

Review

Integrating Competition for Food, Hosts, or Mates via Experimental Evolution

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Competitive interactions shape the evolution of organisms. However, often it is not clear whether competition is the driving force behind the patterns observed. The recent use of experimental evolution in competitive environments can help establish such causality. Unfortunately, this literature is scattered, as competition for food, mates, and hosts are subject areas that belong to different research fields. Here, we group these bodies of literature, extract common processes and patterns concerning the role of competition in shaping evolutionary trajectories, and suggest perspectives stemming from an integrative view of competition across these research fields. This review reinstates the power of experimental evolution in addressing the evolutionary consequences of competition, but highlights potential pitfalls in the design of such experiments.

What Does an Experimental Evolution Approach Add to the Study of Competition?

Competition (see [Glossary](#)) has been extensively studied using mathematical models ever since the Lotka–Volterra equations [1]. Following these classical models, numerous ecological experiments were conducted in the laboratory [2–4] and in natural populations [5], providing many examples of both exclusion and coexistence between species or phenotypes competing for resources. Since then, competition has been studied in many contexts, and three main types of competition have been described ([Box 1](#)).

Darwin identified competition as a source of evolutionary change [1]. In fact, one can argue that all evolution results from a competitive advantage of one genotype over another. However, there are specific questions pertaining to the role of competition, as an ecological interaction, on the evolution of populations. For instance, do traits improving **competitive ability** evolve, especially in the face of trade-offs with other life history traits [6,7]? How does competition drive **niche width**, that is, under which circumstances will individuals expand or contract the range of their resource use? When will **character displacement** evolve [8,9]? How do eco-evolutionary feedbacks, arising from how competition impacts the resource itself, change evolutionary responses? Unfortunately, study systems in which a causal link between competition and these evolved responses can be inferred are scarce [6,10,11]. Moreover, past competitive exclusion is nearly impossible to detect in the wild, a phenomenon coined as ‘the ghost of competition past’ [12]. Therefore, actual forces and mechanisms driving organisms’ distributions and traits, and their impact on ecosystems, are difficult to assess retrospectively, hampering a complete understanding of the reciprocal effects of competition on evolution.

Trends

Organisms compete for several resource types, the most studied being food, mates, and hosts.

The study of each resource type belongs to different research fields, each with its own idiosyncrasies, including distinct vocabulary.

There are similarities in patterns and processes across diverse research fields that implicitly or explicitly study competition, as in all cases, individuals are competing for the use of a limiting resource.

The use of experimental evolution as methodology allows for a complete understanding of the reciprocal effects of competition on evolution.

Experimental evolution can be transversally applied to studies of competition across diverse research fields, in view of establishing a common integrative framework.

An integrative view of competitive interactions creates new predictions and clarifies patterns observed.

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Box 1. Types of Competition

Competition can be categorised according to whether individuals are competing against individuals of the same or a different species (intraspecific and interspecific competition, respectively). Moreover, three types of competition can be distinguished, according to the mechanism that leads to fitness reduction in other individuals [1]:

Exploitative (or resource or scramble) competition is an indirect interaction, in which the consumption of a shared resource by some individuals entails a fitness cost for other individuals because these will be consuming a smaller share of the same resource. A classic example is competition between closely related beetle species (*Tribolium*) feeding on flour [4].

Interference (or contest) competition is a direct, negative interaction, often via attack, between individuals that use a common resource. A classic example of this is males fighting for access to females, for instance, in dung beetles [62].

Apparent competition is a top-down indirect interaction leading to a fitness reduction in individuals that share an upper level resource (predator/host/female) [63]. For example, parasites can trigger the immune system of their host with negative consequences for other parasites sharing the same host [64,65].

Although in some cases the distinction among these three types of competition is straightforward, in others it can be a difficult task. For example, sperm competition can be exploitative if some sperm have better swimming ability, or interference competition when sperm produce toxins that destroy other sperm types (Table 1). For instance, in *D. melanogaster*, it was initially postulated that the ejaculate of the first male was destroyed by that of the second inside the female, suggesting interference competition [66], but later more detailed studies demonstrated that sperm displacement, hence exploitative competition, was the mechanism operating [67]. Furthermore, the success of a particular sperm type might hinge on the female's genetic background, which parallels apparent competition [68,69]. In studies of experimental evolution, the type of competition might be known initially. For example, in Garbutt *et al.* [30], bacteria produce toxins that destroy other bacteria, hence interference competition is operating. However, in many cases, the type of competition is initially unknown and is inferred only after experimental tests are done at the end of the evolutionary process (cf. main text). Note also that even the identification of the type of resource individuals are competing for might be a difficult task [70].

