey type 1 with abundance R_1 . Interaction strength for any given predator–prey pair will be positively related to the space clearance rate (a) but may be dampened by a higher handling time (h).

Because the functional response directly impacts the rate of birth in a predator, increasing a or decreasing h will increase food intake and thus predator fitness (Urban et al. 2020). There has long been an understanding that behaviors and plastic morphologies may alter functional response parameters in different contexts, such as has been proposed for optimal (Charnov 1976) and adaptive (Kondoh 2003) foraging, prey-switching (Oaten and Murdoch 1975) and inducible offenses (Kopp and Tollrian 2003), allowing predators to increase fitness by tailoring predation strategies to the environmental context. Yet, massive variation in functional response parameters across predator–prey pairs and across prey types for particular predators suggests a need to understand the forces that generate average interaction strengths at the population level as well (Roberts et al. 2010, Uiterwaal and DeLong 2020). Recent work indicates that there is considerable scope for natural selection to act on a and h given individual variation in functional responses and associated traits (Schröder et al. 2016, DeLong et al. 2021). This individual variation in functional response parameters is both raw material for selection and likely to have impacts on the ecological dynamics of the predator–prey system through non-linear averaging effects on the overall interaction strength (Bolnick et al. 2011, Coblenz et al. 2021).

When it comes to the act of predation, all relevant biological traits associated with the encounter, detection and successful capture of prey are encapsulated in the parameter a (DeLong 2021), so we focus on this parameter here as the functionally important one. Critically, there are a wide range of traits and behaviors that could be under selection due to their impact on different parts of the predation process (DeLong 2021), but here we focus on the net outcome in the space clearance rate rather than specific underlying traits (while recognizing that space clearance rate is not a trait per se). The effect of space clearance rate on births can be made explicit by considering an ordinary differential equation (ODE) model of a consumer population’s abundance C :

$$\frac{dC}{dt} = e_1 \frac{a_1 R_1 C}{1 + a_1 h_1 R_1} - dC \quad (2)$$

where e_1 is the conversion efficiency (new predators produced per prey type 1 consumed) and d is the per capita mortality rate of the consumer. If we take the per capita rate of growth of the consumer as a proxy for mean fitness (Lande 1982, Abrams et al. 1993), the derivative of this with respect to the space clearance rate is always positive, indicating that increasing the space clearance rate has a positive effect on fitness

and therefore is generally expected to be under selection to be larger:

$$\frac{\partial}{\partial a_1} \frac{1}{C} \frac{dC}{dt} = \frac{e_1 R_1}{(1 + a_1 h_1 R_1)^2} \quad (3)$$

Note, however, that the fitness benefit of having a steeper functional response depends on the conversion efficiency, the prey abundance, the handling time and the space clearance rate itself.

When there is more than one prey type available, however, the impact of the functional response on predator fitness changes. With additional prey types that are included in the diet, the functional response must be expanded to include the time spent handling all S prey types:

$$f_{pc} = \frac{\sum_{i=1}^S a_i R_i}{1 + \sum_{i=1}^S a_i h_i R_i} \quad (4)$$

Likewise, the consumer's population model must be expanded to include the energetic impact of the additional prey types on reproduction. Including just two prey types (types 1 and 2), and assuming that the conversion efficiency for the two prey types is the same, leads to

$$\frac{dC}{dt} = eC \frac{a_1 R_1 + a_2 R_2}{1 + a_1 R_1 h_1 + a_2 R_2 h_2} - dC \quad (5)$$

Following the same steps as above, this leads to a fitness gradient of

$$\frac{\partial}{\partial a_1} \frac{1}{C} \frac{dC}{dt} = \frac{e R_1 (a_2 R_2 (h_2 - h_1) + 1)}{(1 + a_1 R_1 h_1 + a_2 R_2 h_2)^2} \quad (6)$$

Here, if the handling times of the two prey types are the same, the numerator collapses to the single-prey version (Eq. 3) but the denominator gets larger as more prey types are added (both because of the additional aRh terms and because the sum of these terms is squared), making the fitness gradient smaller and reducing the benefit of having a higher functional response on either prey type. This shallowing effect continues with the addition of more prey types (see the Supporting information for a detailed derivation of Eq. 6). This analytical finding indicates that the fitness benefit of a higher functional response becomes small in communities where many prey types are available, creating a potential resolution of the conflict between the community ecology perspective that interactions should be weak and the evolutionary ecology perspective that interaction strengths will evolve to be stronger. Here we see that the strength of selection on the functional response is weakened in diverse

communities, limiting the ability of selection to generate the expected stronger interactions.

