CHAPTER SIX

Individual Trait Variation and Diversity in Food Webs

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Abstract

In recent years, there has been a renewed interest in the ecological consequences of individual trait variation within populations. Given that individual variability arises from evolutionary dynamics, to fully understand eco-evolutionary feedback loops, we need to pay special attention to how standing trait variability affects ecological dynamics. There is mounting empirical evidence that intra-specific phenotypic variation can exceed species-level means, but theoretical models of multi-trophic species coexistence typically neglect individual-level trait variability. What is needed are multispecies datasets that are resolved at the individual level that can be used to discriminate among alternative models of resource selection and species coexistence in food webs. Here, using one the largest individual-based datasets of a food web compiled to date, along with an individual trait-based stochastic model that incorporates Approximate Bayesian computation methods, we document intra-population variation in the strength of prey selection by different classes or predator phenotypes which could potentially alter the diversity and coexistence patterns of food webs. In particular, we found that strongly connected individual predators preferentially consumed common prey, whereas weakly connected predators preferentially selected rare prey. Such patterns suggest that food web diversity may be governed by the distribution of predator connectivity and individual trait variation in prey selection. We discuss the consequences of intra-specific variation in prey selection to assess fitness differences among predator classes (or phenotypes) and track longer term food web patterns of coexistence accounting for several phenotypes within each prey and predator species.

1. INTRODUCTION

Over the past century, ecologists have proposed numerous theories to explain why natural communities have more species than predicted by theoretical models (Cohen et al., 1990a; Hutchinson, 1959; MacArthur, 1955; May, 1973). In recent years, there has been significant progress towards understanding the structure, dynamics, and coexistence of ecological networks (Brose et al., 2006; Gross et al., 2009; Rooney et al., 2006), yet very little is known about the connection between the drivers of intra-specific variation in resource use observed in the empirical data (Bolnick et al., 2002; Cianciaruso et al., 2009; Post et al., 2008) with the observed patterns of diversity in multi-trophic ecosystems (Abrams, 2010; Bolnick et al., 2011; Chesson, 1978; Ings et al., 2009; May, 2006; Murdoch, 1969; Pachepsky et al., 2007; Stouffer, 2010; Svanbäck et al., 2008; Violle et al., 2012). Competition theory predicts that stable coexistence occurs because of a balance between differences in species niches and competitive abilities (Chesson, 1984). However, intra-specific variation in resource use can exceed the
differences in species-level averages within ecological communities, suggesting that individual-level variation might strongly affect community dynamics (Bolnick et al., 2011) and the likelihood of species coexistence (Bolnick et al., 2002; Clark, 2010; Cohen et al., 2005; Lloyd-Smith, 2005; Roughgarden, 1972). Variation in prey selection by predators within natural populations may either promote or limit the diversity of food webs, depending on the number and nature of interactions between individual predators and the abundance of prey populations. Thus, the number of prey an individual predator consumes can be used as a proxy to quantify its effect on prey abundance. On the one hand, where individuals with high feeding rates or fast prey finders (i.e. strongly connected predators) are common and preferentially target rare prey, then we may expect predators to cause declines in prey population size and eventually multiple extinctions in the prey community, increasing the probability of reduction in food web stability (Chesson, 1984; Holt, 1977; Murdoch, 1969). On the other hand, if most individual predators within a population select preferentially common prey, the rare prey species advantage analogous to a Janzen-Connell effect (Janzen, 1970), then most prey populations may coexist in the food web. Thus, the interaction between predator connectivity and prey selection at the individual level can have implications for understanding coexistence of prey and predator species in food webs. There is evidence from both theoretical and empirical work that intra-population variation in prey selection by predators can involve interactions between ecological and evolutionary dynamics. For example, optimal foraging theory with adaptive foragers have shown switching from rare to common prey as prey abundance increase (Beckerman et al., 2010; Kondoh, 2003; Stephens and Krebs, 1986). However, there can be substantial individual variation among predators in the propensity to switch among prey resources (Bolnick et al., 2011) with some individuals switching quickly and others delaying the switch depending on the ecological context (Carnicer et al., 2009). These changes provide intra-specific variation that might include behavioural syndromes associated with individual personalities and may show consistent foraging or mating strategies regardless of the abundance of resources in the environment (Wolf and Weissing, 2012). From the empirical side, individual predator connectivity (i.e. number of interactions) can be estimated from analyzing gut contents, where the number of prey items can give some indicator of an individual’s rate of consumption (e.g., fast vs. slow prey finders) and hence degree of connectivity (e.g., strongly vs. weakly connected) to the prey community. Individual connectivity thus could therefore be a signature of different
feeding rates driven by intra-population trait variation, plasticity, or even behavioural syndromes (Biro and Stamps, 2010). For a given level of connectivity, the individual prey selection (i.e., the nature of interactions) can be estimated from the difference between a predator’s gut contents and independent measures of the empirical abundance distribution of prey in the environment. Previous work has documented extensive individual specialization within predator populations, but the consequences for food web diversity are still unclear (Bolnick et al., 2007; Polis, 1991; Polis and Winemiller, 1996; Tinker et al., 2012; Winemiller, 1990; Winemiller and Layman, 2005). This is partly because obtaining empirical estimations of predator’s gut contents and independent measures of empirical abundance of prey species is difficult in the field and so little is known about intra-population variation in the strength of prey selection. Until now, the lack of high-resolution individual-based data with thousands of individual diets and independent measures of resource abundance, has made it difficult to test the role of intra-specific variation in the distribution of predator connectivity and resource selection on species coexistence in large food webs (Dunne, 2006; Polis, 1991). Here, we propose a method to test whether individual predators with different abundance of prey in their gut differ in their propensity to select rare versus common prey in a species rich food web. We use individual trait-based models and propose predator learning behaviour as a trait (Giraldeau and Caraco, 2000; West-Eberhard, 2003) that may explain the connection between individual rate of consumption (e.g., fast vs. slow prey finders), the degree of connectivity (e.g., strongly vs. weakly connected), and prey selectivity. We take a two-step modelling approach to test for intra-population and sampling variation in the strength of prey selection (Fig. 6.1). First, we compare whether a model with or without predator learning better explains the observed distribution of predator connectivity (Fig. 6.1A). We use learning as our trait that serves as a proxy to quantify the strength of past successful feeding encounters in determining individual diets. We then estimate the speed of learning ($\alpha$) for those occasions where the learning model is the most likely to explain the observed variance in predator connectivity at the individual level (when $\alpha > 0$). Second, to investigate the mechanisms underlying individual variation in the strength of prey selection we used the predicted speed of learning and fit a model of prey selection to test how variation in the number of prey items per individual predator was related to an independent measurement of the observed abundance distribution of resources in the environment (Fig. 6.1B). Overall, the modelling approach uses two-independent sources
Figure 6.1 *Schematic representation of the approach.* (A) Empirical (black dots) and predicted distribution of prey abundance in predator guts (i.e. predator connectivity) with (red (dark grey in the print version)) or without (orange (light grey in the print version)) predator learning. *x*-Axis and *y*-axis represent the predator rank from strongly to weakly connected and prey abundance in guts, respectively. (B) Rank abundance in nature of prey species *i* (*y*-axis) and predicted cumulative abundance of prey *i* in predator guts (Continued)
of data, namely the gut contents of predators and abundance of prey in the environment, and estimates two parameters of ecological relevance, namely the rate of predator learning ($\alpha$) and the strength of prey selection ($\Omega$) (Fig. 6.1).

