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On the evolution of trophic position

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Abstract

The trophic structure of food webs is primarily determined by the variation in trophic position among species and individuals. Temporal dynamics of food web structure are central to our understanding of energy and nutrient fluxes in changing environments, but little is known about how evolutionary processes shape trophic position variation in natural populations. We propose that trophic position, whose expression depends on both environmental and genetic determinants of the diet variation in individual consumers, is a quantitative trait that can evolve via natural selection. Such evolution can occur either when trophic position is correlated with other heritable morphological and behavioural traits under selection, or when trophic position is a target of selection, which is possible if the fitness effects of prey items are heterogeneously distributed along food chains. Recognising trophic position as an evolving trait, whose expression depends on the food web context, provides an important conceptual link between behavioural foraging theory and food web dynamics, and a useful starting point for the integration of ecological and evolutionary studies of trophic position.

KEYWORDS
food webs, intraspecific variation, natural selection, phenotypic plasticity, trait evolution, trophic position

INTRODUCTION

Trophic position is a continuous measure of an organism's position in relation to the transfer of energy from the bottom to the top of a food web (Box 1) (Levine, 1980). The variation in trophic position among species, populations and individuals is a defining feature of food webs, and can strongly influence the dynamics and stability of natural ecosystems (Arim & Marquet, 2004; Ingram et al., 2009; McCann et al., 1998; Pimm, 1991; Post, 2002a; Rooney & McCann, 2012). Ecological research has focused on the causes of variation in trophic structure among food webs across ecosystems (Bell, 2007; Hatton, 2015; Potapov et al., 2019; Shurin et al.,

2006), as well as variation in trophic position among and within the constituent species of food webs (McMeans et al., 2019; Tewfik et al., 2016). In addition, evolutionary research has investigated the origins of trophic novelty (Coll & Guershon, 2002; Cropp & Norbury, 2020; Denno & Fagan, 2003; Herrel et al., 2008) and the phylogenetic patterns of variation in trophic position among species (Burin et al., 2016; Ingram & Shurin, 2009; Muschick et al., 2012; Price et al., 2012). However, few studies have investigated how the ecological dynamics of natural selection can affect the evolution of consumer trophic position (Cropp & Norbury, 2020; Gibert & Yeakel, 2019).

Insights into the ecological causes and pace of trophic position evolution are evident from examples of

Box 1 How to calculate trophic position

The uptake and transfer of energy is a central feature of ecosystems, and consumers often derive their energy through multiple, complex pathways (Polis & Strong, 1996). Contrary to the concept of trophic levels, in which simple trophic topologies (i.e. food chains) and discrete levels of energy processing are assumed, measures of trophic position account for complex food web configurations. Trophic position is the weighted mean path length (i.e. the number of trophic transitions) taken by energy from primary producers to consumers, and thus represents a continuous measure of an individual's function in the flow of energy through a food web (Levine, 1980). Specifically, the trophic position of a consumer can be calculated as:

$$TP_i = 1 + \sum_{j=1}^{n} p_{ij} TP_j \tag{1}$$

where TP_i is the trophic position of consumer i, TP_j is the trophic position of prey type j, and p_{ij} is the relative contribution of j to the diet of i (Adams et al., 1983). Thus, while TP_j is determined by the prey environment of a consumer, p_{ij} can be dependent on consumer properties. For example, Gibert and Yeakel (2019) model p_{ij} as a function of a consumer's type two functional response to different prey types, in which the consumption rate C_{ij} of prey j by predator i, depends on prey-specific abundances R_j, attack rates a_{ij}, and handling times h_{ij}:

$$C_{ij} = \frac{a_{ij} R_j}{1 + a_{ij} h_{ij} R_j} \tag{2}$$

Prey-specific attack rates and handling times can vary among predator individuals, and covary with (potentially heritable) traits in predators, such as body size (Cuthbert et al., 2020). Thus, (heritable) trait variation in a consumer population can introduce variation in functional responses to different prey types, which in turn will affect the diet composition of an individual. This will lead to variation in trophic position among consumers, provided that the prey types differ in trophic positions (Figure 1).

There is a long history of calculating trophic position in ecology, and early approaches relied on estimations based on dietary data (Vander Zanden & Rasmussen, 1996; Williams & Martinez, 2004), however, a broad application of this approach was limited due to the low availability of dietary data for most natural systems. Over the past few decades, isotope analysis has become an increasingly standard method to estimate trophic position and is based on the accumulation of the nitrogen isotope ^{15}N in consumer tissue relative to their resources (Post, 2002b). Such isotope-based approaches have made time-integrated trophic position data more readily available to both ecologists and evolutionary biologist and is widely used to quantify trophic dynamics and estimate the trophic structure of food webs, and the trophic position of individuals.

the adaptation of consumers to new habitats and from adaptive radiations. For example, five rodent lineages in the family Muridae independently increased their degree of carnivory after colonising the Indo-Australian Archipelago (Rowe et al., 2016), whereas lizards from a largely insectivorous ancestral population that were experimentally translocated to an island in the Adriatic Sea evolved morphological features consistent with greater herbivory within ~30 generations (Herrel et al., 2008; Wehrle et al., 2020). The rapid evolution of diet and resource use is also characteristic of many adaptive radiations of consumers, where there is both rapid emergence and sustained diversity of trophic position variation among closely related species (McGee et al., 2020; Muschick et al., 2012; Reding et al., 2009). Radiations of East African cichlid fishes, for example, harbour considerable trophic diversity both among and within species-rich guilds (e.g. omnivores, and predators), providing

evidence for rapid evolution of trophic position of individual species, and rapid divergence among closely related species (Moser et al., 2018; Muschick et al., 2012). The rapid evolution of trophic position is also evident from other instances of ecological speciation of consumers (Arnegard et al., 2014; Matthews et al., 2010; Richards et al., 2021; Shi et al., 2021).