Differences among prey types

In addition to a general constraint on the increase of predator functional responses, diverse communities may have prey types that vary in their benefit to the predator. In Eq. 5 and 6, the two prey types do not differ in their energy yield to the predator (they have the same conversion efficiency). Different traditions in ecology again suggest potential ways that prey might be more or less beneficial to a predator's fitness. In community ecology, there is some expectation that keystone predators have high functional responses on competitively dominant prey, and because of this they can control dominant prey types and prevent competitive exclusion (Paine 1966, 1969, Van Valen 1974, Menge et al. 1994). Keystone predation thus requires predators to evolve high functional responses on specific prey types based on their competitive ability or their potential for becoming abundant. Similarly, viral community ecology suggests the potential for a kill-the-winner strategy, wherein viruses specialize on the most abundant host (Vallina et al. 2014). In contrast, evolutionary ecology has proposed that prey with high net energy yields (ratios of energy yielded to the time cost of handling the prey) should be favored by predators, and total abundance is not a factor in determining whether to include prey in the diet (this is the classic optimal foraging prey model of Charnov 1976). Equation 6 indicates that the benefit of a steeper functional response (again, given by the space clearance rate) depends on several factors. These include the energetic benefit of prey, the abundance of both prey types and the difference between the handling times of the two prey.

Moreover, the fact that the difference in handling time is important to selection on a has a key implication – if $h_1 > h_2$, it is possible that selection would favor a smaller space clearance rate because unlike the single-species version (Eq. 3), the fitness gradient can now be negative. This switch in sign changes the general expectation that functional responses should get steeper. Expanding on Eq. 6 to S species and allowing the conversion efficiency of prey types to differ, the fitness gradient becomes

$$\frac{\partial}{\partial a_1} \frac{1}{C} \frac{dC}{dt} = \frac{R_1 \left(e_1 \left(1 + \sum_{i=2}^S a_i h_i R_i \right) - h_1 \left(\sum_{i=2}^S e_i a_i R_i \right) \right)}{\left(1 + \sum_{i=1}^S a_i h_i R_i \right)^2} \quad (7)$$

This fitness gradient is negative when

$$h_1 \left(\sum_{i=2}^S e_i a_i R_i \right) > e_1 \left(1 + \sum_{i=2}^S a_i h_i R_i \right) \quad (8)$$

or

$$\frac{e_1}{h_1} < \frac{\sum_{i=2}^S e_i a_i R_i}{1 + \sum_{i=2}^S a_i h_i R_i} \quad (9)$$

Thus, when the reproductive benefit of the focal prey is less than the benefit gained by excluding the focal prey from the consumer's diet, the consumer is under selection to reduce its space clearance rate on the focal resource. Note that the left hand side of this expression is the predator's birth rate at the asymptotic foraging rate for prey type 1 (conversion efficiency times foraging rate) and the right hand side is the predator's birth rate given the whole functional response excluding prey type 1. We note the striking similarity between this inequality and the prey choice model of classic optimal foraging theory (Charnov 1976), but here we are focusing on the possibility that a functional response could be under selection to be smaller on a particular prey type, rather than evolve a reaction norm in which the predator chooses to include or not include a prey type in the diet under different conditions.

Equation 7 also indicates that increasing the abundance of a species can potentially lower the fitness gradient, because prey abundance (R_i) shows up as a squared term in the denominator and only a linear term in the numerator. This makes it challenging for selection to drive predators to increase their functional response on abundant prey only by virtue of being abundant in a diverse prey community. However, we have invoked a type II functional response, in which handling time cuts into additional search time. If instead the handling time is negligible, then the type II functional response collapses to the type I, and in this scenario, the fitness gradient $\frac{\partial}{\partial a_i} \frac{1}{C} \frac{dC}{dt}$ becomes $-\frac{C}{\partial a_i} \frac{dC}{dt} = eR_i$, showing that we do expect predators to increase the steepness of their functional response for an abundant prey type if the handling time for that prey is negligible.

As a result, the mechanisms of prey coexistence can influence the functional response. In niche-based communities, additional prey types are accompanied by increased total prey abundance, because reduced competition increases the overall carrying capacity of the system. In neutral communities, however, additional prey types must divide up an overall carrying capacity, as the lack of complementarity does not allow for additional resources to support the system (Loreau et al. 2001). Therefore, the structure of the competitive interactions could indirectly affect selection on space clearance rate, if the handling time is negligible and the fitness gradient actually depends on the abundance of prey.

Together, these analytical results suggest four new hypotheses about the evolution of predator functional responses: 1) functional responses should generally evolve to get steeper, but this outcome should be slower in more diverse prey communities, 2) the evolution of space clearance rate to favor the consumption of more rewarding or abundant prey types should be most detectable in low diversity communities and become less detectable as prey diversity increases, 3)

communities in which prey coexist through neutral mechanisms should allow greater divergence of the functional response between high and low reward prey types than in niche-based communities and 4) evolution of space clearance rate for abundant prey should be greater when handling times are small. We test these new hypotheses using Gillespie eco-evolutionary models (GEMs) (DeLong and Gibert 2016) of a single predator in communities varying in both the number of prey types and the mode of coexistence among prey types.