We tested our method using a community of fish predators from the Guadalquivir estuary community in southwest Spain. We analyzed the stomach contents of 5725 individual fish predators (10 predator species) and identified 88101 prey items (43 taxa). The fish were collected from four daily net hauls at two sites (either oligohaline or polyhaline) once a month for a year ($N = 95$ samplings, one missed sampling, Fig. 6.A1). Hence, the data have sufficient intraday, monthly, and seasonal resolution to make inferences at the individual, species, and food web levels simultaneously (Fig. 6.A2).

This combination of temporal and individual resolution for a larger number of species is not available from previous data sets, which are either focused on a few thousands individuals in a few species or on a few individuals per species in food webs with a large number of species (Dunne, 2006; Polis, 1991; Woodward and Warren, 2007). To simplify the fitting of the prey selection model to the high-resolution food web dataset, we divided predator individuals into four connectivity classes based on the number of prey items per individual predator, ranging from just a few prey items (slow prey finders) to a large number of prey items per predator (fast prey finders, Fig. 6.1C). This model simplification allowed us to test, for example, whether individuals within different classes of predator connectivity preferred either rare or dominant prey items (Fig. 6.1D). We followed this procedure for three different levels of aggregation, (i) for each sampling date, (ii) for each predator species pooled across multiple sampling dates with similar environments (Appendix), and (iii) for all the data pooled together. Overall, this approach allows us to combine high-resolution individual trait-level interaction data with resource abundance data in order to reveal the most likely mechanisms underlying predator preference to select the

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**Figure 6.1—Cont’d (x-axis) in the three scenarios explored:** (1) Predator selecting preferentially rare prey (positive density-dependent prey selection, red (dark grey in the print version) with $\Omega > 0$); (2) no preference (neutral density-dependent prey selection, black with $\Omega = 0$), and (3) selecting preferentially common prey (negative density-dependent prey selection, blue (light grey in the print version) with $\Omega < 0$). Dotted black line represents the identity line to show the different trend between the positive and negative density-dependent prey selection scenarios. (C) Four classes of individual predators ranging from strongly connected (1) or fast prey finders to weakly connected (4) or slow prey finders. (D) Strongly to weakly connected predators targeting dominant ($\Omega < 0$) and rare ($\Omega > 0$) prey, respectively.
common or rare prey that are essential for the maintenance of biodiversity in multi-trophic ecosystems. Overall, we find strong evidence for intra-population variation in the strength of prey selection that could influence food web diversity. In particular, our results suggest that the weakly connected individual predators that favour rare prey have the most pronounced negative effects on food web diversity.

2. MATERIAL AND METHODS

2.1. Stochastic individual trait-based predator–prey model

Following the schematic in Fig. 6.1, we present an approach that models individual-level variation in the predator connectivity (i.e. the number of prey items) and the strength in prey selection. Our model is a stochastic, predator–prey model with $N_1, N_2, \ldots, N_S$ the prey population abundance of species $n$, and $w_1, w_2, w_3, \ldots, w_T$ the number of prey items in the gut of individual predator $j$ (Table 6.1). Prey population abundance is sorted from the most common, $N_1$, to the rarest species, $N_S$, with $S$ the observed prey species number and $T$ the number of individual predators sampled. In the next section, we expand the model by considering learning as a trait to test whether the model with learning behaviour is a plausible mechanism to connect the degree of connectivity (e.g., strongly connected and fast prey finders vs. weakly connected and slow prey finders) with prey selectivity.

2.1.1 Speed of learning and the distribution of predator connectivity

We model variation in predator connectivity assuming identical learning abilities among individual predators. We model this learning ability using a single parameter, $\alpha$, which we refer to as the learning rate. To investigate how learning rate affects the distribution of predator connectivity, we consider that the probability to find a prey item is driven by an individual prior experience in catching a prey. The probability to find a prey item is then given by the number of items in the stomach content of each individual predator $j$, $w_j$, and the speed of learning, $\alpha$. For each time step, an individual predator $j$ at time $t$ has probability of catching a prey given by

$$
P_{jt} = \frac{\mathcal{K}}{1 + \mathcal{K}e^{-\alpha w_{j-1}}} \sum_{i=1}^{T} \frac{\mathcal{K}}{1 + \mathcal{K}e^{-\alpha w_{i-1}}} \tag{6.1}
$$
Table 6.1 Glossary of mathematical notation, dimensions, and values used

<table>
<thead>
<tr>
<th>Variable or parameter</th>
<th>Definition</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$N_n$ [inds]</td>
<td>Abundance of prey species $n$</td>
<td>State variable</td>
</tr>
<tr>
<td>$N$ [inds]</td>
<td>Abundance all prey species</td>
<td>Empirical value</td>
</tr>
<tr>
<td>$S$ [species]</td>
<td>Number prey species</td>
<td>Empirical value</td>
</tr>
<tr>
<td>$T$ [inds]</td>
<td>Number of individual predators sampled</td>
<td>Empirical value</td>
</tr>
<tr>
<td>$\omega_{jt}$ [prey items]</td>
<td>Number of prey items in stomach content of predator $j$ at time $t$</td>
<td>State variable</td>
</tr>
<tr>
<td>$\alpha$ [dimensionless]</td>
<td>Speed of learning</td>
<td>$[10^{-5}, 10^{-1}]$</td>
</tr>
<tr>
<td>$K$ [dimensionless]</td>
<td>Learning capacity</td>
<td>$[10^2, 10^3]$</td>
</tr>
<tr>
<td>$\tau_c$ [inds]</td>
<td>Number of individuals in class $c$ obtained by simulations</td>
<td>$[0, T]$</td>
</tr>
<tr>
<td>$P_{\alpha}$ [dimensionless]</td>
<td>Probability class $c$ catch a prey item at time $t$</td>
<td>$[0, 1]$</td>
</tr>
<tr>
<td>$p_{cn}$ [net energy (time)$^{-1}$]</td>
<td>Profitability of prey species $n$ for individuals in class $c$</td>
<td>$U[1, 101]$</td>
</tr>
<tr>
<td>$P_{cn}$ [dimensionless]</td>
<td>Probability class $c$ eat prey species $n$ with profitability $p_{cn}$</td>
<td>$[0, 1]$</td>
</tr>
<tr>
<td>$\Omega_c$ [net energy (time)$^{-1}$]</td>
<td>Prey selection strength individuals in class $c$</td>
<td>$U[-10^2, 10^2]$</td>
</tr>
<tr>
<td>$\Omega_{c-}$ [net energy (time)$^{-1}$]</td>
<td>Negative prey selection strength individuals in class $c$</td>
<td>$U[-10^2, &lt;-30]$</td>
</tr>
<tr>
<td>$\Omega_{co}$ [net energy (time)$^{-1}$]</td>
<td>Neutral prey selection strength individuals in class $c$</td>
<td>$U[-30, 30]$</td>
</tr>
<tr>
<td>$\Omega_{c+}$ [net energy (time)$^{-1}$]</td>
<td>Positive prey selection strength individuals in class $c$</td>
<td>$U[&gt;30, 100]$</td>
</tr>
<tr>
<td>$\mu$ [ind (time)$^{-1}$]</td>
<td>Prey mortality rate</td>
<td>1</td>
</tr>
<tr>
<td>$\lambda$ [ind (time)$^{-1}$]</td>
<td>Prey birth rate</td>
<td>1</td>
</tr>
</tbody>
</table>

where $K$ defines the learning capacity for all individual predators, $\alpha$ is the speed of learning equal for all individual predators regardless their number of items, $\omega_{jt}$ is the number of prey items in the stomach content of predator $j$ at time $t-1$, and $T$ is the number of individual predators. A larger value of $\alpha$ implies a higher finding rate of prey (Giraldeau and Caraco,
Note the probability to find a prey item is a function of predator density and what other predators ate in the previous time step. Thus, we assume that with more number of individual predators in a given environment or volume the lower the probability to catch a prey for each of these predators. If there are huge numbers, density-dependent probability can collapse for each individual predator and some individuals predators may starve.