While considerable work has documented dramatic patterns of variation in trophic position among and within consumer species, much less is known about the ecological drivers underlying the expression and evolution of trophic position in food webs. The expression of an organism's heritable traits, such as body size (Bergland et al., 2008; Lafuente et al. 2018) and habitat choice (Rodriguez et al. 1992; Via & Hawthorne 2002), emerges from gene expression in a relevant environmental context. For trophic position of consumers, the food web is the relevant environmental context, and trophic
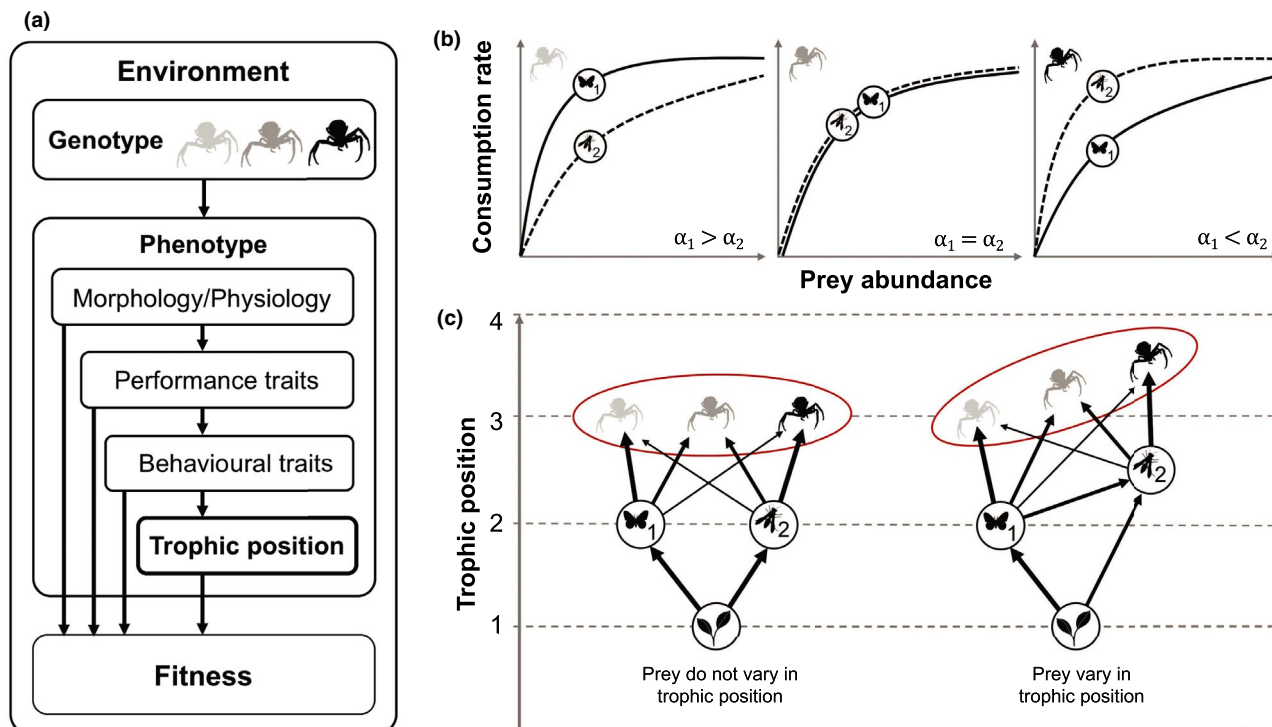
FIGURE 1   The food web context and consumer characteristics determine trophic position variation. (a) In a given environmental context, genetic differences between individuals can lead to phenotypic variation throughout the trait hierarchy that affects diet composition, which ultimately determines the trophic position of an individual. (b) For example, genotypes can differ in attack rates (α) on prey species (1 and 2), which affects their functional response (Box 1; Equation 2) and their diet composition (Gibert & Yeakel, 2019). (c) Such differences in diet (thickness of arrows) among genotypes leads to heritable variation in consumer trophic position when the prey species differ in trophic position (which is the case in the scenario on the right but not on the left)

position of consumers can evolve either when it is a direct target of selection or when it is correlated with other heritable traits under selection (Box 2). However, as we discuss below, the food web context of trophic position expression and evolution presents a challenge for (1) identifying the determinants of trophic position variation, (2) quantifying the heritability and genetic architecture of trophic position, (3) identifying putative mechanisms of the adaptive evolution of trophic position and (4) understanding the relevance of these mechanisms for explaining macroevolutionary patterns of trophic diversity in natural food webs.

DETERMINANTS OF TROPHIC POSITION VARIATION AMONG INDIVIDUALS

Trophic position is a quantifiable aspect of an individual organism that is expressed in a food web resulting from the sum of its trophic interactions (Box 1) (Levine, 1980). As a result, trophic position can change not only due to changes in an organism's diet (e.g. due to changes in foraging behaviour and/or performance) but also due to changes in the trophic position of dietary items. Thus, a challenge when identifying evolutionary shifts in trophic position is to distinguish variation in trophic position

due to phenotypic change in the focal population from variation arising solely from changes in the underlying food web structure. The dependence of trophic position expression on other organisms is somewhat analogous to the context-dependency of expression for other evolving traits: social dominance and social network position require meaningful variation in social interactions (Moore et al., 2002; Wice & Saltz, 2021), and boldness requires meaningful variation in risk (Réale et al., 2007). In natural populations, there is substantial opportunity for diet variation among individuals (Bolnick et al., 2003) to translate into intrapopulation variation in the expression of trophic position (Vander Zanden et al., 2000). Such diet variation can result from differences in the abundance, diversity and trophic structure of prey (Gibb & Cunningham, 2011; Lei et al., 2019; van Rijssel et al., 2017; Tewfik et al., 2016), as well as from individual differences in the ability to capture prey with different trophic positions (Araújo et al., 2011; Bolnick et al., 2003). Trophic position can also change over the lifespan of individuals, often as a consequence of transitions in resource use among different life stages or with increasing body size (Werner & Gilliam, 1984). For example, in some Lepidopterans trophic position changes following metamorphosis: in Hawaiian *Eupithecia sp.*, insectivorous caterpillars transition to herbivorous imagos (Montgomery, 1983), while in *Calyptra sp.* ('vampire