One way to overcome this is using experimental evolution. This methodology consists of following real-time evolution of populations subjected to specific selection pressures under controlled conditions. Its explanatory power relies on: (i) knowledge of the ancestral (i.e., initial) state, (ii) easy manipulation of selection pressures, (iii) replication at the population level, and (iv) the ability to follow the dynamics of a process (i.e., evolutionary change over time), instead of measuring only the end product – the pattern [13,14]. Although this methodology has been used extensively to study other biotic interactions, such as antagonistic host–parasite interactions [15], its use to address the evolutionary consequences of competition is relatively recent [16].

Organisms might compete for several resource types, the most studied (and probably biologically relevant) being food, mates, and hosts (Table 1). The mechanisms of competition for these resources are shared, yet their study belongs to different research fields, each with its own idiosyncrasies, including distinct vocabulary. Indeed, whereas competition for food is usually stated explicitly, competition for mates can be masked behind terms such as ‘sexual selection’ or ‘sexual conflict’, and competition for hosts is usually referred to as ‘coinfection’. However, in all cases, individuals are competing for the use of a limiting resource. Experimental evolution, as a methodology that is transversally applied to studies of competition across resource types, opens a unique opportunity to (i) establish parallels across research fields, in view of establishing a common integrative framework, and (ii) highlight potential lessons from one field to the other. Those are the aims of this review.

Measuring Evolutionary Change: The Importance of the Ancestral State

One significant advantage of experimental evolution is knowing the ancestral state of populations before selection [13,14]. In studies of competition for food or hosts, the ancestral state is often no competition. Evolutionary change can be directly inferred, by comparing traits in their ancestral state to those following selection in a competitive environment. For example, experimental evolution clearly demonstrated character displacement for carbon source exploitation in *Escherichia coli* strains as a result of evolving in competition [17]. Establishing such causality is

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Table 1. Expected Evolutionary Outcomes of Competition^a

Type or Resource	Type of Competition		
	Exploitative	Interference	Apparent
	Within		
Mates	Increase sperm swimming ability	Increase production of toxins against other sperm, or resist toxins of other sperm	Increase evasion of, or resistance to toxins produced by females
Food	Increase feeding rate	Increase weapons or resist those of competitors	Resist or evade antipredator (resource) traits
Host	Increase strain growth and virulence	Increase production of or resistance to toxins produced by competitors	Increase evasion of, or resistance to host immunity
	Among		
Mates	Increase females' searching and monopolising ability	Increase weapons or resist those of competitors (e.g., horns)	Increase male persistence to overcome female's increased resistance to mating
Food	Increase home range/searching ability	Increase traits that allow defence or attack of territories	Evade antipredator (resource) traits by exploiting a novel food source
Hosts	Increase strain transmission/searching ability/infectivity/survival outside the host	Increase production of or resistance to toxins produced by competitors	Overcome host resistance to superinfection

^aExamples of expected evolutionary outcomes for interference, exploitative, and apparent competition when competition is for mates, food, and hosts. Expected outcomes are given for competition occurring at different hierarchical levels: either within or among resources. Competition within resources refers to sperm competition (in competition for mates), competition for nutrients within a territory (in competition for food), and for resources within a host (in competition for hosts). Competition among resources refers to male–male competition (in competition for mates), competition for territories (in competition for food), and for access to hosts (in competition for hosts).

difficult in natural populations [10]. By contrast, studies of competition for mates are often initiated from panmictic populations with many interacting males and females, suggesting that competition is the ancestral state. However, often the intensity of competition among same-sex individuals in the ancestral population is unknown. This uncertainty over the ancestral state hampers a clear inference of the direction of evolution (Figure 1; see Outstanding Questions [18,19]). These studies might assume that monandry is the derived state, but this assumption should be clearly stated and tested (e.g., [20]). In fact, it should be clear whether the **operational sex ratio (OSR)** imposed in 'control' lines corresponds to that of the ancestral state, in which case these lines can effectively be used as control. For example, in a study of experimental evolution of the bruchid beetle *Callosobruchus maculatus*, both the ancestral state and the control populations were monandrous [21] (see also [22]).