In summary, the number of prey items in the stomach content of each individual $j$, $w_j$, and the speed of learning, $\alpha$, capture the probability to find a prey. We remark that when $\alpha = 0$, that is, when learning is not present, there is no effect of previous successful encounters to find new prey items. We remark that the model without the learning trait may represent a prey population dynamics with predators that are represented as individuals instead of species (Cohen et al., 1990b; Wilson et al., 2003). In the scenario without learning, it is expected that the variance in the number of prey items among individuals is lower than in the model with learning, leading to a homogeneous number of prey items per individual predator. The model with and without learning can be used to compare the expected distribution of predator connectivity with the empirical observations (Fig. 6.1A).

### 2.1.2 Profitability and the strength of prey selection for individual predators

In order to predict whether strongly (i.e. fast prey finders) or weakly connected predators (i.e. slow prey finders) tend to favour rare versus dominant prey items, respectively, we further expand the learning model to individual predators by considering that the profitability of a given prey varies among individual predators. We model this function as an individual-level trait, and use it to estimate variation in prey selection for a given speed of learning (as estimated above) and an observed prey abundance distribution. By explicitly including individual-level variation in predator profitability functions along with the distribution of prey abundance, we can estimate the strength of the individual predator preference for rare or common prey.

We modelled the profitability function based on the idea that the ratio of energy gained for a given handling time is an essential variable to distinguish random encounters from active searching of common or rare prey by each individual predator. Short handling times have a marked effect on profitability of prey (Catania and Remple, 2005), and variation in each individual predator in handling time (capture, killing, eating, or digesting) can have large consequences for profitability of foraging on a particular prey. We take into account variation in handling time in each individual predator by defining the profitability of prey species $n$ for individual predator $j$ as a function of
the ratio of energy gained to handling time, \( p_{jn} = (E/h)_{jn} \). This profitability for individual \( j \) can be defined as a probability as \((\text{Stephens and Krebs, 1986})\)

\[
P_{jn} = \frac{p_{jn}}{\sum_{i=1}^{S} p_{jn}},
\]

where \( S \) is the number of prey species. Because we do not have empirically derived estimates of energy gained and handling time for the sampled prey species, in the simulations we provide each predator with a vector of profitabilities that includes all prey species and this vector of profitabilities is decoupled from abundance. In other words, an individual predator may have a low number of prey items (i.e., slow finder) but this individual may have a set of traits that favour high profitability values for rare prey. The same situation may occur for individual predators with a large number of items (i.e., fast prey finder), who may spend a long time capturing or killing a rare prey species \( n \), while an individual with a low number of items can find the same rare prey highly profitable. In summary, we relax the profitability ranking and decouple it from abundance of prey to allow for variation in handling versus searching time or when digestive abilities vary greatly among individual predators.

We define the strength in prey selection for predator \( j \), by \( \Omega \), as the difference in profitability for foraging on the rarest, \( N_S \), and the most common prey, \( N_1 \). The following three scenarios are possible for each individual predator \( j \)

\[
\begin{align*}
\Omega_j & = \left\{ \begin{array}{ll}
\Omega_{j-} (< 0) & = p_{jS} - p_{j1} \\
\Omega_{j0} (= 0) & = p_{jS} - p_{j1} \\
\Omega_{j+} (> 0) & = p_{jS} - p_{j1},
\end{array} \right.
\end{align*}
\]

where \( \Omega_{j-}, \Omega_{j0}, \) and \( \Omega_{j+} \) represent the negative, neutral, and positive density-dependent prey selection by individual predator \( j \), respectively. The strength of prey selection will be a negative number when predator \( j \) choose preferentially common prey (i.e., negative density-dependent prey selection or the fitness of prey population increases as it becomes less common, thus \( p_{j1} > p_{jS} \)). In the case of no preference, profitability is equal across all the prey species and the individual predator chooses prey according to their abundance. In this scenario, the value will be zero or close to zero (i.e., neutral or nearly-neutral prey selection, respectively, with \( p_{j1} \approx p_{jS} \)). The strength of prey selection will be a positive number when predator \( j \)
preferentially selects rare prey (i.e., the advantage of the common prey satisfying \( p_{j1} < p_{jS} \)). In this scenario, the cumulative abundance of rare prey in predator guts will grow faster than in the neutral or the negative density-dependent prey selection scenario (Fig. 6.1B). The vector of profitabilities is included in the simulations as a monotonic function with decaying (negative density-dependent prey selection), equal (neutral), or increasing (positive) values from the most common to the rarest species.

### 2.1.3 Profitability and the strength of prey selection for connectivity classes

At this point, the model is still too complex to recover predator estimates of the strength of prey selection given the food web and abundance data. In order to compare food web and species abundance data with model predictions, we have to divide the predator population into four classes (\( c \)) of varying connectivity (Fig. 6.1C), which are (1) strongly connected predators (or fast prey finders); (2) medium-strongly connected predators; (3) medium connected predators, and (4) weakly connected individuals (or slow prey finders).

Equation (6.1) for each individual predator \( j \) can be now written for each class, such that, an individual in class \( c \) at time \( t \) has probability of catching a prey given by

\[
P_c = \frac{\sum_{i=1}^{T_c} \frac{K}{1 + Ke^{-aw_{i-1}}}}{\sum_{i=1}^{T} \frac{K}{1 + Ke^{-aw_{i-1}}}}
\]

(6.4)

where \( T_c \) is the number of individuals in class \( c \) at time \( t \). The profitability of prey species \( n \) for an individual predator in class \( c \) is now given by \( p_{cn} = (E/h)_{cn} \), and the profitability for class \( c \) can be written in probabilistic terms as

\[
P_{cn} = \frac{p_{cn}}{\sum_{i=1}^{S} p_{in}}.
\]

(6.5)

The strength of prey selection for each class, \( \Omega_c \) (i.e., Strongly (\( \Omega_1 \)), medium–strongly (\( \Omega_2 \)), medium (\( \Omega_3 \)), and weakly (\( \Omega_4 \)) connected individuals) now follows these scenarios
\[ \begin{align*} \Omega_t & \begin{cases} \Omega_{c^-} (< 0) = p_{cS} - p_{c1} \\ \Omega_{c^0} (\equiv 0) = p_{cS} - p_{c1} \\ \Omega_{c^+} (> 0) = p_{cS} - p_{c1}, \end{cases} \end{align*} \tag{6.6} \]

where \( \Omega_{c^-}, \Omega_{c^0}, \) and \( \Omega_{c^+} \) represent the negative, neutral, and positive density-dependent prey selection values for each class \( c \), respectively. We can now study the strength of prey selection in four classes of predators by using the speed of learning, \( \alpha \), and the strength of prey selection for each class, \( \Omega_c \).