Box 2   A formal description of selection and evolution of trophic position

We can formally describe the evolutionary change in trophic position (TP) by substituting in the mathematical definition of TP (Box 1, Equation 1) into Price's theorem (Frank, 2012; Price, 1970), which provides a complete description of evolutionary change in a trait, yielding

$$\Delta \overline{TP} = cov\left(w, 1 + \sum_{j=1}^{n} p_j TP_j\right) + E(w\Delta TP)$$
$$= \sum_{j=1}^{n} cov(w, p_j TP_j) + E(w\Delta TP) \tag{3}$$

where $\overline{TP}$ is the mean TP of the focal consumer population and w is individual relative fitness. The first term on the right-hand side of Equation 3 describes the covariance between relative fitness and TP. This term is a selection differential describing within-generation change in TP due to selection ($\Delta\overline{TP}_s$; Lande & Arnold, 1983). The second term in Equation 3, $E(w\Delta TP)$ describes transmission bias, or fidelity of transmission of TP from parents to offspring. Thus, this second term captures effects such as imperfect heritability and changes in prey trophic position, including independent environmental changes in prey TP (e.g. arising from the insertion mechanism).

We can expand the first selection differential term of Equation 3 (assuming no third moments; Bohrnstedt & Goldberg, 1969), to gain insight into the contributions to selection of TP,

$$\sum_{j=1}^{n} cov(w, p_j TP_j) =$$
$$\sum_{j=1}^{n} [\overline{p_j} cov(w, TP_j) + \overline{TP_j} cov(w, p_j)] \tag{4}$$

Equation 4 indicates that two main sources contribute to the total selection of TP. The first term, $\sum_{j=1}^{n} \overline{p_j} cov(w, TP_j)$, describes the covariance between prey TP and consumer fitness, weighted by the proportional diet content of each prey type. This covariance term will be nonzero when prey j vary in their TP and this variation covaries with consumer fitness. The second term in Equation 4, $\sum_{j=1}^{n} \overline{TP_j} cov(w, p_j)$, fitness effects arising from variation in consumer diet content weighted by the average TP of the prey item.

Partitioning this selection differential illustrates that selection of TP can occur through independent contributions from the selection of prey TP and of diet content. These terms will reflect total selection; including that arising from selection for correlated traits even if diet or TP have no causal effects on fitness. To explore how causal effects on fitness contribute to total selection, we can define individual fitness explicitly,

$$w = \mu_w + \beta_{TP} TP + \sum_{j=1}^{n} \beta_{p,j} p_j + \epsilon \tag{5}$$

where a consumer's fitness is causally determined by both its TP ($\beta_{TP}TP$) and independently by its diet content ($\beta_{p,j} p_j$) (see also Lande & Arnold, 1983). Although we focus on selection on the actual traits (diet proportions), selection on linear combinations of traits (e.g. a PCA of diet content) can readily be transformed to such (Chong et al., 2018). Substituting this definition of fitness into Equation 4 and expanding yields

$$\Delta\overline{TP}_s = \sum_{j=1}^{n} \beta_{TP} \left[\overline{p_j} cov\left(TP, TP_j\right) + \overline{TP_j} cov\left(TP, p_j\right)\right]$$
$$+ \sum_{j=1}^{n} \sum_{k=1}^{n} \beta_{p,k} \left[\overline{p_j} cov\left(p_k, TP_j\right) + \overline{TP_j} cov\left(p_k, p_j\right)\right] \tag{6}$$

Equation 6 illustrates that direct selection on TP (β_{TP}) and direct selection on diet content (β_p) can both contribute to the total selection of TP. In both cases, the effects are mediated by the phenotypic (co)variances

Box 2   Continued

between TP and diet content. Note that we can arrive at an analogous expression to Equation 6, but where covariances are genetic, by expanding $cov\left(w, a_{TP}\right)$, where $a_{TP} = [\mu_{p_j} a_{TP_j} + \mu_{TP_j} a_{p_j} + a_{TP_j} a_{p_j}]$ is the genetic value for individual consumer TP, resulting in the breeders equation for TP.

This model *of TP evolution yields several insights. First, it illustrates that consumer TP* can influence fitness and selection completely independently of variation in diet content if variation in trophic position within a prey type exists. If such within-prey variation does not exist, causal fitness effects of consumer TP (β_{TP}) can still exist and contribute to total selection on TP and its evolution, and these effects are mediated by variation in diet (e.g. see Figure 4), specifically the phenotypic covariance between diet proportions and consumer TP, $cov(TP, p_j)$. Direct selection on diet content, β_p, generates a selection of TP even if there is no causal relationship between TP and fitness, and this effect is mediated by the phenotypic variance in diet, $cov\left(p_k, p_j\right)$ (note that this is variance where k = j), and the covariance between prey TP and diet, $cov\left(p_k, TP_j\right)$.

Second, this model illustrates that selection on TP can readily be measured and partitioned empirically. When fitness measures or proxies are available, total selection cov(w, TP) can be calculated and the parameters of Equation 5 estimated in a multiple regression (Lande & Arnold, 1983).

Although selection on TP may occur regardless of how variation in TP arises, TP must be transmitted from parents to offspring (measured at the same life stage) for evolutionary change in TP to occur. Although we may expect diet content to often be heritable (see main text), our model also illustrates that transmission fidelity of within-prey TP (TP_j), when it occurs, will also be important for the evolution of TP.

moths') herbivorous larva transition to blood feeding adults (Hill et al., 2010). In *Micropterus salmoides* (largemouth bass) trophic position increases as individuals grow larger, allowing them to switch from feeding on invertebrates to fish (Post, 2003). In this case, even within an age cohort of largemouth bass (i.e. young-of-the-year), individuals that hatched earlier in the season with higher growth rates were the first to transition to piscivory. While such ontogenetic niche shifts are common, studies rarely focus at the individual level on the developmental reaction norms of trophic position, so it is often unknown whether the trophic position trajectories over an individual's lifespan are heritable and how they might evolve, or not, over time.