Simulations of functional response evolution

The model

We use a standard ODE predator-prey model that includes Lotka-Volterra-type competition among prey, a type II functional response following Eq. 4, and a conversion efficiency for each prey type. The predator equation is

$$\frac{dC}{dt} = C \frac{\sum e_i a_i R_i}{1 + wC + \sum a_i R_i h_i} - dC \quad (10)$$

Here we have added a predator interference term with wasted time w because interference is a widespread factor influencing foraging in populations and has a stabilizing effect on population dynamics (DeAngelis et al. 1975, DeLong and Vasseur 2011). Note that when $w=0$ this model collapses to the model used in our analytical results above. The prey models (for $S=1, 2, 4$ and 8 prey types) are the birth-death version of the logistic growth equation including competition coefficients among all prey types:

$$\begin{aligned} \frac{dR_i}{dt} = & (b_{\max,i} - \beta_i R_i - \sum \alpha_{ij} R_j) R_i \\ & - (d_{\min,i} + \delta_i R_i + \sum \alpha_{ij} R_j) R_i - \frac{Ca_i R_i}{1 + \sum a_j h_j R_j} \end{aligned} \quad (11)$$

Here, $b_{\max,i}$ is the intercept of a line relating the realized birth rate to the abundance R_i with slope β_i . Similarly, $d_{\min,i}$ is the intercept of a line relating the realized death rate to the abundance R_i with slope δ_i . Thus, β_i and δ_i characterize the effects of population abundance (intraspecific competition) on the realized birth and death rates, respectively, for prey type i . In Eq. 11, as R_i increases, the birth rate drops and the death rate increases by β_i and δ_i per prey, respectively. The effect of other prey types on the birth and death rates of prey type i are given by α_{ij} . This model is a simple expansion of the logistic model, with maximum rate of population growth given as $r_{\max} = b_{\max} - d_{\min}$ and a carrying capacity defined as $K = \frac{b_{\max} - d_{\min}}{\beta + \delta}$ whenever the α s are zero. We use this expansion of the logistic model rather than the standard version because GEMs require separate birth and death terms rather than a net rate of population growth to allow for the

stochastic birth–death process that underlies the evolution of traits (Dieckmann and Law 1996).

We parameterize the model using a set of global mean parameters for both predator and prey (Table 1). For each simulation, we select a number of prey types and then draw prey-related parameters (a_i , b_i , e_i , M_r , α_{ij}) from lognormal distributions that have a specified global mean and variances (Table 1). Here, M_r is the mean body mass of the prey species, with M_c being the mean body mass of the predator species set at 10× the mean prey body mass. Other parameters were constant (Table 1). In this way, every simulation represents a unique community, allowing variation in all parameters to be an inherent aspect of our simulation results, rather than requiring us to control each parameter in turn to determine their effect. The outcome is a series of simulations that encompass variation in the underlying parameters. As our simulations are a test of hypotheses, we only require that our parameter set reflect scenarios in which persistence is generally achievable such that predators have the capacity to evolve space clearance rates on all prey types (see the Supporting information for example dynamics). Our parameter set is roughly in the range of small aquatic predators foraging on fast-growing phytoplankton or zooplankton (DeLong 2021). Our starting point for the functional response was the functional response of the backswimmer *Notonecta hoffmanni* foraging on mosquito larva *Culex quinquefasciatus* (Fox and Murdoch 1978). We do not invoke specific tradeoffs between space clearance rates and other model parameters, as there is limited evidence and justification for such connections. Such tradeoffs, however, would likely alter our results, by either reducing or accelerating evolution.

Simulation technique

We use GEMs, implemented in Matlab, to conduct our simulations. GEMs are a simple modification of the standard

Gillespie algorithm (DeLong and Gibert 2016, DeLong and Belmaker 2019). In short, GEMs transform the rate terms of ODEs into discrete ‘events,’ such as births and death by predation, and use these events to update population sizes and trait distributions through time. To determine which event occurs at a given time step, each model term is divided by the sum of all model terms, providing a probability of occurrence for each event that can be randomly sampled. Each population in a GEM is represented not by a number of individuals (as in a standard Gillespie simulation) but by a matrix of traits. For each event, instead of using a constant parameter (as in a standard Gillespie simulation), a trait value is drawn from the current population distribution and that value is used to set up the event probabilities. When an individual dies, the current individual is removed from the population; when an individual is born, the new individual takes on a trait similar to that of its parent (given its heritability). The outcome is that a trait that is relatively likely to lead to death gets removed from the population, and one that is relatively likely to lead to a birth gets bolstered in the population via offspring. Thus, GEMs are a computational analog of natural selection, allowing the distribution of traits in a population to change with each time step alongside changes in population size. One of the most useful aspects of GEMs for the current study is the ability to allow multiple parameters to evolve at once without having to write down explicit equations for their change. This allows us to simply invoke additional prey types – and allow the space clearance rate on all prey types to evolve – without needing additional equations that describe the change of each evolving space clearance rate.