### 2.1.4 Dynamics of prey populations driven by predators

Prey dynamics were modelled as a function of predator events. Thus for each predation event a prey population decreases. Suppose the population size of prey species \( n \) at some time \( t \) is \( N_n \). What will it be after a small increment in \( \delta t \) in time? Call births and deaths “events”. Then the population size at the later time \( t + \delta t \) depends on which events occur during the small interval \( \delta t \) (Yodzis, 1989). For \( \delta t \) sufficiently small, an individual of prey species \( n \) at time \( t \) dies by an individual predator in connectivity class \( c \) with probability

\[ D_{N_n}(t + \delta t) = \mu P_c P_{cn} \left( \frac{N_n}{N} \right) \delta t, \]

where \( P_c \) is the probability of catching a prey by an individual in class \( c \) at time \( t \) (Eq. 6.4), \( P_{cn} \) is the profitability of species \( n \) for connectivity class \( c \) (Eq. 6.5), and the last term is the frequency of prey species \( n \) with \( N \) the total number of individuals. We scale time to prey dynamics, so mortality rate of prey species, \( \mu = 1 \), and the attack rate of individual predators in class \( c \) on prey species \( n \) is given by \( P_c P_{cn} \). At the same time, each birth event produces an offspring in the prey species \( n \). This probability is described as

\[ B_{N_n}(t + \delta t) = \lambda \left( \frac{N_n}{N - 1} \right) \delta t, \]

and we scale time to prey dynamics, so the birth rate of prey species \( \lambda = 1 \). The changes in prey abundance for the individual-learning based model with prey selection are described as

\[ \mathcal{P}[N_n - 1|N_n] = D_{N_n} B_{N_{\neq n}} \]

\[ \mathcal{P}[N_n + 1|N_n] = D_{N_{\neq n}} B_{N_n}, \]

where \( B_{N_{\neq n}} \) and \( D_{N_{\neq n}} \) are the probabilities that a birth or a death occur in a species other than species \( n \), respectively.
2.2. Guadalquivir estuary food web as a case study: Sampling of gut contents and resource distribution

**Gut contents**—We analyzed the stomach contents of 5725 fish individuals (total length < 140 mm), including mainly postlarvae and juveniles but also adults of small resident species of the 10 most abundant fish species (*Engraulis encrasicolus*, *Sardina pilchardus*, *Pomatoschistus* spp., *Dicentrarchus punctatus*, *Cyprinus carpio*, *Pomadasys incisus*, *Argyrosomus regius*, *Liza saliens*, *Liza ramada*, and *Aphia minuta*). We analyzed 95 distinct sample collections (12 months × 2 stations × 4 samplings, minus 1 missing sampling, Fig. 6.A1) and identified a total of 88,101 prey items spanning 43 taxa, mostly zooplankton—including copepods, cladocerans, ostracods, and cirripids as the dominant groups—and hyperbenthic species (e.g. mysids, gammarid amphipods and larval decapods and fishes), but also endobenthic (e.g. polychaetes and gastropods) (Baldo and Drake, 2002). Four connectivity classes were extracted from the empirical variance in the number of prey items per individual predator (Fig. 6.A1): (1) strongly connected predators (or fast prey finders) contain equal or more than 200 prey items; (2) medium-strongly connected predators contain equal or more than 100 and less than 200; (3) medium connected predators contain equal or more than 10 and less than 100; and (4) weakly connected individuals (or slow prey finders) are those individuals with equal or more than 1 and less than 10 prey items in the stomach.

**Distribution of prey resources**—The species abundances were estimated from samples collected using nets of two different sizes (1 mm, and 250 μm), where the abundance of the different species were given per $10^5$ m$^3$ of filtered water, as estimated either from the current speed measurements taken made a digital flow meter for each net. To estimate the abundance of edobenthic preys, five replicate samples of the macrobenthic community were monthly taken randomly at each sampling site, with an Ekman–Birge grab ($15 \times 15$ cm$^2$).

**Aggregation**—Many food web studies aggregate species across samplings and environmental gradients (Dunne, 2006). In order to test for the robustness of the strength of prey selection pattern across environmental gradients, we aggregated each predator species across sampling dates that have similar environmental conditions and analyzed groupings with more than 2000 individual prey and predators sampled (Figs. 6.A1A, 6.A2A, and 6.A3). Similarly, we analyzed each sampling date pooled across all predator species (Figs. 6.A1B, 6.A2B, and 6.A4), and for the entire dataset. Additional sampling details are described in the supplement.
2.3. Fitting the model to the data: Speed of learning ($\alpha$) and the distribution of predator connectivity

To compare the empirical observations with model predictions of the distribution of predator connectivity across samplings and populations, we used previous experience of the predator given by the number of prey items in the stomach content of each individual predator $j$, the speed of learning, $\alpha$, and the learning capacity, $K$, as the drivers of variability in predator connectivity. The number of prey species and individual predators in the model are the same than in the empirical observations for those observations with more than 2000 individual prey and predators (Figs. 6.2, 6.A3, and 6.A4). Results for Figs. 6.2, 6.A3, and 6.A4 were obtained after running $10^5$ replicates. Each replicate was run for the observed number of prey items sampled within the same predator population and temperature–salinity range.

![Figure 6.2](image)

**Figure 6.2 Distribution of predator connectivity.** $x$-Axis and $y$-axis represent the predator rank from strongly to weakly connected and prey abundance in guts, respectively. (A) For the species *Engraulis encrasicolus* in the temperature and salinity range 22–29 °C (summer) and 6–12 (medium salinity), respectively. (B) For all the predators in the sampling number 33 in the temperature and salinity range 22–29 °C (summer) and 0–6 (low salinity), respectively. (C) For the data pooled in the temperature and salinity range 9–29 °C and 0–36, respectively. Black circles represent the empirical data, solid and dotted red (dark in print version) and orange (light grey in the print version) lines are the mean and confidence interval (CI) from the model with ($\alpha > 0$) and without ($\alpha = 0$) learning, respectively.
(Fig. 6.2A and 6.A3), the observed number of prey items within the same sampling using all the predators sampled (Fig. 6.2B and 6.A4), and for all the data pooled (Fig. 6.2C).

In Figs. 6.2, 6.A3, and 6.A4, we simulated the distribution of the number of items of per individual predator $j$ denoted as $\mathbb{W} = [w_1, w_2, \ldots, w_T]$, with $T$ the number of predators sampled, and compare it with the empirical data, $\mathbb{D} = [d_1, d_2, \ldots, d_T]$. All individual predators have equal $w_j$ at the outset with $w_j$ values larger than 0 for all individual predators. We calculated the distance between model predictions and the empirical data as the sum of the absolute values of the misfits as follows (Tarantola, 2006)

$$
\rho(d_1, d_2, \ldots, d_T | \alpha, K) = \sum_{j=1}^{T} \log \left( \frac{P(d_j | w_j)}{C_0} \right) \quad \text{(6.11)}
$$

where $\log(P(d_j | w_j))$ captures the difference between the observed ($d_j$) and simulated ($w_j$) number of prey items of individual predator $j$ and used the standard rejection-ABC algorithm (Beaumont, 2010; Sunnåker et al., 2013; Toni and Stumpf, 2010) that works as follows

1. Draw $\theta$ from the prior where $\theta = [\alpha, K]$. In absence of field estimations of the speed of learning, $\alpha$, and the learning capacity, $K$, the values were randomly chosen from a uniform distribution with range $U[10^{-5}, 10^{-1}]$ and $U[10^2, 10^3]$, respectively.
2. Simulate $\mathbb{W}$ from each run with parameter $\theta$.
3. Calculate distance for $\rho(\mathbb{W}, \mathbb{D})$ between simulated ($\mathbb{W}$) and empirical data ($\mathbb{D}$).
4. Reject $\theta$ if $\rho(\mathbb{W}, \mathbb{D}) > \epsilon$.