In addition to arising from diet variation among individuals, trophic position can also change in response to changes in the underlying structure of trophic interactions in the food web (Figures 1c, 2). This can occur when determinants of food web structure, such as ecosystem size and productivity (Post, 2002; Post et al., 2000), are independent of a focal consumer's diet. For example, non-prey species of a focal consumer could be added or removed from a food web, causing a change in the trophic position of the focal consumer without any change in its diet (insertion mechanism; Figure 2) (Post & Takimoto, 2007). A similar effect could arise from altered trophic interactions among prey species in the food chain leading up to the focal consumer (Post & Takimoto, 2007). Such changes in trophic position might be prevalent in natural systems, however, they do not represent evolutionary change in trophic position because they are entirely driven by the external environment and can occur without any genetic or phenotypic changes in the focal population (e.g. if trophic structure changes but diet does not).
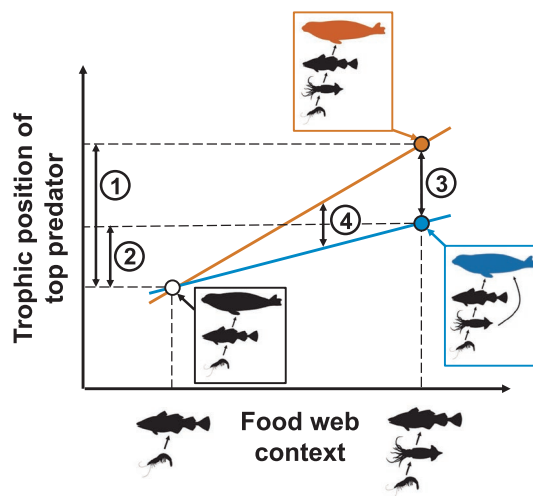

FIGURE 2 Shifts in the trophic position of a focal species (e.g. a seal in a marine food web) can result from multiple mechanisms. When there is a new food web context (e.g. the addition of squid to the food chain) the trophic position expression of a focal consumer can change either (1) without a diet change (see 'insertion mechanism' described in main text) or (2) with a diet change. Evolutionary change in trophic position can occur either (3) when there is heritable change in the mean trophic position of the population within a given food web context or (4) when there is a change across generations in the population distribution of norms of reaction for trophic position of different genotypes (i.e. orange and blue lines) and a variable food web context (i.e. variation in squid occurrence over time or space)

As we discuss further below, the more relevant sources of variation to understand the evolution of trophic position arise from the determinants of individual variation in diet, and the extent to which variation in the trophic position of dietary items can explain fitness variation within consumer populations.

The variation in trophic position relevant to understanding its evolution is that which arises from heritable phenotypic differences among individuals. There is growing evidence that variation in trophic position within populations can be correlated with heritable traits that are associated with foraging performance, such as body size, aspects of the foraging apparatus and behaviours (Cucherousset et al., 2011; Dumont et al., 2016; Matthews et al., 2010; McCarthy et al., 2004; Musseau et al., 2020; Post, 2003; Wagner et al., 2009). For instance, Matthews et al. (2010) showed a correlation between trophic position and gill raker morphology in *Gasterosteus aculeatus* (threespine stickleback)—a heritable trait that is relevant for foraging performance in the pelagic habitat of lakes (Robinson, 2000). Heritable behavioural traits, such as boldness, activity levels or prey selectivity, could also prove to be important determinants of trophic position variation. For example, intraspecific variation in the predatory seabird *Stercorarius skua* (great skua) likely arises from dietary specialisation (fish vs. seabirds), which in turn affects the levels of contamination with biomagnifying pollutants (Leat et al., 2019). However, previous reviews of such behavioural traits highlight the ongoing challenge of quantifying both their heritability and their role as determinants of individual diet variation (Araújo et al., 2011; Bengston et al., 2018; Sih & Bell, 2008).

Trophic position evolves within a hierarchy of heritable traits that collectively influence an individual's fitness in a given food web. Variation in survival and reproduction directly result from individual performance differences in an environmentally relevant context, such as foraging, avoiding predators and finding mates (Arnold, 1983; Garland & Losos, 1994). Underlying this variation are 'performance traits', such as prey capture rate, locomotor speed and olfactory perception that constrain which behaviour an animal can express in a given environment (Garland & Losos, 1994). Performance traits, in turn, are determined by multiple underlying morphological and physiological traits (Arnold, 1983). This morphology/physiology → performance → behaviour → fitness paradigm is a useful starting point for thinking about how selection acts on ecologically relevant traits, such as trophic position (Figure 1a) (Bolnick & Araújo, 2011). Trophic position is at a high-level in the trait hierarchy, arising from dietary differences among individuals that result from variation in behaviour, performance, physiology and morphology (Bolnick et al., 2003). As such, trophic position might integrate some of the fitness effects of multiple subordinate traits, as we discuss below.

HERITABILITY OF TROPHIC POSITION

Intraspecific variation in consumer trophic position likely emerges from both environmental and genetic determinants, though our understanding of the latter is relatively poor. Environmental variation can affect the availability and accessibility of resources, along with the distribution of trophic positions among prey (Gibb & Cunningham, 2011; Lei et al., 2019; van Rijssel et al., 2017; Tewfik et al., 2016). For example, the trophic position of *Ocypode quadrata* (ghost crabs) varies in relation to the width of their beach habitat, which determines the composition and trophic structure of their prey communities (Tewfik et al., 2016). Alternatively, variation in trophic position within a population may arise from phenotypic differences in resource exploitation that have underlying genetic causes (Figure 1). Heritability is crucial for traits to evolve by natural selection, and a variety of approaches exist to help understand how genetic and environmental factors interactively shape trait variation (Lynch et al., 1998). While these approaches have not been used to explicitly address the heritability of trophic position or its reaction norms, studies on the heritability and genetic basis of dietary variation, such as the degree of omnivory (Dumont et al., 2016), predation (Konczal et al., 2016), cannibalism (Wagner et al., 1999) or dietary specialisation (Richards et al., 2021) suggest that trophic position likely has underlying genetic causes. For instance, both predation rate and diet preference (animal vs. plant diet) of the omnivorous insect *Campylomma verbasci* (mullein bug) exhibit heritable variation, and jointly affect the expression of omnivory by individuals (i.e. trophic positions are between 2 and 3) (Dumont et al., 2016, 2017).