Experimental Manipulations of Competition and Their (Hidden) Assumptions

Intraspecific Competition for One Resource

When competition concerns one species/strain and one resource, it is manipulated by either increasing the number of competitors or reducing the amount of resources per capita. Although these manipulations are equivalent from an ecological standpoint, they are not from an evolutionary perspective. Indeed, adding more competitors also potentially increases the amount of genetic variation, the raw material upon which evolution acts. This implies that responses to selection might differ among treatments, independently of the selection differential due to competition (Box 2). Therefore, manipulating resources leads to more straightforward evolutionary interpretations. Indeed, *Drosophila melanogaster* populations exposed to high competition increased their niche width (i.e., diet breadth with increasing cadmium) at a faster rate than populations under low competition. In this study, competition was manipulated by exposing the

Glossary

Character displacement: the divergence of traits in individuals sharing the same environment.

Competition: interaction between individuals that share a common resource, in which the presence of one negatively impacts the fitness of the other.

Competitive ability: comparative advantage of one competitor, relative to another, in a shared environment. This can be measured as the relative ability to exploit a shared resource, or their relative growth, in the presence of the competitor.

Correlated responses to selection: evolution of traits that are not directly targeted by the selection regime to which populations are exposed, usually due to genetic correlations among traits, and that do not necessarily improve an individual's competitive performance.

Disruptive selection: selection favouring divergent trait values, where phenotypes at the extreme of the distribution will have a fitness advantage over intermediate phenotypes.

Functional diversity: the range of trait values in communities that either respond to ecosystem disturbance or that affect ecosystem fluxes.

Niche width: the distribution range of organisms in an *n*-dimensional resource–environmental space, as a function of their biotic and abiotic interactions.

Operational sex ratio (OSR): the ratio of males to females that are available for mating.

Resource utilisation: the ability to exploit a resource, not necessarily measured in the presence of competitors.

Sexual conflict: occurs when the evolution of traits in one sex towards their optimum entails a concomitant evolution of traits away from the other sex's optimum. Sexual conflict might fuel an evolutionary arms race between sexes, where adaptations in one sex are followed by counter-adaptations in the other.

Virulence: parasite-induced reduction in host fitness.

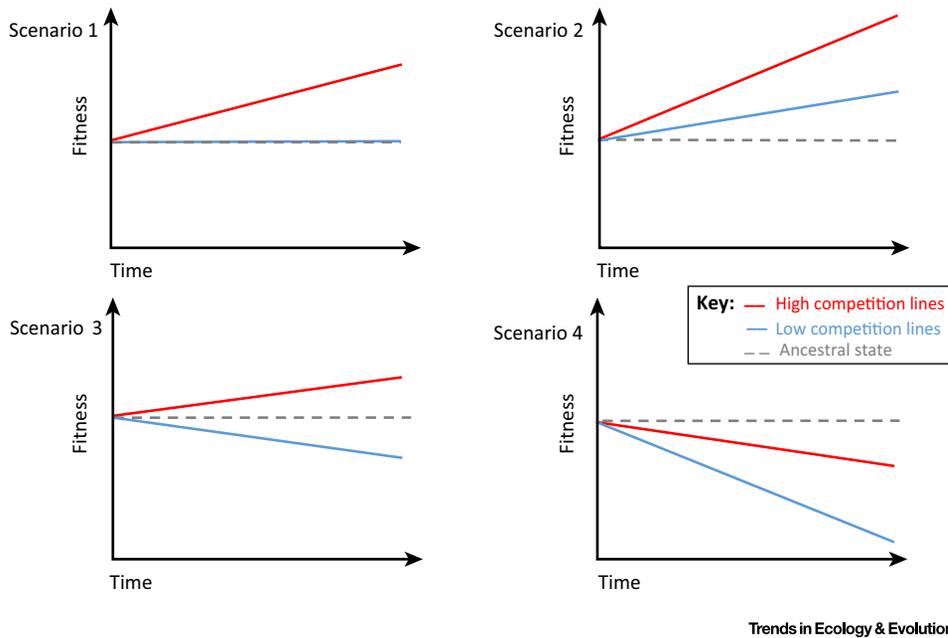


Figure 1. Measuring Evolutionary Change. Four possible scenarios of evolutionary trajectories of populations undergoing experimental evolution. The red line represents populations in which evolutionary change is expected ('high competition' lines), whereas the blue line represents 'low competition' lines, which are expected to reflect the ancestral state (dashed grey line). However, note that control lines might be lines in which competition is high (usually in competition for mates – where polyandrous lines are assumed to represent the ancestral state of the population). Because the distance between trajectories of the two selection regimes is the same in all graphs, the conclusion drawn from that comparison is always that selected lines have adapted to the regime they were exposed to (they increased in fitness). However, in Scenario 2 this fitness increase is underestimated, in Scenario 3 it is overestimated, and in Scenario 4 the conclusion of a fitness increase is incorrect. Therefore, it is important that control lines reflect the ancestral state.

same number of flies to varying numbers of food vials containing different cadmium concentrations, while keeping the proportion of each concentration constant [23].