The tolerance $\epsilon \geq 0$ is the desired level of agreement between the simulations ($\mathbb{W}$) and the empirical data ($\mathbb{D}$) (Toni and Stumpf, 2010). Accepted model replicates to calculate the confidence interval (CI) taking the percentiles 0.05 and 0.95 were generated using a family of $\theta = [\alpha, K]$ parameter values with tolerance $\epsilon = 2 \times$ minimum log-distance where the minimum log-distance refers to the replicate that minimizes the absolute difference between the empirical and simulated data.

2.4. Choosing among alternative models: Strength of prey selection ($\Omega$)

2.4.1 Negative, neutral, and positive density-dependent prey selection

Results for Figs. 6.3 and 6.4 were obtained by using the information gained from the simulations with the speed of learning. We used the CI range of
Figure 6.3 *Strength of prey selection.* (A) Predicted cumulative abundance of prey in predator guts ($x$-axis) with predator selecting preferentially rare prey (red (dark grey in the print version), $\Omega > 0$), no preference (black, $\Omega = 0$), and common prey (orange (light grey in the print version), $\Omega < 0$). (B and C) Predicted (blue (light grey in the print version)) and empirical (black) cumulative abundance of prey in predator guts ($x$-axis) for the strongly (B) and medium-strongly (C) connected individual predators for the data pooled. Strongly (B) and medium-strongly (C) connected predators select preferentially common prey ($\kappa_{\Omega_1, H_1} = 14$, $\Omega_1 = -61$, $\alpha = 0.009$, and $\kappa_{\Omega_2, H_2} = 36$, $\Omega_2 = -41$, $\alpha = 0.0072$, respectively). (D and E) Predicted (red (dark grey in the print version)) and empirical (black) cumulative abundance of prey in predator guts ($x$-axis) for the medium (D) and weakly (E) connected individual predators for the data pooled. Weakly (B) and medium (C) connected individuals select preferentially rare prey ($\kappa_{\Omega_3, H_3} = 82$, $\Omega_3 = 91$, $\alpha = 0.001$, and $\kappa_{\Omega_4, H_4} = 107$, $\Omega_4 = 73$, $\alpha = 0.0062$, respectively). Solid and dotted red (dark grey lines in the print version) and orange (light grey lines in the print version) lines are the mean and CI from the best-fit values given by the model with learning. Dotted black lines represent the identity line to show the different trend between the strongly and medium-strongly connected individuals (B and C) and the medium and weakly connected individuals (D and E).
speed of learning values that best fitted the data (see for example the distance profile in sampling 27 in Fig. 6.A4). As in the previous section, results were obtained after running $10^5$ replicates for each population and sampling with more than 2000 individual prey and predators. We simulated the diet of each individual predator $j$. The diet is given by the number of items of each prey species $n$ in the stomach content of individual predator $j$. We also simulated the number of individuals within each connectivity class $c$. We denote each simulated individual predator diet in class $c$ for all prey species $S$ as $x_{jc} = \{x_{Ja}, x_{Jb}, \ldots, x_{Jn}\}$. We compare the simulated diets with the empirical ones, $y_{jc} = \{y_{Ja}, y_{Jb}, \ldots, y_{Jn}\}$, across all the empirically observed and simulated predators (i.e., $D_c = [D_1, D_2, \ldots, D_T]_c$ and $S_c = [S_1, S_2, \ldots, S_T]_c$, respectively). $S$, $T_c$, and $\tau_c$ are the total number of prey species, the number of individual predators empirically sampled in class $c$, and the number of individual predators in class $c$ obtained by simulation, respectively. All individual predators $j$ have equal values at the outset with at least one of the $x_{jc}^S$ values larger than 0 for all $j$.

Figure 6.4  **Strength of prey selection (species, sampling dates, and data pooled).** Strength of prey selection, $\Omega$ (y-axis), as a function of strongly (1) to weakly (4) connected predators (x-axis). (A) Strongly to weakly connected predators target preferentially dominant ($\Omega < 0$) and rare ($\Omega > 0$) prey, respectively. (B) Strongly and weakly connected predators target both dominant and rare prey. (C) Strongly to weakly connected predators target preferentially dominant and rare prey, respectively. Red, orange, blue and black (Filled dots in the print version) dots represent the classes for the species, sampling dates and the pooled data outside the range predicted by the neutral density-dependent prey selection model, respectively. Strength of prey selection values plotted in these colours has Bayes factor values $>3$. 

![Figure 6.4](image-url)
As in the fitting for the speed of learning, we calculated the distance between model predictions and the empirical data as the sum of the absolute values of the misfits for each connectivity class $c$ as follows (Tarantola, 2006)

$$\rho\left(d^1_{c}, d^2_{c}, \ldots, d^S_{C} | \alpha, \Omega_c\right) = \left[\sum_{j=1}^{\nu} \sum_{n=1}^{S} \log \left( P\left(d_{j,n}^c | s_{j,n}^c\right) \right)\right] \times \left| T_c - \tau_c + 1 \right| \xi,$$

(6.12)

where $d_{j,n}^c$ and $s_{j,n}^c$ are the empirical data and the model prediction of the number of prey items per individual predator $j$ for prey species $n$ for each of the four connectivity classes, respectively. $\nu$ is the smallest number after comparing the empirical with the simulated individual predators in class $c$ and $\xi$ represents the number of comparisons when $d_{j,n}^c > 0$ and $s_{j,n}^c > 0$. The best fit is given by the parameter combination that: (1) maximizes the similarity between the empirical ($T_c$) and simulated ($\tau_c$) number of individuals in class $c$, (2) maximizes the number of comparisons between the empirical and simulated values, $\xi$, and (3) minimizes the absolute differences in the number of prey items per prey species across all prey species and across all the individual predators in class $c$. We used the standard rejection-ABC algorithm (Beaumont, 2010; Sunnåker et al., 2013; Toni and Stumpf, 2010) that works as follows

1. Generate $\theta$ from the prior where $\theta = [\alpha, \Omega_c]$. $\alpha$ values were randomly chosen from the CI range that best fitted the data for each population and sampling. The strength of prey selection values for each class, $\Omega_c$, were chosen from a uniform distribution with ranges $U[-30,30]$, $U[-100,-30]$, and $U[30,100]$ for the neutral, ($H_{0\nu}$, negative, ($H_{-\nu}$, and positive, ($H_{+\nu}$, density-dependent prey selection models, respectively. For the negative and positive density-dependent prey selection scenarios, we ranked the randomly obtained $\Omega_c$ values for each class with the abundance values.

   We remark an strict neutral model would imply to sample values close to 0. We relax the neutral model to allow for a more conservative nearly neutral model and use strength of prey selection values in the range $U[-30,30]$.

2. Simulate the diets, $S_c$, from each run with parameter $\theta$.

3. Calculate distance for $\rho(S_c, D_c)$ between simulated ($S_c$) and empirical data ($D_c$).

4. Reject $\theta$ if $\rho(S_c, D_c) > c$. 
2.4.2 Occam factor

The best-fit distance value gives us a first support for each model. In order to find the evidence supporting each model, we also need to quantify the penalization for each model given the data. That is to say, how much of the prior variance, the one given by the initial uniform distribution, is lost after taking the data into account, the variance in the posterior distribution. One way to find evidence for each model is by taking the best-fit distance that the model can achieve and multiplying it by an “Occam factor” (MacKay, 2003). The “Occam factor” is a term whose value is less than one that penalizes each model for having the strength of selection parameter, \( \Omega_c \).