Despite our lack of understanding about the genetic basis of trophic position, its position in the trait hierarchy means it will likely be correlated with other heritable traits. In simple terms, if trophic position is largely determined by the expression of a heritable trait, then variation in trophic position would also have underlying genetic causes via mediated pleiotropy (Solovieff et al., 2013). There are some trivial situations, for example, when the potential for phenotypic variation is low (Figure 1c), where we would not expect to find heritability. We would expect limited heritability in populations where individuals feed on either few diet items (i.e. species with highly specialised diets), or many diet items with limited variation in trophic position (e.g. strict herbivores). Importantly, we expect limited heritability when the environmental conditions do not provide an opportunity for the expression of trophic position variation among individuals. The expected amount of heritability in trophic position will also depend on the underlying structure of the trait hierarchy. High-level traits, such as life history and behaviour, generally have low heritability (Mousseau & Roff, 1987) due to their proximity to fitness and cumulative environmental contributions to their expression (Price & Schluter, 1991). Therefore, as an increasing number of traits contribute to trophic position, we might expect the contribution of environmental sources of variation to increase and heritability to decrease.

As with other heritable traits whose expression varies with the environment, trophic position can be understood in the context of phenotypic plasticity, with the norms of reaction of trophic position measured in relation to variation in food web configuration (Figure 2). For example, Dumont et al. (2017) exposed multiple families of *Campylomma verbasci* to two different resource settings (diets of either only animals, or animals and pollen), and found that the time spent foraging on animals (i.e. a behavioural trait associated with trophic position) was heritable in both settings. Furthermore, families differed in their phenotypic response to the environmental treatments, such that some remained largely carnivorous irrespective of the resource environment, while others adopted a more herbivorous strategy when pollen was available (Dumont et al., 2017).

It is increasingly recognised that phenotypic plasticity may facilitate the emergence of morphological and dietary novelty (Sommer, 2020). For example, tadpoles of the genus *Spea* (western spadefoot toads) express plastically induced alternative morphs (omnivores vs. carnivores), depending on the presence of large animal prey in the environment (e.g. other tadpoles, fairy shrimp), whereas most closely related anurans produce only omnivorous tadpoles (Levis et al., 2018). These morphological and behavioural innovations in *Spea* that go along with an increase in trophic position, likely arose from the selection on ancestral, non-adaptive variation in reaction norms (refinement) between alternative resource environments that is still present in contemporary populations of closely related species (Levis et al., 2018). While the carnivorous morph is environmentally induced in most *Spea* species, some populations of *S.bombifrons* that live in sympatry with another *Spea* species produce carnivorous tadpoles irrespective of the environment (Levis et al., 2017). In these populations, genetic assimilation has likely led to the loss of environmentally induced variation in gene expression and the emergence of environment-independent novelty in morphology (Levis et al., 2017), and ultimately, to the evolution of trophic position within and among species (Levis et al., 2018).

EVOLUTION OF TROPHIC POSITION BY NATURAL SELECTION: DIRECT AND INDIRECT MECHANISMS

The environmental causes of fitness variation (agents of selection) can vary in consistent ways along food chains, and thereby generate covariation between trophic position and fitness (i.e. selection) (Box 2). Identifying these general patterns in how selective environments vary along food chains can help us predict whether shifts in trophic position result either directly from a covariance between trophic position and fitness, or indirectly from covariances between trophic position and other traits under selection (Box 2; Equation 6) (Price & Langen, 1992). With increasing height in the food chain, for example, we might expect: (1) a decrease in the overall biomass and thus of available energy (Arim et al., 2007), (2) a change in the strength of species interactions (e.g. competition) (Cropp & Norbury, 2020), (3) an increase or decrease in food quality (Denno & Fagan, 2003) and (4) an increase in the concentration of toxicants (Vander Zanden & Rasmussen, 1996). We explore each of these in turn.

Biomass is often unequally distributed across food webs and typically decreases with increasing trophic position (Hatton et al., 2015; Trebilco et al., 2013), although inverted trophic pyramids do exist (Woodson et al., 2018). As a result, trophic structure may constrain the upper trophic position limit of consumers, due to energy limitations on the maintenance of viable predator populations (Arim et al., 2007). However, the distribution of biomass along food chains can also impact fitness variation among individuals within consumer populations, and this relationship can change over time. For example, the evolutionary assembly of trophic structure in Lake Victoria, occurring over the past 15 000 years, has culminated in an incredibly trophically diverse food web of over 500 cichlid fish species (McGee et al., 2020; Seehausen, 2015). The evolution of predatory cichlid species probably occurred only after considerable population expansion and diversification of more generalist cichlids at lower trophic positions (Seehausen, 2015). At some point over the course of the radiation, omnivorous populations probably experienced positive selection for trophic position, potentially when there was sufficient fish biomass to favour more predatory individuals (Harmon et al., 2019).

The distribution of competitors along food chains can impose strong selective gradients that may influence the likelihood of trophic position evolution. In some cases, competition could promote the evolution of a higher consumer trophic position, for example, if it becomes more beneficial to prey upon a competitor than to compete for the common resource (Cropp & Norbury, 2020). In other cases, competition may cause the evolution of lower trophic positions of consumers. For example, the invasion of centrarchids (*Micropterus dolomieu* and *Ambloplites rupestris*) to lakes inhabited by *Salvelinus namaycush* (lake trout) has led to steep declines in the trophic position of *S. namaycush*, as they shift from a more piscivorous to planktivorous diet (Vander Zanden et al., 1999). In this particular example, the shift was likely due to plasticity, but such competitive interactions might cause selection against lake trout individuals that were less proficient at planktivory (e.g. due to morphological constraints).