Competition for mates is manipulated by varying the number of males (competitors) accessing females and/or the number of females (resource) offered to a male and/or density, sometimes resulting in changes in OSR. Stronger competition (i.e., more polyandry) is achieved when more males compete for fewer females [16]. This implies that most treatments differ in genetic variability, since the effective population size is reduced with uneven sex ratios [24]. This can confound observed evolutionary responses [25]. Although, in some studies, treatments varying in sex ratio do not differ significantly in effective population size, as explicitly demonstrated in *D. melanogaster* [26], this might not always be the case. By increasing the population size in parallel with the increase in female bias, it is possible to overcome this effect ([25], see also [26] for additional strategies).

Interspecific Competition for One Resource

In competition studies between species or strains, two main designs are implemented: the 'substitution design', where the overall density is maintained across treatments and, consequently, the competition treatment contains half as many individuals of each species/strain as the single species/strain treatments (2A, 1A:1B, 2B; e.g., [27]), and the 'addition design', where the competition treatment contains the same number of each competitor as the single species/strain controls, entailing an increased overall density in this treatment (2A, 2A:2B, 2B, e.g., [28]). The addition design is used in competition for hosts, although sometimes not explicitly stated [29,30]. In competition for food, both designs are used ('substitution' = [27], 'addition' = [28,31]).

These designs are absent in competition for mates, as interspecific interactions were not addressed (but see [32]).

Each of these designs has its flaws, as discussed in the ecological literature [33]. Indeed, in the addition design, the competition regime differs from controls in that (i) two species/strains are present instead of one, and (ii) there is a twofold increase in the overall density. Therefore, which of these factors affects differential trait evolution between treatments is unclear. Equalising per capita resources across treatments might minimise this problem. This, however, requires knowledge on species functional responses, as doubling resources does not necessarily imply doubling feeding rates. The advantage of the addition design is that the intensity of intraspecific competition is maintained across treatments. Still, this only holds if we assume that interspecific individuals do not alter intraspecific interactions.

In the substitution design, all treatments have the same density hence, if intra- and interspecific/strain competition have similar strengths, global competition levels are maintained across treatments. However, this implies lower intraspecific/strain density, hence lower intraspecific competition, in the 'competition' treatments. Thus, observed responses might be attributed to this rather than to interspecific/strain competition. Moreover, and importantly, differences in the number of individuals of each species result in differences in genetic variability. As in the single species case, this implies that responses to selection can differ among treatments, independently of the selection differential due to competition (Box 2). This can be overcome by seeding each of the intra- and interspecific/strain treatments with combinations of individuals from the same number of isogenic lines (Figure 2).

More than One Resource

Although the addition and substitution designs have been used to describe the manipulation of competitors, they can also serve to describe manipulations of the resource. Indeed, competition can be manipulated by replacing half of the original resource by a novel one, or by adding a novel resource, while keeping the amount of the original constant. For example, Barret and colleagues manipulated competition by varying the number of carbon substrates involved in different *Pseudomonas* metabolic pathways by keeping the concentration of each substrate constant, thus increasing substrate availability in treatments with more substrate types [34]. It should be noted that only in the substitution design is competition increased (assuming that novel resources are initially of poorer quality than the original). The addition of novel resources can promote niche expansion or character displacement leading to a decrease in competition, at least transiently.

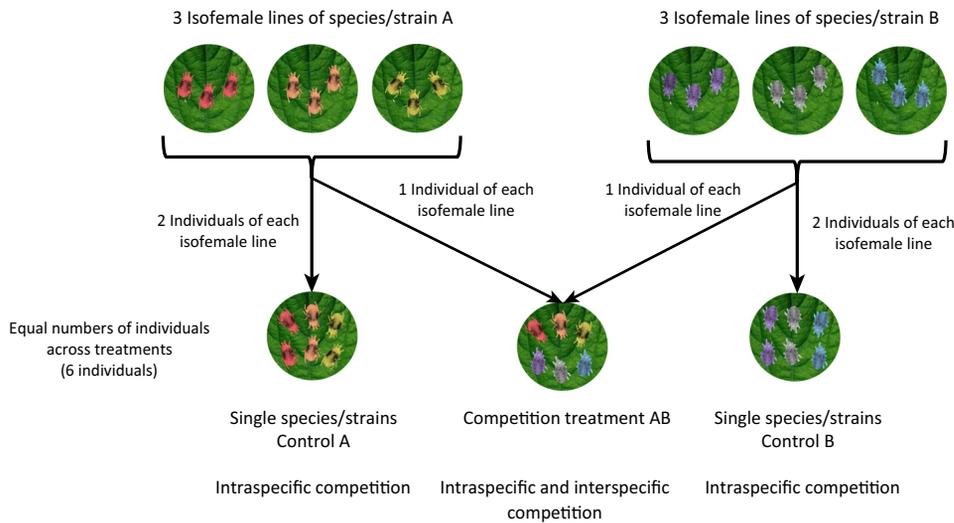
There are other, more subtle ways of addressing the role of competition, for example, by manipulating the spatial scale at which competition is operating [35,36]. For instance, Macke *et al.* [36] varied the number of founders per patch to test whether local mate competition leads to a more female-biased offspring sex ratio [37].