The evidence for each model, \( (H_{ci} = [(H_{c0}, (H_{ci} \rightarrow), and (H_{ci}^{+}]), or the probability to reproduce the empirical data for each connectivity class \( c, D_i \), given each model, \( H_{ci}, P(D_i | H_{ci}) \), reads as follows

\[
P(D_i | H_{ci}) \sim P(D_i | L'(\alpha, \tilde{\Omega}_c), H_{ci}) \times \sigma_{H_{ci}} / \sigma_{H_{ci}} \tag{6.13}
\]

where \( P(D_i | L'(\alpha, \tilde{\Omega}_c), H_{ci}) \) is the minimum distance from model \( H_{ci}, \sigma_{H_{ci}} | D_i \) is the posterior variance of the strength of selection parameter, \( \Omega_{ci} \) given the data, and \( \sigma_{H_{ci}} \) is the prior variance of the strength of selection parameter, \( \Omega_{ci} \). As we have assumed that the prior is uniform on a fixed interval, representing the range of values of the strength of prey selection that were possible a prior, then the Occam factor is

\[
\text{Occam factor} = \frac{\sigma_{H_{ci}} | D_i}{\sigma_{H_{ci}}} \tag{6.14}
\]

or the factor by which each model space collapses when the data arrive (Gregory, 2005; MacKay, 2003).

2.4.3 Bayes factor

Once we have the metrics to quantify the best-fit distance values given by each model and the penalization for each model given the data, we can now compare each pair of models to quantify the model that best explain the data. We will use the Bayes factor, \( K_{H_{ci}}, (H_{cj}) \), to do so and it is given by

\[
K_{H_{ci}, H_{cj}} = \frac{P(D_i | H_{ci})}{P(D_i | H_{cj})} \tag{6.15}
\]
where $K_{H_dH_g} < 1 : 1$, $K_{H_dH_g} > 3 : 1$, $K_{H_dH_g} > 10 : 1$, and $K_{H_dH_g} < 100 : 1$, supports model ($H_{g}$), supports model ($H_{d}$), substantial support for model ($H_{d}$), and strongly supports model ($H_{d}$), respectively (Jeffreys, 1961). Bayes factor values reported were obtained by comparing the positive (or negative) density-dependent prey selection model with the neutral density-dependent prey selection model with the condition $K_{H_cH_o} + K_{H_cH_o}/C_0 > 3:1$ provided $K_{H_cH_o} + K_{H_cH_o}/C_0 > 3:1$. Otherwise we consider there is no support for the positive or negative density-dependent prey selection model.

3. RESULTS

3.1. Rate of learning and the distribution of predator connectivity

In order to estimate the rate of learning, we used groups with greater than 2000 predator and prey individuals sampled. This sampling size was sufficient to stabilize the variance in connectivity (Fig. 6.A2). A total of 13 of the 62 predator populations (Fig. 6.A2A) and 11 of the 95 samplings (Fig. 6.A2B) have more than 2000 prey and predator individuals sampled and were used to estimate the speed of learning, followed by an analysis to detect individual variation in prey selection. In all of these cases, including for the pooled analysis of all the data, the distribution of predator connectivity obtained from the model without learning (i.e. $\alpha = 0$ in Eq. 6.1) strongly deviates from the empirical data (Fig. 6.2). By contrast, the learning model ($\alpha > 0$ in Eq. 6.1, and red lines in Fig. 6.2) predicts the variance of the distribution of predator connectivity at population level (Figs. 6.2A and 6.A3), across multiple samplings (Figs. 6.2B and 6.A4), and for all the data pooled (Fig. 6.2C). Overall, the distribution of the speed of learning values, $\alpha$, was always in the range [0.01–0.5]. The learning model consistently captured the strongly and weakly connected individual predators, but it often failed to capture the distribution of the medium and medium-strongly connected predators (Appendix Figs. 6.A3 and 6.A4). Nevertheless the dramatic improvement of the model with versus without learning suggests that this learning trait is an important parameter to model and to carry forward for the analysis of individual variation in prey selection (from Fig. 6.1A to B).

The length of individual predators at intra-specific level explains both the mean length of prey and the total number of prey in 6 of the 13 environmental conditions with more than $2 \times 10^3$ prey and predator sampled ($R^2 = [0.22, 0.46]$, and $R^2 = [0.21, 0.61]$ and all $p < 0.01$, respectively) (Appendix Fig. 6.A5). At the sampling level, the length of individual
predators explains the mean length of prey and the total number of prey in 3 and 1 samplings of the 11 samplings with more than 2000 prey and predator sampled, respectively. These patterns suggest there is a trend at intra-specific level with individuals with a few or several prey of small and large size, respectively, but there is also substantial variation across individuals with few or several prey of similar length.

3.2. Variation in the strength of prey selection among individuals

Our observation of non-zero rates of learning estimated at the population level, suggests that successful prey captures leading to an increasing probability of future predation success (i.e., learning) is an important mechanism driving predator connectivity. This is true, even in absence of individual-level variation in the speed of learning. However, to discriminate active prey selection from a random encounter model we need to take into account the empirical observations of resource abundance and the profitability function for each predator individual. If prey occurs in the observed gut of individual predators more or less frequently than prey abundance in the environment, then these deviations suggest density-dependent resource selection by individual predators. In such a scenario, diversity in food webs will depend on the preference of predators for rare versus common prey (Fig. 6.1B). To detect such scenarios, we tested for prey selection for each sampling date (pooling across species), for each predator species (pooling across sampling dates in similar environmental conditions), and for the entire dataset.

Analysis of pooled dataset— We found that predators with many prey items in their gut preferentially consume common resources (i.e., negative density-dependent prey selection, best fit and CI in orange lines (light grey lines in the print version), Fig. 6.3B and C), while predators with few prey items preferentially select rare prey (i.e., positive density-dependent prey selection, best fit, and CI in red lines (dark grey lines in the print version), Fig. 6.3D and E). The best fits for the speed of learning, \( \alpha \), did not differ significantly across connectivity classes (Kolmogorov–Smirnov test for all pairwise comparisons, \( p > 0.1 \)), but the sign and the strength of prey selection, \( \Omega_c \), differed significantly between the weakly (and medium) and strongly (and medium-strongly) connectivity classes (Kolmogorov–Smirnov test for all pairwise comparisons between predator connectivity classes, \( p < 0.01 \), Figs. 6.3 and 6.4C).

Analysis by predator species—Strongly and weakly connected individual predators selecting preferentially common (i.e., positive prey selection,
Ω₁ > 0) and rare (i.e., negative prey selection, Ω₄ < 0) resources were observed in 22 of the 48 groupings of predator species pooled across samplings. Weakly and medium connected individuals select preferentially rare prey in 12 combinations (positive density-dependent prey selection, Fig. 6.4A) whereas medium-strongly and strongly connected individuals select preferentially common prey in six combinations (negative density-dependent prey selection, Fig. 6.4A).

Analysis by sampling date—Strongly and weakly connected individual predators selecting preferentially common (i.e., positive prey selection) and rare (i.e., negative prey selection) resources were observed in 31 of the 43 sampling dates pooled across species. Weakly and medium connected individuals select preferentially rare resources in 8 samplings (positive density-dependent prey selection, Fig. 6.4B), while medium-strongly and strongly connected individuals select preferentially common resources in 10 samplings (negative density-dependent prey selection). Strongly and weakly connected individuals select preferentially rare and common resources in 4 and 9 combinations, respectively (Fig. 6.4B). Similar to our analysis by predator species, our analysis of each sampling date revealed that predators in different connectivity classes shared both evidence for positive and negative density-dependent prey selection. In contrast, however, the shift from negative to positive prey selection with decreasing predator connectivity was less evident (Fig. 6.4A vs. B).