Resource quality can vary in predictable ways between adjacent trophic levels, setting up the possibility for adaptive evolution of consumer trophic position. For arthropod consumers, food quality (in terms of nitrogen

content) differs between plants (poor quality) and herbivorous prey (high quality), and further increases with the trophic position of animal prey (Denno & Fagan, 2003). This distribution of nitrogen along the food chain may have fitness implications for consumers such as the jumping spider *Portia fimbriata*, which have better survival when feeding on higher trophic level prey (Denno & Fagan, 2003; Li & Jackson, 1997). As another food quality example, many of the phytosterols that are essential for the reproduction of the lady beetle *Coccinella septempunctata* are produced only by plants but not aphids. Therefore, lady beetles with a trophic position of 3 (foraging exclusively on aphids), would have lower fitness than those feeding as omnivores (i.e. trophic position <3) (Ugine et al., 2019).

Directional selection gradients for trophic position could result from biomagnification of organochlorine pollutants in food webs (Kiriluk et al., 1995; Vander Zanden & Rasmussen, 1996). If there is a positive correlation between the trophic position of organisms in a food web and pollutant concentration in tissues, then individual predators might face fitness costs when feeding on organisms at higher trophic levels (Leat et al., 2019). This could lead to negative selection gradients for trophic position within such predator populations. Indeed, for *Larus hyperboreus* (glaucous gulls), a top predator in arctic food webs, trophic position is positively correlated with pollution load (Sagerup et al., 2002), which, in turn, is negatively correlated with reproductive success and adult survival (Bustnes et al., 2003).

In addition to the food chain distribution of individual selective agents, covariation among multiple selective agents along food chains can also affect trophic position evolution. For example, the distribution of resource quality along food chains can covary negatively with the distribution of resource biomass (Fagan et al., 2002). Because both resource biomass and quality are potential agents of selection on the trophic position of consumers,

their covariation can lead to consumers trading off between foraging on high-quality and rare resources rather than low-quality and abundant resources. Such a trade-off has been proposed to explain the evolution of omnivory and intraguild predation in arthropods (Denno & Fagan, 2003). More generally, selection gradients for trophic position can emerge from the interaction of multiple, putatively independent, agents of selection (e.g. resource biomass and quality, pollutants, etc.), and from how such agents of selection are distributed across food chains (Figure 3).

In addition to the direct causal relationships between trophic position and fitness mentioned above, trophic position can also evolve as a correlated response to selection on genetically correlated traits (Box 2; Equation 6; second term). Genetic correlations between phenotypes can arise when a locus independently affects two phenotypes (biological pleiotropy) or when one heritable phenotype is causal for another phenotype (mediated pleiotropy) (Solovieff et al., 2013). It is well known that selection acting on one trait can affect genetically correlated traits, leading to an evolutionary response of traits that are unrelated to fitness (Price & Langen, 1992). For instance, artificial selection on four different behavioural traits underlying predation behaviour (consumption rate, conversion efficiency, dispersal and olfactory attraction to prey) of predatory mites (*Phytoseiulus persimilis*), led to correlated responses among these traits, and revealed genetic correlations in phenotypes related to predation (Nachappa et al., 2010). However, in this example the trophic position would not be affected, since the consumer is a specialist, (i.e. the evolution of predation behaviour is not affecting diet composition). Yet, similar heritable variation exists in consumers with diverse prey spectra (Dumont et al., 2017), and selection on phenotypes in the trait hierarchy might cause the evolution of trophic position, without it having direct fitness consequences (Dumont et al., 2018).
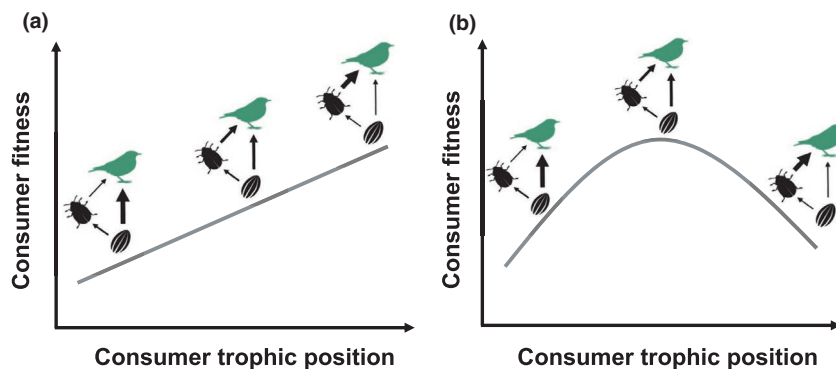

FIGURE 3 Trophic position can become associated with fitness variation when the fitness effects of the resources are structured along the food chain. (a) In a population of omnivores (i.e. individual birds ranging between trophic position 2 and 3) feeding on a higher trophic position can be positively correlated with fitness, for example, because animals are generally higher quality food than plants. (b) However, foraging entirely on animals might come with a fitness cost if they are less abundant than plants. This might create a trade-off between foraging on abundant resources (usually plants) and food quality (usually animals), creating selection gradients with an optimal trophic position for individuals with intermediate levels of animal prey in their diet

A prevailing challenge in evolutionary ecology is to determine the ecological mechanisms underpinning trait evolution (Henshaw et al., 2020; MacColl, 2011; Wade & Kalisz, 1990), and the same challenge holds for understanding the evolution of trophic position by natural selection. In a study of *Gasterosteus aculeatus* populations, Bolnick and Araújo (2011) found covariation among trophic position, foraging traits (gill raker morphology), and individual growth rate (a proxy for fitness). They used path analysis to partition the fitness effects of diet (trophic position and habitat use; estimated using isotopes analyses) and morphology, and found that diet explained fitness variation better than morphology, and that the apparent correlation between foraging morphology and fitness arises indirectly from a correlation between morphology on diet. In one (but not all) of the lakes in this study, individuals foraging at a lower trophic position diet attained higher growth rate, and trophic position explained more of the variation between individuals in growth rate than did habitat use (Bolnick & Araújo, 2011). Thus, in some situations trophic position can be under selection due to its effects on fitness, however, the ecological mechanisms that promote such situations are largely unknown.