Evaluating the Effect of Competition

In Table 2 and Table S1 in the supplemental information online, we compile representative examples of experimental evolution studies that manipulated competition for food, mates, or hosts.

Measuring the Evolutionary Response to Competition

In experimental evolution, adaptation is typically tested by comparing trait values in populations evolving under a given selection pressure (selection lines) with those evolving in conditions pertaining to the ancestral environment before the experiment (control lines). The general assumption is that control populations are at a steady state for the traits measured, hence



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Figure 2. How to Manipulate Competition while Keeping Genetic Diversity Constant. One possible way to keep overall densities the same across treatments (hence reducing the number of each species in competition) while maintaining similar levels of genetic variability is to use mixes of isogenic lines from each species in all treatments. In this way, all treatments could be drawn from the same number of isogenic lines (thus maintaining genetic diversity across treatments) but using a different number of individuals from each line (thus varying the intraspecific density as required in the substitution design). In the diagram, as an example: create three isofemale lines for species A and for species B; single species treatment A: use two individuals from each species A isofemale line, with a total of six individuals; single species treatment B: use two individuals from each species B isofemale line, with a total of six individuals; two species competition treatment A and B: use one individual from each isofemale of species A and species B, with a total of six individuals. Note: (i) a much higher number should be used; (ii) this solution is not valid if strong sib competition is an important concern in the system under study.

differences observed can be attributed to evolutionary changes occurring in evolved populations [13] (Figure 1).

In lines selected under competition, a higher competitive ability is expected to evolve. This can be evaluated by comparing the performance of individuals evolving in competition with that of individuals evolving under controlled conditions, in a competition environment. This is a typical test of local adaptation [38] and this prediction is generally met (Table 2).

Evolving under competition might also affect **resource utilisation**. Testing this requires evolved and control lines to be tested in a competition-free environment. In some cases, such as in *Tribolium castaneum* feeding on wheat, evolution of resource utilisation in competitive and non-competitive environments is positively correlated [39]. Other studies find trade-offs. For example, *Drosophila* evolving with competitive fungi perform better than control lines in the presence of the competitor, but this comes at a cost of performance in the ancestral, competitor-free environment [31]. In another study, *Drosophila* evolving in crowded conditions increased resource acquisition, but had higher mortality when tested in uncrowded conditions [40]. Therefore, the direction in which resource utilisation evolves varies among studies.

Competition for or within Resources

Competition can concern access to an entire resource or a portion of it (Table 1). Indeed, males can compete for access to females and/or their sperm might compete for egg fertilisation within the female – sperm competition; parasites can compete for access to hosts, and for resources within the host; individuals can compete for territories, or for food within territories. In studies of competition for food and hosts, however, evolutionary responses to competition for territories or among hosts remain to be investigated (Box 2; see Outstanding Questions).