We ran our simulations for 1, 2, 4 and 8 prey types. There was one type of predator in the model, and the predator had a different, independently evolving space clearance rate (a_i) for each prey type. We implemented two different scenarios for the relationship among prey types. First, we chose an approximately neutral scenario, where the average of all

Table 1. Parameters and the values and variance of parameters used in the simulations. For each separate replicate simulation, the global mean and variance was used to set the overall values. Each of 50 simulations was run with a set of starting parameters drawn from a lognormal distribution with the global mean and variance. Then, each of 30 replicate runs within each simulation was run with that same set of initial parameters. Thus, each simulation encompassed variation in the initial parameters.

Parameter	Symbol	Global mean	Variance
Maximum birth rate	b_{\max}	5	0.1
Minimum death rate	d_{\min}	0.2	0.01
Density dependence of birth rate	β	0.005	0.002
Density dependence of death rate	δ	0.005	0.002
Interspecific competition coefficient	α_{ij}	0.5 × mean(β, δ) – niche-based communities 1 × mean(β, δ) – neutral communities	
Space clearance rate	a_i	0.21	0.02
Handling time	h_i	0.012 – initial 0.12 – test higher h	0.0012 0.012
Wasted time (interference)	w	0.1	
Predator background death rate	d	0.04	
Prey mass	M_r	10	0.3
Predator mass	M_c	10 × M_r	–
Gross growth efficiency	GGE	0.1	–
Predator conversion efficiency	e_i	$e = \text{GGE} \frac{M_r}{M_c}$	

interspecific competition coefficients ($\bar{\alpha}$) was approximately one, generated by setting the mean $\bar{\alpha}$ in the distribution equal to the mean of the density-dependence parameters on birth and death rates (β and δ). This means that the addition of prey types caused the system to divide up the total carrying capacity of the system among prey types, reducing the abundance of each prey type as more types are included. In the second scenario, we allowed complementarity among prey types, with the average $\bar{\alpha} = 0.5$, generated by setting α equal to half of the mean of the density-dependence parameters on birth and death rates. This allowed the total prey community to get larger as more prey types were added, as each new prey type is implicitly accessing different resources. Other features of the models did not change as prey levels increased. We ran 50 simulations for all seven treatments (that is, we ran 50 1-prey simulations, 50 2-prey niche simulations, 50 4-prey neutral simulations and 50 8-prey neutral simulations). For each of the 50 simulations within treatment, we used a different parameter set by drawing values from a lognormal distribution with a global mean and variance for that parameter (Table 1). Then, we ran 30 replicates for each simulation, generating eco-evolutionary dynamics for each parameter set. For all simulations, we set the narrow-sense heritability (h^2 , not to be confused with handling time squared) of evolving space clearance rate traits at 0.75 and the coefficient of variation of the trait within the evolving population at 0.3.

As a result, our simulations represent a wide range of outcomes that we then evaluate for the impacts of prey level, competitive scenario and differences among prey types on the evolution of space clearance rate. Our main experimental outcome that we evaluate is the trajectory of the space clearance rate through time. We look at the average trajectory across our treatments to determine whether adding prey types limits the evolution of the space clearance rate, and whether the impact of prey types is different in the two competitive scenarios.

We use the 1 prey type scenario as the baseline, as there are no competitive interactions or differences among prey types with only one type of prey. With 1 prey type, we expect space clearance rate to increase through time. With 2 or more prey, we look at the evolution of space clearance rate for the best and the worst prey. The best and the worst prey are defined in three different ways based on the above discussion from evolutionary and community ecology. First, prey differed in net energy gain e_i/h_i , where e_i is the conversion efficiency and h_i is handling time. Thus, net energy gain is more directly the reproductive benefit of a prey, but since conversion efficiency is based on prey mass, it also represents the energy yield given the size of a prey type. Here, the best prey has the highest gain and the worst prey has the lowest. Second, prey also differed in handling time, with the best prey having the smallest handling time. Finally, prey differed in average abundance, with the best prey being the most abundant and the worst being the least abundant. We contrasted the space clearance rate trajectories for the best and worst prey to determine whether

evolution favors predators evolving to have higher predation on prey with specific benefits. We then determined whether prey diversity or the mode of coexistence influences these outcomes. For a comparison of the trajectories, we refrain from using a statistical test, as even small differences could be made to be significant if we increased the number of simulations (White et al. 2014). We standardized all trajectories by subtracting the starting value of the space clearance rate from all population means through time and dividing by the initial value. This standardized all trajectories to an initial value of zero and showed change as a fraction of the initial value, facilitating a visual comparison.