DISCUSSION

Phylogenetic analyses of dietary preferences have revealed that macro-evolutionary shifts in both diet and trophic position are common in many clades, and often associated with eco-morphological variation among species (Burin et al., 2016; Ingram & Shurin, 2009; Muschick et al., 2012; Price et al., 2012; Román-Palacios et al., 2019; Shi et al., 2021). Such diversification is ultimately responsible for the emergence of trophic structure in ecosystems, and there is growing evidence that evolutionary processes play an important role in the emergence and structure of ecological networks in general (Segar et al., 2020), and food webs in particular (Gibert & Yeakel, 2019; Loeuille & Loreau, 2005; Segar et al., 2020). Trait differences among species arise from processes acting on intraspecific variation, and some study systems provide insight into how differences in trophic position between species can arise from genetic variation within populations (Levis et al., 2018; Richards et al., 2021). For instance, the increase in trophic position in *Spea* tadpoles likely arose from a refinement of ancestral variation in phenotypic plasticity in an omnivorous ancestral population, which led to the emergence of a novel polyphenism, and the subsequent fixation of carnivory (Levis et al., 2018). However, we know little about how ecological processes and natural selection jointly act on intraspecific variation in trophic position, and how this affects the evolutionary trajectories of populations, creating a gap in our understanding of how macroevolutionary patterns arise from microevolutionary processes.

So far, we have discussed the sources of intraspecific variation in trophic position and highlighted that variation among individuals is not only determined by the food web context but also by genetic factors underpinning associated fitness-relevant traits. We argue that trophic position, measured at the individual level, can be studied as a heritable quantitative trait that can evolve via natural selection (Box 2). However, whether it is generally useful to study trophic position as an evolving trait depends on its importance in explaining fitness variation relative to other causally linked traits, such as dietary variation (Figure 4). If the fitness of consumers is determined by the position of their prey in the food
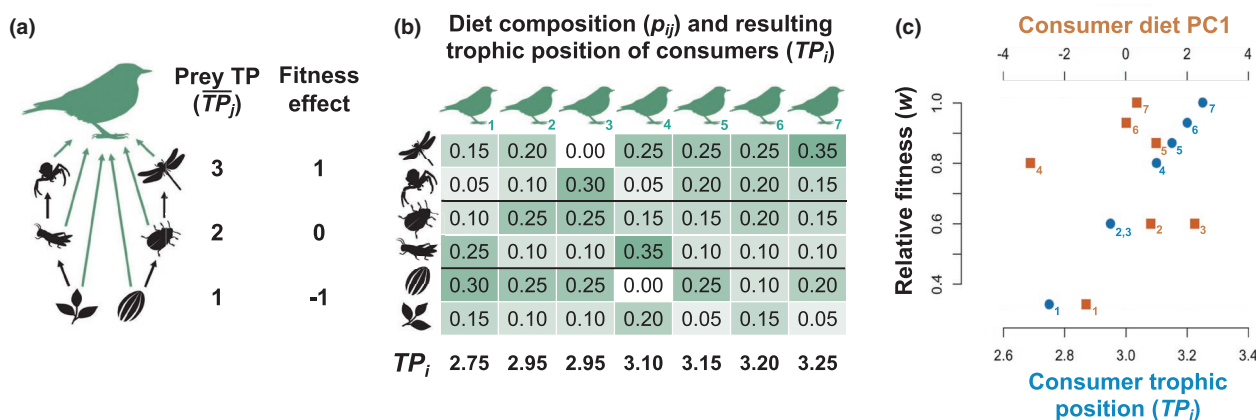

FIGURE 4 Causal fitness effects of consumer trophic position (β_{TP}) can be mediated by dietary variation (Box 2). (a) Prey items may vary in trophic position $\overline{TP}_j$ and in their effect on consumer fitness, and these fitness effects can be structured along the food chain (e.g. when nutritional quality increases along the food chain). (b) Differences in the dietary composition among consumers then lead to variation in consumer trophic position (TP; Box 1; Equation 1), as well as variation in fitness resulting from the covariance between p_j and fitness (Box 2; Equation 4). When consumers forage on a variable diet (in terms of both trophic position and prey identity) the link between diet and trophic position can decouple (i.e. individual consumers can have the same trophic position but different diets; note birds 2 and 3). (c) If the trophic position of prey has casual effects on fitness, the trophic position of the consumer can explain fitness variation that is unexplained by diet composition (i.e. illustrated here by a principle component analysis of the diet - PC1)

web, rather than other aspects of the prey, then trophic position will be the target of selection and diet will change as a correlated response. Identifying the target of selection is especially important because consumers can have different diets but identical trophic positions (Vander Zanden et al., 1997). Such 'many-to-one' mapping presents a general challenge for understanding the evolutionary causes of phenotypic variation because it decouples selection on high-level traits from the selection on underlying traits. For example, organism can apply different morphological solutions to resolve selection on mechanical performance (e.g. locomotion), which weakens parallel morphological evolution (Muñoz, 2019). 'Many-to-one' mapping of diet to trophic position may lead to different dietary outcomes resulting from selection on trophic position (Figure 4).