Table 2. Experimental Evolution Studies Manipulating Competition^a

Type of Resource	Organism	Manipulation	CA	RU	Correlated Response	Refs
Food	<i>Drosophila melanogaster</i>	Number of competitors	↑	↔↓↑	↔ Parasitoid resistance	[40,77–79]
Food	<i>D. melanogaster</i>	Resource quality	↑	↔↓↑	↑ Cannibalism ↓ Motility	[52,80–82]
Food	<i>D. melanogaster</i>	Resource quantity	–	↑	Niche expansion	[23]
Food	<i>D. melanogaster</i>	Type of competitors	↑	↓	–	[31,83]
Food	<i>Escherichia coli</i>	Resource diversity	–	–	Character displacement	[17,84]
Food	<i>E. coli</i>	Type of competitors	↑	–	Character displacement	[85]
Food	<i>Fagus sylvatica</i>	Type of competitors	–	↓↑	Character displacement	[27]
Food	<i>Pseudomonas fluorescens</i>	Resource diversity	↑	↑	–	[34]
Food	<i>P. fluorescens</i>	Type of competitors	–	–	Niche expansion, contraction	[50]
Food	<i>Tribolium castaneum</i>	Number and type of competitors	–	–	Niche expansion	[39]
Mates	<i>Caenorhabditis elegans</i>	Outcrossing/selfing	–	–	↓ Genetic variability	[86]
Mates	<i>Callosobruchus maculatus</i>	OSR, age at reproduction	–	–	Sexual conflict affects lifespan	[87]
Mates	<i>C. maculatus</i>	M/P	↔	↔	↑ Sexual conflict	[21]
Mates	<i>D. melanogaster</i>	OSR	↑	↓?	↑ Sexual conflict, body size	[20,42,43]
Mates	<i>D. melanogaster</i>	OSR (female-biased)	↓	–	–	[25]
Mates	<i>D. melanogaster</i>	M/P	↑	↔	↑ Male cognitive ability	[44]
Mates	<i>Drosophila pseudoobscura</i>	OSR	–	–	Song elements, character displacement?	[88]
Mates	<i>Megabrychidius tonkineus</i>	OSR	–	↑	↔ Sexual conflict	[89]
Mates	<i>Mus domesticus</i>	OSR	↑	–	↓ Sexual conflict	[90,91]
Mates	<i>Onthophagus taurus</i>	M/P	↑	↑	↔ Sexual conflict	[92]
Mates	<i>Rhizoglyphus robini</i>	M/P	↑	–	↑ Sexual conflict	[93]
Mates	<i>Scathophaga stercoraria</i>	OSR	↑	–	↑ Sexual conflict	[94]
Mates	<i>Sepsis cynipsea</i>	M/P	–	–	↑ Character displacement	[95]
Mates	<i>Tetranychus urticae</i>	Local/global competition	–	–	Sex ratio adjustment varies with scale of competition	[36]
Mates	<i>Tribolium castaneum</i>	OSR	↑	–	↑ Sexual conflict	[96]
Mates	<i>T. castaneum</i>	OSR, resource quality	–	↓↑	↑ Sexual conflict	[97]
Hosts	<i>Bacillus thuringiensis</i>	Type of competitors	↑	–	↓ Virulence	[30]
Hosts	Vesicular stomatitis Indiana virus	Type of competitors	↑	–	–	[98]
Hosts	Vesicular stomatitis Indiana virus	Number and type of competitors	↑↓	–	–	[99]
Hosts	Lytic phage φ2	Type of competitors	↑	↓	↑ Virulence	[49]
Hosts	<i>Lysiphlebus fabarum</i>	Type of competitors	–	↔	–	[100]

^aExamples of experimental evolution studies that have manipulated competition for food, mates, or hosts. Our aim is to use representative examples, not to summarise all available literature. Abbreviations: CA, competitive ability; RU, resource use; M/P, monogamy and polygamy treatments; F-biased, female-biased. ↑, increase; ↓, decrease, ↔, no change. In Table S1 in the supplemental information online, we provide more details and references.

The traits that respond to selection might differ depending on the level where competition is strongest. For example, mating rate is associated with competition for mates – between resources – whereas fertilisation success is a measure of sperm competition – within a resource. Furthermore, trade-offs can occur between levels. For example, higher mating rates can trade off with sperm competitive ability. In the same way, defending a larger territory might be incompatible with the defence of particular resources within it, and within-host competition for resources might trade off with competition for new hosts. Hence, experiments should be designed such that the level at which selection is acting (within or between resources) is clear. For example, Fricke and Arnqvist [41] exposed bruchid beetle females to several males sequentially, thus only allowing for competition within the female to occur (within resource). Alternatively, traits acting on each of these levels should be measured, so that responses to selection do not go undetected.

Correlated Responses to Selection: Commonalities and Specificities across Resource Types

Competition for Mates: Sexual Conflict and Secondary Sexual Traits

Sexual conflict is perhaps the most studied correlated response to selection using experimental evolution. When evolving in competitive environments, males typically become more harmful towards females. This can in turn select for female resistance. By contrast, under low male competition, male harassment and female resistance are no longer advantageous. For example, offspring of *D. melanogaster* females mated with males evolved in monandry, compared with polyandry, have lower mortality [42]. Moreover, ejaculates from males evolving in monandry are less effective at manipulating female behaviour towards being less receptive [43]. Conversely, females evolving in polyandry have higher mating rates, suggesting higher resistance to ejaculate manipulation [43]. Note that, when tested in a competitor-free environment, higher female fertility might be interpreted as relaxed sexual conflict (a correlated response to selection) or reduced resource exploitation by males (a direct response).