Simulation results

As expected from Eq. 7, the impact of prey species richness and abundance had a clear impact on the fitness gradients on space clearance rates (Fig. 1). Using a randomly chosen set of parameters from our simulations, increasing both prey richness and abundance had a decelerating negative impact on the fitness gradient. Consistent with this effect, our simulations indicated that predators can evolve toward higher space clearance rates, but the magnitude of this effect decreased with increasing number of prey types (Fig. 2–4). Compared to the single-prey type baseline, the trajectories of space clearance rate increase were less and less dramatic as the number of prey types increased. There was little apparent difference between the simulations given niche-based or neutral coexistence mechanisms for the prey.

The simulations also showed that predators can evolve steeper functional responses for the most rewarding prey relative to the least rewarding prey. When prey quality was determined as net energy yield, space clearance rates for the

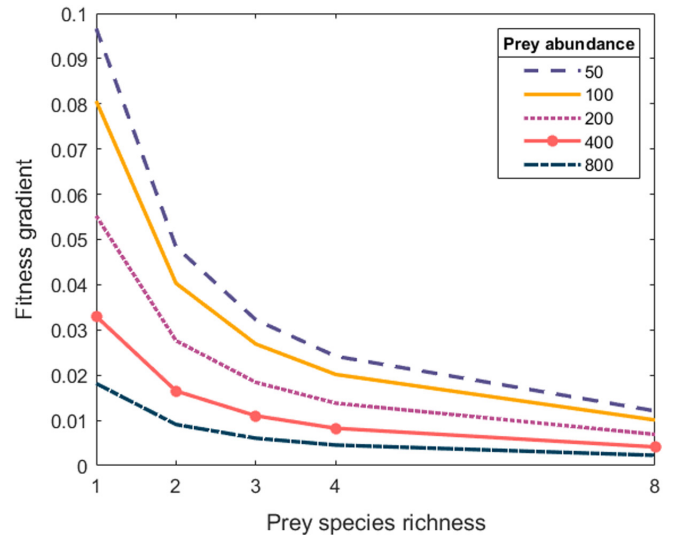


Figure 1. Fitness gradients decline with the addition of more prey types and greater prey abundance. Curves generated by Eq. 7 parameterized using a randomly drawn parameter set of eight prey types.

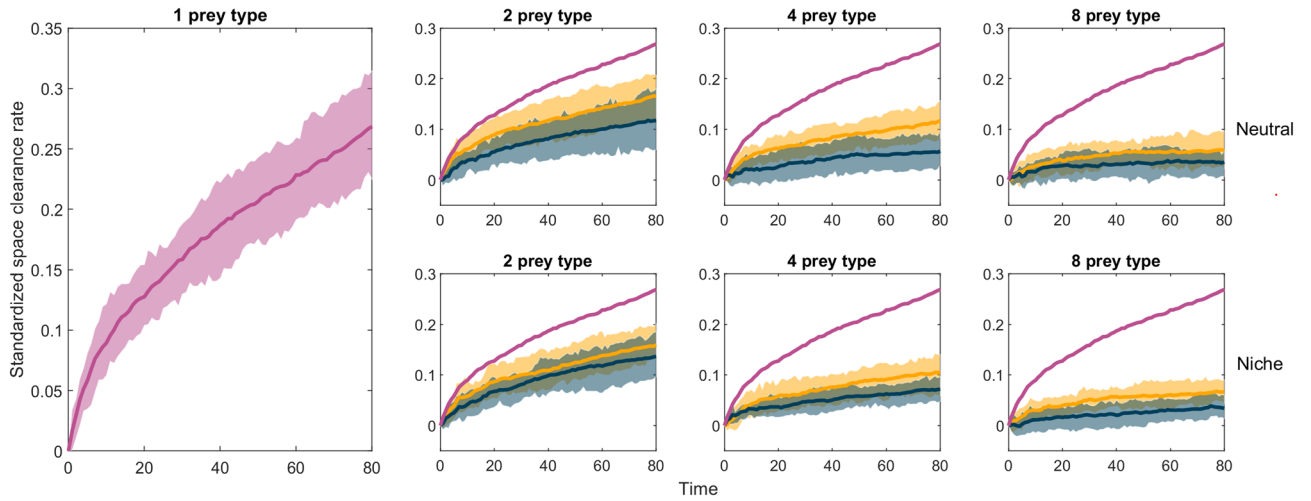


Figure 2. Differences in evolutionary trajectory for the best and worst prey when prey quality is measured as the net energy value. The trajectories of space clearance rate through time are shown standardized to a starting value of zero and the changes represent a fraction of the initial value. The panels show from left to right an increasing number of prey types (1, 2, 4 and 8 prey types), with the single prey trajectory (burgundy) being repeated as a baseline in all panels. The orange lines show the trajectories for the best prey type, while the dark blue lines show the trajectories for the worst prey type. The shaded areas show the middle 50% of all simulations.