Summary—Overall, these results suggest that there is ample evidence for intra-population variation in the strength of prey selection by predators. It is equally common to observe such variation within species as across species within a given sampling. Our results also suggest neutral density-dependent prey selection with rare and common resources occurring in the observed gut of the weakly and strongly connected individuals, respectively.

4. DISCUSSION

The patterns of predator connectivity and prey selection presented in this study may be a consequence of strongly and weakly connected predators actively foraging in a system in which prey are distributed in a spatially heterogeneous and patchy manner. Strongly connected predators (or fast prey finders) could result from individuals preferentially searching the most abundant prey species in high-density but species poor patches. A strongly connected predator that finds this kind of patch will then be highly connected to just one or a few common prey species that are highly profitable for this
individual predator. Conversely, weakly connected predators could result from individuals preferentially searching low-density patches with a large number of rare prey species. A weakly connected predator will then be weakly connected to more than one rare prey species that are highly profitable for these weakly connected predators. These mechanisms are taken into account in our modelling framework and suggest that individual-level traits in prey selection of spatially heterogeneously distributed resources can drive patterns of species diversity and coexistence in multi-trophic ecosystems. Patterns of coexistence will ultimately depend on the frequency of individual predators that promote (i.e., strength of prey selection $\Omega < 0$) or inhibit diversity (i.e., strength prey selection $\Omega > 0$) (Fig. 6.1).

### 4.1. Intra-specific variation in prey selection

The patterns of intra-specific variability reported in this study may help to reconcile the mechanisms promoting variation within natural populations with the patterns that promote or inhibit diversity in ecological networks. It has been shown that non-random interactions among species can increase diversity (Bastolla et al., 2009), but non-random interactions among species can also decrease diversity if, as shown here, most weakly connected individuals across predator populations are preferentially selecting rare prey. Nestedness and compartments may increase coexistence and diversity in food webs (Bastolla et al., 2009), but the connection between the empirical evidence of nested diets within populations (Araújo et al., 2010; Bolnick et al., 2007; Cantor et al., 2012; Pires et al., 2011) and food web diversity is still at an incipient stage. Nestedness and compartments at species level can be obtained from at least two scenarios of intra-specific variability with opposite consequences for species diversity: either strongly and weakly connected individuals selecting common and rare prey, respectively, or alternatively strongly and weakly connected individuals selecting rare and common prey, respectively. Because the number of strongly connected individuals in large networks may be orders of magnitude lower than the number of weakly connected individuals, the species-level effects on diversity and stability of these two opposite intra-specific level patterns may differ significantly. We found that highly connected individual predators are preferentially selecting common prey, so they promote rather than limit prey diversity because their overall effect on extinction probability of resource species is lower than we would expect based on their number of interactions. The opposite is true for weakly connected individuals. They preferentially
select rare resources and thus their effect on extinction probability of resource species is larger than we expect based on their low number of interactions. Hence, the greater the proportion of weakly connected individuals consuming rare resources, the more pronounced their negative effect on diversity in the network will be.

### 4.2. Connecting the strength of prey selection and diversity in food webs

In the context of biodiversity theories, current models can explain species abundance patterns for many groups (Allen and Savage, 2007; Rosindell et al., 2011), but most of these approaches do not explain patterns of intra-specific variation in ecological interactions nor their implications for diversity patterns in ecological networks and multi-trophic ecosystems (Bolnick et al., 2011; Violle et al., 2012; Volkov et al., 2009). The models we have developed in this study explore a plausible set of mechanisms that may be useful as a benchmark to predict the empirical patterns of predator connectivity within samplings and populations. In cases where we do not identify significant prey selection, this could occur due to the lack of power or because of stochastic variation in prey selection driven by random encounter processes (Fig. 6.4, open circles). Further work is needed to investigate the temporal consistency of individual diet variation (Bolnick et al., 2003; Sih et al., 2012), for example, by exploring patterns between individual diet variation and morphology (Matthews et al., 2010).

In general, the fit of our models might be improved by considering additional traits. We have studied only learning as a trait involved in prey selection but individuals may differ in diet and prey selectivity for a variety of additional reasons including genetic components, size, sex, morphology, metabolic rates, or physiology (Bolnick et al., 2003). Traits involved in these characteristics of individuals may combine in unexpected ways to improve predictions in resource selection in heterogeneously distributed resources. Analysis combining some of these components like individual size and morphology (Beckerman et al., 2006; Ingram et al., 2011; Woodward et al., 2010), learning in foraging groups (Giraldeau and Caraco, 2000), and genetic and phenotypic characteristics are likely required to improve the predictions we present in this study so as to further disentangle the effect of multiple traits in resource selection at individual level and their effect on diversity in food webs (Bolnick et al., 2011). From our results, it is not entirely straightforward to infer the consequences for food web stability...
and dynamics. Although the majority of individuals exhibit destabilizing preference for rare prey (≈95% of individuals in our food web are weakly connected), these same individuals consume comparatively few prey per capita, which may mitigate their destabilizing effect. Conversely, highly connected individuals tend to prefer common prey with stabilizing effects on prey populations and although these strongly connected individuals are rare in the samplings they also consume large number of prey. Previous theoretical studies have shown the allocation of species diversity to slow energy channels within food webs and how these slow energy channels result in the skewed distribution of interaction strengths that has been shown to confer stability to food webs (Rooney and McCann, 2012). Further theoretical and empirical research are required to explore the connection between slow and fast prey finders (i.e., weakly and strongly connected individuals, respectively) to slow or fast energy channels and the net effect of these opposing trends within species on interaction strength and food web dynamics and stability. For example, under which conditions does interaction strength driven by intra-specific variation in prey selection embedded in food web dynamics yield different outcomes than a species-mean based approach?

4.3. Connecting trait variation with eco-evolutionary food web dynamics

In the present study, we develop individual trait-based models that contain two basic parameters, namely, the speed of learning and the strength of prey selection. These two parameters drive individual choices of resource selection with fast prey finders preferentially targeting common prey and slow prey finders preferentially targeting rare prey. The model predicts that given a non-zero and equal rate of learning for all the individuals, variation in prey selection among individuals is driven by the different rates in successful experience attacking common and rare prey. This result suggests that accumulation of experience from successful prey captures lead to an increasing probability of predation of similar prey types. Some individuals become highly specialized fast prey finders in a type of prey that is, as observed in the empirical data (Figs. 6.3 and 6.4), a common resource. On the other hand, there are individuals that become highly specialized slow prey finders in a type of prey that is rare in the environment, even if they have the same speed of learning as the fast prey finders (Figs. 6.3 and 6.4).
The observed individual variation in prey selection within and among predator populations is a first step towards understanding the potential for eco-evolutionary dynamics in natural populations. It has been shown that feedbacks between the ecological and evolutionary time scales may be common in prey–predator interactions (Yoshida et al., 2003), but it is an ongoing challenge to obtain datasets to infer both the fitness variation among individual predators so as to estimate subsequent evolutionary effects (Fig. 6.5). Consider a scenario where a population of predators consists of both strongly (Fig. 6.5A, red bars (light grey bars in the print version)) and weakly connected predators (Fig. 6.5A, black bars) selecting preferentially common and rare prey, respectively. In order to test for eco-evolutionary dynamics in such a scenario, we would want to assess fitness differences among predator classes (or phenotypes) and track longer term patterns in class (phenotype) frequency through time (Fig. 6.5C). With the present data and modelling we were able to infer different types of density-dependent prey selection from individual predators for a given ecological time scale, but we were unable to estimate how such variation in prey

\[ \Omega(x) \]