Another potential correlated response is the evolution of secondary sexual characters. For example, males evolving under relaxed sexual selection showed reduced cognitive abilities, considered a secondary sexual character because it permits discrimination of receptive and non-receptive females [44]. To our knowledge, few experimental evolution studies have investigated this [44,45].

Competition for Host Resources: Evolution of Virulence

Within-host competition among parasites is expected to select for higher growth rates to overcome competitors [46]. As more parasites supposedly induce more harm, theory assumes that within-host growth rates are positively correlated with **virulence** [47]. Alternatively, evolution of lower virulence is predicted if competing strains engage in interference competition [48] (Box 1). Moreover, between-host competition can favour lower virulence if there is a trade-off with transmission [47].

The link between virulence evolution and within-host competition (i.e., single versus multiple infections) has been the subject of many theoretical studies and an excellent recent review [46]. However, to date, only two empirical studies test these predictions using experimental evolution. The first shows that virulence decreases in coinfections with *Bacillus thuringiensis*, probably due to the production of bacteriocins that kill competitors [30]. In the second, virus strains become more virulent when evolving with other strains compared with single infections, when tested in competition [49]. This result is consistent with exploitative competition between parasites, although this has not been explicitly tested.

Competition for Food: Niche Width

Competition can select for traits allowing new regions of resource space to be explored, leading to niche expansion [11]. Alternatively, it can favour traits that decrease niche overlap, leading to

niche contraction. If sufficiently intense, these processes can lead to **disruptive selection**, in which both tails of the phenotypic distribution are favoured, potentially leading to character displacement [11]. Whether traits evolve in one direction or the other depends on the relative availability of the different resources.

Results of experimental evolution studies on the role of competition on niche width are variable. For example, relaxing competition between two different *E. coli* populations adapted to different carbon sources resulted in their phenotypic convergence; the reintroduction of competition led to character displacement, as predicted [17]. However, this outcome might be contingent on the diversification ability of the competitor strain. Indeed, in *Pseudomonas fluorescens*, niche expansion of a focal strain is slowed when competing with generalist strains able to thrive in all environments. By contrast, competition with strains with reduced niche width promotes the diversification of the focal strain, facilitating the colonisation of a new environment [50]. Other studies show that strong intraspecific competition selects for niche expansion [23,39,51].

Other correlated responses can also evolve, such as cannibalism in *Drosophila* as a result of competition for food [52] and reduced immunocompetence following competition for mates in the Indian mealmoth *Plodia interpunctella* [53] and the beetle *C. maculatus* [54]. Moreover, one can establish parallels between correlated responses: both virulence and sexual conflict, by-products of competition, induce harm to the resources (hosts and mates, respectively). Additional parallels are explored in Box 2. These could drive new research or reinterpretation of existing studies.

Box 2. Learning from Parallels Involving Different Resource Types

Female Aggregation and Evolution of Mating Rate

In polygynous systems, evolution of mating rates is a function of their variance (e.g., [71]). Hence, if some males can monopolise females, selection intensity for mating rates will be stronger than in systems with no female aggregation [72–74], leading to runaway sexual selection, stopping when males cannot defend more females. Hence, selection intensity is not simply dependent on the ratio between competitor number and resource availability.

Extrapolating to competition for food, it implies that the more resources (some) individuals can monopolise, the stronger selection for food acquisition. Hence, explicitly measuring standing genetic variance for resource acquisition might help to predict evolution. Moreover, if competition is experimentally manipulated through fewer resources, the opportunities for resource monopolisation can decrease, which might invalidate the prediction that more competition drives faster evolution. Similarly, parasites can evolve the ability to monopolise hosts, for example, by increasing host resistance to superinfection with other parasitoid wasps, as *Hamiltonella defensa* in aphids [29]. This might modify the evolution of virulence in such populations.

Niche Width

Evolution of niche width has been tackled mostly as a consequence of competition for food (cf. main text). A host is also an ecosystem within which parasites exploit different niches [58]. Competition might thus select for parasites colonising novel hosts, or using different resources within a host [64]. For example, some trematodes specialise on different species or portions of the intestine [75]. Experimental evolution could establish causal links between competition avoidance and within-host parasite distributions (e.g., evolution of niche expansion in viruses [51]).

Similarly, competition for mates can select for alternative tactics to acquire mates [11], such as monopolising females or sneaking [62]. However, the evolution of such morphs does not necessarily result from character displacement. Experimental evolution on alternative morphs is scarce [32,45], and such studies are needed to establish causality (cf. Outstanding Questions).