most energetically rewarding prey increased more than they did for the least rewarding prey (Fig. 2). This differentiation appeared somewhat dampened at higher prey levels, but was likely due to the overall reduced magnitude of change. When prey quality was determined by handling time, however, we saw no difference between the trajectories of space clearance rate for the best and worst prey (Fig. 3).

When prey quality was determined as abundance, predators were again able to evolve higher space clearance rates on the more abundant prey types, with an overall dampening of the effect at higher prey types (Fig. 4). As indicated in Eq. 6, however, we predicted that higher abundance would reduce the fitness gradient of space clearance rate when the handling time was high enough to make the functional response

meaningfully type II. As predicted, raising the handling time from 0.012 to 0.12 eliminated the separation of space clearance rate trajectories between the most and least abundant prey types (Fig. 5).

Discussion

The evolution of predator foraging traits is a key process that influences interaction strengths in food webs. In general, we expect that predators will be under selection to be better foragers while prey are under selection to avoid predation, creating an ongoing eco-evolutionary tug-of-war between predator and prey (Brodie and Brodie 1999). Such evolution could be

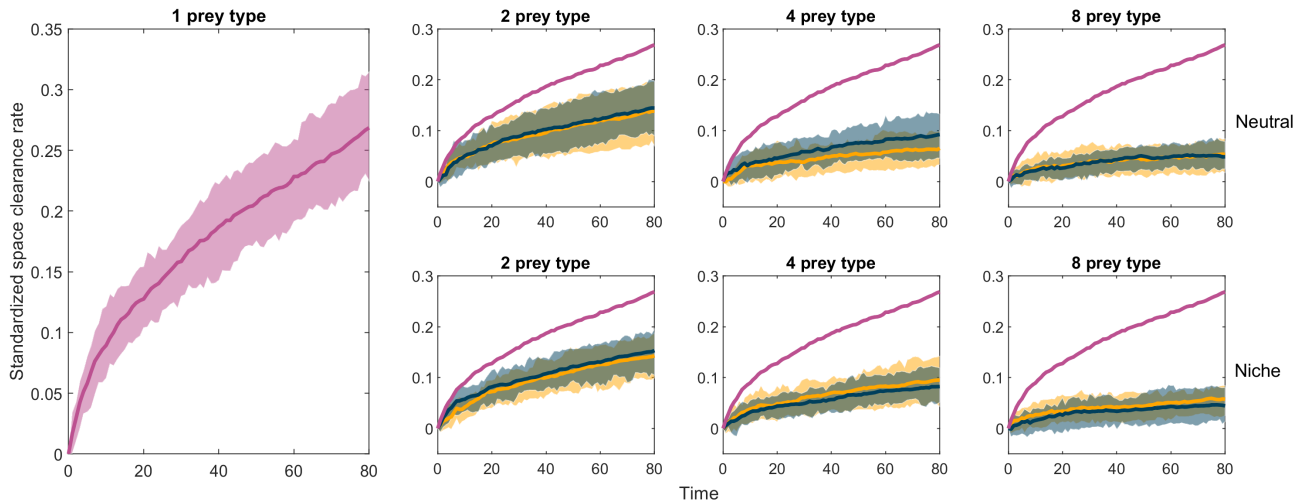


Figure 3. Differences in evolutionary trajectory for the best and worst prey when prey quality is measured as handling time. Figure set up as in Fig. 2.