Figure 6.5  Strength of prey selection, fitness, and frequency in time. (A) The frequency of strongly (red (light grey in the print version)), medium, and weakly (black) connected individuals as a function of the strength of prey selection, \( \Omega \) (x-axis), for the species *Engraulis encrasicolus* in the temperature and salinity range 22–29 °C (summer) and 6–12 (medium salinity). (B) A hypothetical scenario where the fitness of each class varies as a function of the strength of prey selection, \( \Omega \) (x-axis). In this scenario, strongly connected individuals (red dot (light grey dot in the print version)) selecting preferentially the most common prey have higher fitness than weakly connected individuals (black dots). As a consequence, the frequency of the strongly and weakly connected individuals increases and decreases in this population with time, respectively (C).
selectivity might drive frequency-dependent selection pressures experienced by these interacting populations.

4.4. Conclusion

Understanding the mechanisms driving predator connectivity, and how such variation determines the strength of prey selection in high-resolution food web data present several open challenges. In the present study, we have developed individual-based models (Figs. 6.1 and 6.2, orange lines (light grey lines in the print version)) to quantify the speed of learning and the strength in resource selection across predators with different connectivity. By examining these models under different parameter combinations and confronting them with high-resolution individual-level data, we can ascertain the factors driving resource selection in weakly and strongly connected individual predators. The more standard approach of using population level to develop food web and ecological network theory, may fail to anticipate the mechanisms driving species extinction, coexistence, and diversity in multi-trophic ecosystems.

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APPENDIX. SAMPLING METHODS

Four daily samples were collected monthly for 1 year period (February 1998 to January 1999) at two sites (oligohaline, o, and polyhaline, p, stations) in the Guadalquivir estuary, southern Spain. The Guadalquivir estuary is a well-mixed temperate estuary with a gradual horizontal change in salinity and a clear seasonal temperature cycle. We selected polyhaline (20 ± 10.1) and oligohaline (3.7 ± 2) sampling stations, situated at 8 and 32 km, respectively, from the river mouth. The samples were collected at the new moon at each sampling site from a traditional fish boat anchored on the left river side. Samples consisted of passive hauls, lasting 2 h, made during the first 2 h of each diurnal and nocturnal flood and ebb tide. Sampled were taken with three nets working in parallel. Nets were made with polyamide gauze of 1 mm and an opening of 2.5 m (width) × 3 m (depth). At the start of each sampling, water temperature and salinity were measured.
SAMPLINGS AND POPULATIONS ACROSS ENVIRONMENTAL GRADIENTS

To test whether patterns of individual-level variation are robust across environmental gradients, we have categorized the samplings in 9 conditions of salinity and temperature: [0–6 (low salinity), 9–16 °C (winter), green (medium grey in the print version)], [12–36 (high salinity), 9–16 °C (winter), light grey], [0–6 (low salinity), 16–22 °C (spring-fall), blue (dark grey in the print version)], [6–12 (medium salinity), 16–22 °C (spring-fall), cyan (medium grey in the print version)], [>12–36 (high salinity), 16–22 °C (spring-fall), turquoise (medium grey in the print version)], [0–6 (low salinity), 22–29 °C (summer), orange (medium grey in the print version)], [6–12 (medium salinity), 22–29 °C (summer), brown (medium grey in the print version)], [12–36 (high salinity), 22–29 °C (summer), red (dark grey in the print version)], and [6–12 (medium salinity), 9–16 °C (winter), violet (dark grey in the print version)]. At population level, all individuals of the same species were pooled in each of the nine conditions even if individuals

Figure 6.A1 Distribution of predator connectivity. (A and B) The number of connections observed in each individual predator (number of prey items, y-axis) in each of the 95 oligohaline, (o), or polyhaline, (p), samplings since February 1998, $F_o$ and $F_p$ to January 1999, $J_o$ and $J_p$ (x-axis) for the fish species Engraulis encrasicolus, a, and for all the fish predators, b. Colours tones (Grey tones in the print version) indicate samplings in each salinity and temperature combination.
Figure 6.A2 Sampling effort. (A) Represents the variance in the number of prey items (y-axis) as a function of the number of prey and predator individuals sampled for all the species (x-axis). Predator species are: *Aphia minuta* (black), *Argyrosomus regius* (violet; dark grey in the print version), *Cyprinus carpio* (blue; dark grey in the print version), *Dicentrarchus punctatus* (orange; grey in the print version), *Engraulis encrasicolus* (red; dark grey in the print version), *Liza ramada* (green; dark grey in the print version), *Liza saliens* (maroon; black in the print version), *Pomatoschistus* spp. (cyan; grey in the print version), *Pomadasys incisus* (magenta; grey in the print version), and *Sardina pilchardus* (indigo; dark grey in the print version). (B) Represents the variance in the number of prey items (y-axis) as a function of the number of prey and predator individuals sampled (x-axis) for all the samples. To detect shifts in the relationship between the number of individuals sampled and the variance in the number of prey items, we used split-line regression. Provided that a shift was detected in the slope of the regression, a threshold of approximately 2000 individuals was detected for both the species and the sampling data. We analyzed the data points that were higher than 2000 individuals (dotted line).
Figure 6.A3  Distribution of predator connectivity in populations. x-Axis and y-axis represent the predator rank from strongly to weakly connected and prey abundance in guts, respectively. Black dots represent the empirical distribution for each temperature-salinity combination with more than 2000 individual prey and predators sampled. Solid red (dark grey lines in the print version) and orange lines (light grey lines in the print version) represent the mean and CI from the model with and without learning after $10^5$ replicates, respectively.
**Sampling 1**

*T*(9–16), *S*(12–36)

**Sampling 9**

*T*(16–22), *S*(12–36)

**Sampling 17**

*T*(16–22), *S*(12–36)

**Sampling 24**

*T*(22–29), *S*(0–6)

**Sampling 27**

*T*(16–22), *S*(12–36)

**Sampling 32**

*T*(22–29), *S*(12–36)

**Sampling 48**

*T*(22–29), *S*(12–36)

**Sampling 56**

*T*(22–29), *S*(6–12)

**Sampling 80**

*T*(9–16), *S*(12–36)

**Sampling 95**

*T*(16–22), *S*(6–12)

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**Figure 6.A4 Distribution of predator connectivity in samplings.** Represents the distribution in individual connectivity for each sampling. x-Axis and y-axis represent the predator rank from strongly to weakly connected and prey abundance in guts, respectively. Black dots represent the observed species distribution for samplings with a specific temperature–salinity combination and with more than 2000 individual prey and predators sampled. For the Sampling 27, we show the distance profile with the x-axis and y-axis representing the speed of learning, \( \alpha \), and the distance values (Eq. 11 in the main text), respectively. Solid red (dark grey lines in the print version) and orange lines (light grey lines in the print version) represent the mean and CI from the model with and without learning after \( 10^5 \) replicates, respectively.
belonging to the same species were collected in different samplings (Figs. 6.2A, 6.4A, and 6.4A). At sampling level, all individuals from the different predator species were pooled (Figs. 6.2B, 6.4B, and 6.4A). Finally we pooled all samplings and all predators (Figs. 6.2C, 6.3, and 6.4C).

REFERENCES