Virulence

How coinfections affect virulence evolution is discussed in the main text. Virulence can be paralleled with sexual conflict, and one can predict that exploitative or interference competition between sperm within females will lead to more or less male harm, respectively.

The competition/colonisation trade-off in competition for food [76] mirrors the virulence/transmission trade-off. Extending the parallel leads to predicting that under exploitative competition patches would be depleted at a faster rate in the presence of competitors, the reverse being true under interference competition (cf. Outstanding Questions).

Perspectives for Future Research

Addressing All Possible Scenarios (Coexistence versus Exclusion)

In studies of interspecific/strain competition, experimental conditions are conceived such that species/strain exclusion is prevented, forcing coexistence to be maintained across generations. This means that only one of the Lotka–Volterra scenarios is considered, that in which intraspecific is stronger than interspecific competition. Hence, by narrowing down the conditions used, the experimenter is directing the evolutionary outcomes. To test for alternative scenarios (i.e., where competitive exclusion is expected), one could replenish the outcompeted player at regular intervals and measure evolution in the superior competitor.

This set-up would also allow to test how coevolution among competitors affects trait values as well as the maintenance of diversity [11]. Although this possibility has been theoretically proposed [55], it has never been tested in experimental evolution studies. Indeed, when competitors coexist, one can generate treatments in which both species coevolve and contrast them with treatments in which only one species evolves, the other being systematically replenished from the ancestral population at each generation, as in studies of host–parasite [15] or male–female coevolution [56]. This set-up allows singling out the role of coevolution in shaping trait values, the rate of evolution and/or the maintenance of genetic diversity [11] (cf. Outstanding Questions).

Experimental Evolution Studies Should be Strongly Rooted upon Ecological Knowledge

Much theory has been developed to understand the ecological outcomes of competition. This knowledge might help interpret experimental evolution studies. For example, a clear definition of the type of competition helps refine predictions concerning experimental outcomes (Box 1). In fact, this approach has been taken to interpret the outcomes of coinfection scenarios [57,58] and could also be applied to competition for mates or food. When the type of competition is unknown, it can later be inferred from the observed outcomes following evolution (i.e., which traits are affected and in which direction). In this case, evolution would inform ecology, providing knowledge on interactions among species or strains.

Experimental Evolution Can Shed Light on Functional Traits and Functional Diversity

Competition is a major component of ecosystems. As such, it is likely to affect the **functional diversity** of such ecosystems. Unfortunately, knowledge on which functional traits are affected by competition within a species community is in its infancy [59]. In this context, experimental evolution can be instrumental to identify which traits respond to selection imposed by competition. Those traits are likely to be ecologically relevant, as they will affect other competitors as well as resource levels. Hence, they are expected to act as effect traits (i.e., traits that have an effect on the functioning of the ecosystem [60]). Moreover, the strength of competition is, by definition, linked to the amount of resource present. Thus, traits involved in competitive interactions are also expected to act as response traits (i.e., traits that change after environmental disturbance). Often, traits that respond to perturbations are also the same traits that have a relevant role in ecosystem functioning. In light of the recent evidence for widespread rapid evolution and eco-evolutionary dynamics in nature [61], it is clear that traits that respond to selection may be functional both in the evolutionary and in the ecological sense. Thus, knowledge stemming from experimental evolution might significantly contribute to strengthen the ongoing link between ecology and evolution, as it would contribute to merge ecosystem functioning to eco-evolutionary dynamics (cf. Outstanding Questions).

Concluding Remarks

In summary, we aimed to highlight similarities in patterns and processes across diverse research fields that implicitly or explicitly study competitive interactions (parasitology, sexual selection, foraging ecology). We have shown how this integration helps generate novel predictions and

Outstanding Questions

The comparison of the literature regarding experimental evolution of competition for hosts, food, or mates revealed a few questions that remain largely unexplored. Addressing these questions will contribute to a better understanding of the reciprocal effects of competition on evolution.

Does competition lead to coevolutionary dynamics between competitors? If so, when is it characterised by arms race or fluctuating selection dynamics? And when does it allow for the maintenance of genetic variation in populations?

Can character displacement evolve as a result of competition for mates or hosts?

Does evolution towards monandry or polyandry evolve at different rates?

How does competition between resources (e.g., competition for territories) affect competition within resources (within-territory competition for food)?

How does the evolution of competition affect functional diversity in communities and ecosystems?

clarify patterns observed in experimental evolution studies. Clearly, competition is a major biotic selection pressure imposed on organisms, the evolutionary outcomes of which are still largely unclear. Further experimental evolution studies addressing the rich diversity of competitive interactions across organisms will help clarify the commonalities among evolutionary responses to competition.

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