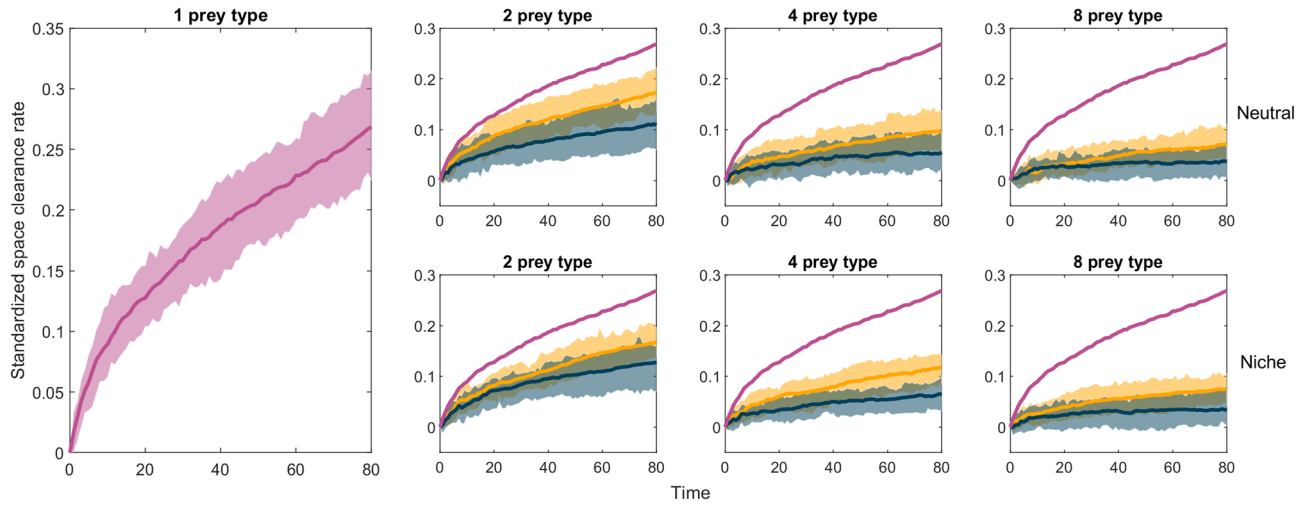


Figure 4. Differences in evolutionary trajectory for the best and worst prey when prey quality is measured as abundance. Figure set up as in Fig. 2.

mediated by a wide range of behavioral, morphological or physiological traits that influence encounters, detection and successful attacks of predators on prey (DeLong 2021). Eco-evolutionary dynamics among predator and prey play out in communities containing multiple prey types (Fussmann et al. 2007), but surprisingly, the potential effect that prey diversity per se could have on the evolution of foraging interactions has not been evaluated. Our results indicate that increasing prey diversity can reduce the benefit of increased foraging on any given prey type, relaxing the overall pressure for predators to have steeper functional responses and thus greater interaction strengths. Overall, our simulation results supported our hypotheses that 1) increasing prey richness would slow the rate of increase in space clearance rate, 2) specialization for rewarding prey would be more detectable at low prey richness and 4) that predators would be more likely to increase

their space clearance rate on abundant prey when handling times are small. However, hypothesis 3) that evolution for higher space clearance rates would be more pronounced in neutral than niche-based communities, was not supported. These results have implications for several features of ecological communities.

First, many predators have broad diets that include numerous prey types across different taxonomic groups. For example, the spider *Pardosa glacialis* takes prey from at least 51 different arthropod families (Eitzinger et al. 2019), and the flycatcher *Nesotriccus ridgwayi* takes prey from multiple orders and classes of arthropods using a range of foraging tactics (Sherry 1985). Why do so many predators have such broad diets? Our results suggest that broad diets should generally be expected wherever there are many prey types to be had, as the selective pressure to have a high functional

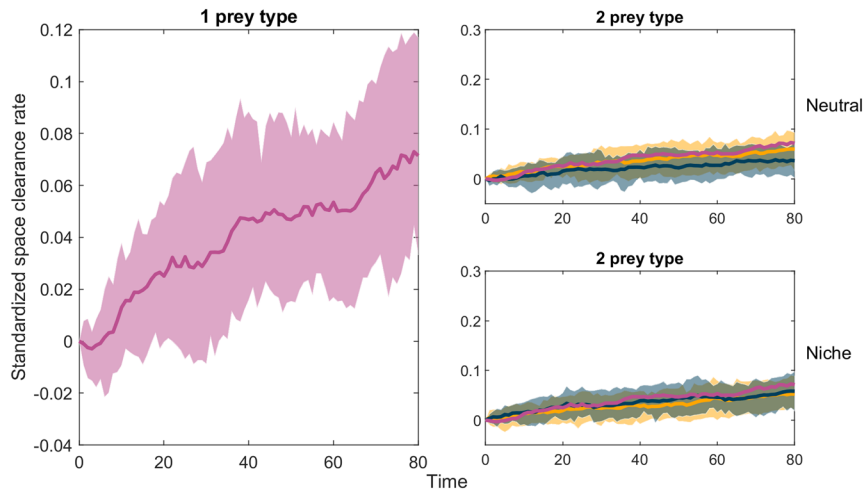


Figure 5. Differences in evolutionary trajectory for the best and worst prey when prey quality is measured as abundance. These simulations, only for 1 and 2 prey types, show the impact of increasing handling time so that the functional response is saturating. Figure set up as in Fig. 2.

response on any particular prey type is very small. And if the functional response on any one prey type is small, then the predator's time budget will not be dominated by the handling time on focal prey types, freeing them up to forage on a variety of prey types that are encountered, broadening their realized diet. This scenario, however, presupposes that predators have the morphological capability of taking a wide range of prey types. Predators with morphologies that mechanically limit the range of their prey types – such as *Didinium*, a ciliate *Paramecium* specialist and snail kites, a raptor well-known for its specialization on freshwater apple snails – would be limited to a smaller diet breadth. Even so, such 'specialist' predators often take multiple prey types within their specialization (Hewett 1987, Beissinger 1990), suggesting that the selective pressure to specialize within prey categories also is small.