Gathering evidence of trophic position evolution

The strong environmental dependence of the expression of trophic position poses some challenges for comparative and experimental studies of trophic evolution. In the wild, patterns of trophic position variation along environmental gradients (i.e. phenotype-environment correlations: Figure 5a) can help generate some hypotheses about the drivers of trophic position evolution. However, such comparative approaches need to account for ontogenetic

(a) Phenotype-environment correlation

(b)　　　　　(c)　　　　　(d)

FIGURE 5 Hypothetical outcomes of a reciprocal transplant experiment on two populations with divergent trophic position: (a) From observational data, it is not possible to infer whether divergence in trophic position between two populations (fish) arises from different food web contexts or from genetic differences between the populations. Exposing individuals to the respective other food web context might reveal that (b) trophic position variation is entirely driven by the food web context (i.e. is fully plastic), (c) is entirely driven by the genetic identity of the individuals or (d) a combination of the two (i.e. genotype-by environment-interaction)

sources of variation in trophic position, and, more generally, variation that arises from genetic and/or environmental causes, specifically food web configurations. This can be done, for example, with breeding experiments and quantitative genetic analyses (Lynch et al., 1998), but such approaches have not been explicitly applied to trophic position. Indeed, combining estimates of trophic position (e.g. from stable isotopes, or dietary studies) with pedigree data (Kruuk et al., 2008), either in a comparative or experimental context, could reveal new statistical insights into the genetic variation underlying trophic position. Additionally, as with any heritable phenotype, one could attempt to identify regions of the genome that are associated with trophic position variation. This could involve treating trophic position as a continuous trait within a QTL framework (quantitative trait loci; where laboratory crosses have the possibility to feed on a variety of prey with varying trophic position, and the subsequent variation in offspring trophic position can be linked to inherited allelic variation) or in a GWAS (genome-wide association studies; where individual markers along the genome are correlated with trophic position across a large number of individuals) (Bengston et al., 2018). In both of these cases the number and distribution of loci associated with trophic position, along with the variance in trophic position explained by these loci could be elucidated. While challenging for behavioural traits, such approaches might help identify the genetic basis of trophic position variation and its underlying traits (i.e. traits lower in the hierarchy), provided that such studies are applied in appropriate food web contexts (Arnegard et al., 2014; Bengston et al., 2018).

Common garden experiments are another useful approach to isolate the influence of the food web context and genetic background on trophic position variation. By establishing a common garden food web design, one can isolate the role of genetic variation in determining trophic position. Furthermore, by including more than one common environment (e.g. food webs with contrasting structure), potential interactions between genotypes and environments can be revealed (i.e. variation in phenotypic plasticity/non-parallel reaction norms). A general challenge with trophic position is that it is highly dependent on the food web context, and artificial experimental food webs might not provide the meaningful context for trophic position expression. Therefore, common garden experiments involving reciprocal transplants in the wild (Figure 5) could be applied to ensure a more meaningful food web context. This approach would have the additional benefit of providing information about the fitness relevance of trophic position variation.
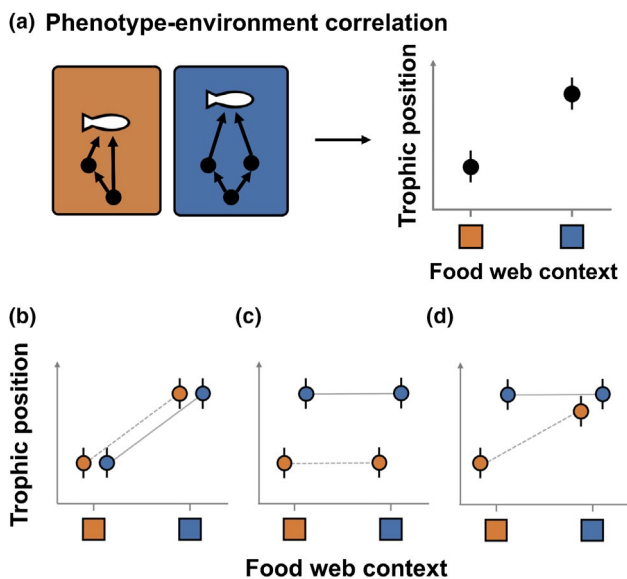
Concluding remarks

The idea of an evolving trophic position is not new to evolutionary biology. The origin and maintenance of trophic diversity is a central theme in adaptive radiation

research (Harmon et al., 2019; Muschick et al., 2012), and phylogenetic studies often focus on broad patterns of trophic position variation and transitions between trophic strategies across the tree of life (Burin et al., 2016; Price et al., 2012; Román-Palacios et al., 2019). Evolutionary ecologists often quantify variation in the trophic ecology of populations in contrasting environments (Zandonà et al., 2017), as well as in the context of micro- and macroevolutionary analyses (Arnegard et al., 2010; Ingram & Shurin, 2009; Wagner et al., 2009). At microevolutionary scales, models often describe shifts in resource use, including those that affect trophic position, and culminate in the emergence of multiple trophic levels (Cropp & Norbury, 2020; Ingram et al., 2009).

Here, we argue that viewing trophic position as a quantitative trait that can be correlated with fitness variation can provide novel insights into causal mechanisms of natural selection (i.e. how do traits evolve?). The robustness of such inferences inevitably depends on understanding the relationships between traits, fitness components and the environment (Henshaw et al., 2020). For example, classical evolutionary hypotheses linking intraspecific variation in morphology, diet and fitness, such as the niche variation hypothesis (Van Valen, 1965), are often not explicit about the trophic structure of the consumers' resources (Bolnick et al., 2007).

Models that examine the role evolutionary processes in structuring food webs typically involve selection on traits governing species interactions (e.g. via attack rates, body size, etc.) that ultimately lead to shifts in trophic position (Cropp & Norbury, 2020; Gibert & DeLong, 2017; Gibert & Yeakel, 2019; Loeuille & Loreau, 2005). However, they usually do not consider variation in trophic position as a potential source of fitness variation. In Box 2, we outline a standard evolutionary framework for studying trophic position of single consumer species that can also be expanded to understand coevolution of trophic position in complex food webs and other interactions. For example, when fitness functions of interacting species depend on evolving traits of each species, these interactions can be explicitly defined in the equations for fitness that are then used to expand Price's theorem to explore models of between-species coevolution (De Lisle et al. 2021). Such an integration of trophic position into the hierarchy of traits that contribute to fitness, might help discover new causal pathways connecting ecologically relevant traits with fitness, and improve our understanding about the evolutionary determinants of species interactions and food web structure.

AUTHORSHIP
All authors conceived and formulated the ideas presented. MM and BM led the writing of the manuscript, SDL formulated the mathematical model in box 2, and all authors provided critical feedback.

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