Second, predators should have broader diets – and thus lower pairwise interaction strengths – in areas with high prey diversity. This outcome suggests that functional responses should get shallower and thus interaction strengths weaker in the tropics relative to temperate areas. Although total rates of foraging may actually increase toward the tropics (Roslin et al. 2017), in part due to increases in mean temperature, our results suggest that the distribution of pairwise interactions would be weaker and more even in the tropics, and that predator diets would likely include more prey types as well because of the availability of more prey types. In other words, we would generally expect predators with narrower diet breadth and some larger pairwise interaction strengths more commonly at higher latitudes. Although it is unclear whether such a pattern generally occurs for predators, for herbivorous insects there is conflicting evidence for a link between resource specialization and latitude (Novotny et al. 2006, Dyer et al. 2007).

Third, it would be difficult for predators to evolve to become keystone predators in diverse communities. Although keystone predators must have some tendency to focus on competitively dominant prey types more than others, if this tendency did not exist prior to the formation of the diverse prey base, our results suggest it would be difficult for it to evolve. Although predators can evolve to have higher space clearance rates for the most abundant prey types, this effect was limited with eight prey types. Further, when handling times were higher (Fig. 5), the separation of space clearance rate trajectories for high and low abundance prey types was eliminated. This result suggests the possibility that keystone predation may arise in less diverse systems that facilitate increased functional responses on individual prey types, allowing other prey types to enter the system, rather than evolving within diverse prey systems. The results also suggest that keystone predation is more likely to occur when competitively dominant prey types also have a high energetic yield to the predators. This pairing of traits could arise if being a good

competitor arose through strong allocation of resources to reproduction at the expense of predator defenses. Otherwise, their abundance alone is not likely to lead to a high space clearance rate on that prey type and an effective interruption of competitive exclusion.

Fourth, the loss of prey species from food webs could further destabilize food webs. As the selective pressure to increase functional responses gets stronger as prey diversity declines, the loss of species from a food web would have the effect of generating stronger selection for predators to increase their foraging on the remaining prey types. Thus, the loss of prey could destabilize the dynamics of the remaining predator–prey pairs because of the stronger interactions, increasing the risk of further extinctions. However, given the decelerating effect of prey diversity on the strength of selection, this effect might be weak in communities that are not already very depauperate in prey diversity.

A major theme in ecological research for the last half-century has been to identify and understand mechanisms that would stabilize ecological communities in the face of destabilizing consumer–resource interactions (Yodzis 1981, McCann 2000, May 2001). From trait-based links in food webs (Brose et al. 2006), to interference competition (Arditi et al. 2004) and network structure (Allesina and Pascual 2008), several key stabilizing forces may be operating in ecological systems. However, none of these mechanisms alter the expectation that natural selection would continue to favor stronger interactions due to the fitness benefits they provide to predators, and it is even possible that stabilizing mechanisms have their own unexplored effects on the evolution of functional responses. Although natural selection could just as easily act on prey to reduce the strength of interactions, our results show that in addition to a variety of ecological processes, prey diversity per se has the effect of simply constraining fitness gradients such that predators may not be under as much selection for strong interactions in the first place. If selection on prey types further reduces interaction strengths, then the general observation of widespread weak interactions in food webs (McCann et al. 1998, Wootton and Emmerson 2005) can be understood as originating with wide-diet breadth predators simply being under little pressure to increase interaction strengths on any individual prey type.

In conclusion, we suggest that the general conflict between the observation and theoretical need for weak interactions to dominate food webs and the expectation that selection favors stronger interactions can be resolved by the recognition that selection for stronger interactions is actually weak in diverse communities. Our analytical predictions of reduced evolution of steeper functional responses with increasing availability of prey types was supported by simulations using a stochastic birth–death framework (GEMs), suggesting that predators should generally be under little pressure to develop narrow diet breadth.

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Author contributions

John P. DeLong: Conceptualization (lead); Formal analysis (lead); Methodology (equal); Project administration (equal); Software (lead); Writing – original draft (lead); Writing – review and editing (equal). **Kyle E. Coblenz:** Conceptualization (supporting); Investigation (equal); Methodology (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.j6q573nfn>> (DeLong and Coblenz 2021).

Supporting information

The supporting information associated with this article is available from the online version.

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