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Disruptive selection and then what?

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Disruptive selection occurs when extreme phenotypes have a fitness advantage over more intermediate phenotypes. The phenomenon is particularly interesting when selection keeps a population in a disruptive regime. This can lead to increased phenotypic variation while disruptive selection itself is diminished or eliminated. Here, we review processes that increase phenotypic variation in response to disruptive selection and discuss some of the possible outcomes, such as sympatric species pairs, sexual dimorphisms, phenotypic plasticity and altered community assemblages. We also identify factors influencing the likelihoods of these different outcomes.

Introduction

A population experiences disruptive selection (see Glossary) on a quantitative trait when intermediate phenotypes have a fitness disadvantage compared with more extreme phenotypes. During the 1950s and 1960s, disruptive selection figured prominently in mainstream evolutionary thinking, with the realization that it might have several consequences for the evolution of phenotypic variability [1–6], including the maintenance of high levels of genetic variation, sympatric speciation, the emergence of allelic switches between alternative phenotypes and the evolution of phenotypic plasticity. After a period of diminished interest in the idea [7,8], renewed attempts at understanding disruptive selection were made during the 1990s [9–13]. An important new insight was that two types of disruptive selection must be distinguished, of which only one has a diversifying effect (Box 1).

Two types of disruptive selection

For disruptive selection to occur, the mean phenotype has to experience the lowest fitness. In the first type, which does not lead to diversification, selection prevents a population from experiencing such a situation for any significant amount of time. Instead, the population evolves away from the region of disruptive selection (Box 1, Figure Ia). For example, imagine a situation where a consumer feeds on two resources, say, large and small seeds, whose abundance is maintained at relatively constant levels by other factors. Consumers with intermediate phenotypes perform poorly on both resources and have a smaller energy intake rate than do either of the more extreme phenotypes. Thus, directional selection acts towards specialization in the direction of the closer fitness peak.

For the second type of disruptive selection, we can imagine a situation where a population exploits a continuously varying resource, such as seeds that range from very small to very large and where the level of consumption influences seed abundance. Individuals that efficiently exploit the most abundant resource (e.g. seeds of intermediate size) have a fitness

Glossary

Assortative mating: when sexually reproducing organisms tend to mate with individuals that are similar to themselves in some respect. Can be caused by assortative mate choice, or by environmental factors that cause non-random associations between mating partners.

Attractor: in dynamical systems, an attractor is a set to which the system approaches given enough time. Trajectories moving close to the attractor remain close when slightly disturbed. Stable equilibrium points, cycles and strange chaotic attractors are all different types of attractor. Evolutionary systems are usually described by the dynamics on a trait space and the attractors of such systems are trait values observed given enough time.

Bet hedging: type of risk aversion strategy. It is present when identical individuals experiencing the same unpredictable environment take mixed decisions or produce a variety of phenotypes.

Convergent selection: selection on two or more different species or morphs that increases the similarity of the different types.

Directional selection: favors traits that differ from the current value in a particular direction.

Disruptive selection: favors both types of more extreme phenotypes over intermediates.

Evolutionary branching: originally used to denote a set of conditions on fitness landscapes that lead to an adaptive splitting of clonal lineages. These conditions cause directional evolution of the mean trait of a population to a fitness minimum, where selection turns disruptive. In a genetic context, evolutionary branching denotes conditions where a homozygous lineage evolves through a series of allele substitutions to a certain trait value where disruptive selection favors different alleles that coexist.

Negative frequency-dependent selection: causes the fitness of a phenotype to depend on its frequency, such that rare phenotypes have an advantage over common ones.

Linkage disequilibrium: non-random association of alleles at two or more loci, such that certain haplotypes occur more frequently than would be expected based on allele frequencies alone.

Polygenic traits: determined by many loci, often all with relatively small effects.

Quantitative traits: traits measured on a continuous scale, such as height or weight.

Protected polymorphism: each type present in the polymorphism has a selective advantage relative to more common types whenever it becomes rare. Therefore, all types in such a polymorphism are protected from extinction. Protected polymorphisms are maintained by negative frequency-dependent selection.

Repellor: a set from which a dynamical system evolves away after a sufficiently long enough time. Analogous to an attractor.

Stabilizing selection: favors intermediates over extremes in the frequency distribution of traits.

Sympatric speciation: the origin of new species from a single local population. Most mathematical models of sympatric speciation assume that mating is random with respect to the birthplace of the mating partners [25].[25]

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Box 1. When does disruptive selection have a diversifying effect?

Under disruptive selection, an intermediate phenotype resides at a minimum of the fitness landscape (Figure Ia). Fitness landscapes exerting disruptive selection can be either U- or M-shaped (two peaks separated by a valley) with most phenotypes being located near the fitness minimum at intermediate phenotypes. Two different types of disruptive selection must be distinguished. In the first, persistent disruptivity only acts on a population when its mean phenotype is exactly at the minimum (Figure Ia). A population with a mean phenotype displaced from the minimum of the fitness landscape evolves in a direction away from that minimum (Figure Ia). If evolution is viewed as a dynamical system on a trait space, such fitness minima act as repellors of the evolutionary dynamics. Proximity of the mean phenotype to a minimum can occur owing to the arrival of a population in a new habitat, or to a major environmental change in its original habitat, but cannot occur through evolutionary change.

In the second case, a population with a mean phenotype in the neighborhood of a fitness minimum experiences directional selection towards the minimum (Figure Ib), which occurs for populations with an initial mean trait value that is either smaller or larger than that of the fitness minimum. From the viewpoint of the theory of dynamical systems, such minima act as attractors of the evolutionary dynamics. This scenario requires strong negative frequency-dependent selection, which causes the position of the minimum of the moving fitness landscape to shift further and in the same direction as a shift in the mean trait value (Figure Ib). It is this process that drives an evolving population toward a fitness minimum. An ecological scenario causing a population to evolve towards a fitness minimum where it subsequently experiences disruptive selection is given in Figure 1 (main text).

The crucial difference between these two scenarios is that, in the second one, a population is exposed to disruptive selection for an extended period of time during which selection acts to increase phenotypic variation. In asexual populations, this occurs when mutants come to lie on opposite sides of the fitness minimum, in which case both types can coexist in a protected polymorphism and evolve toward different fitness peaks (Figure Ic).

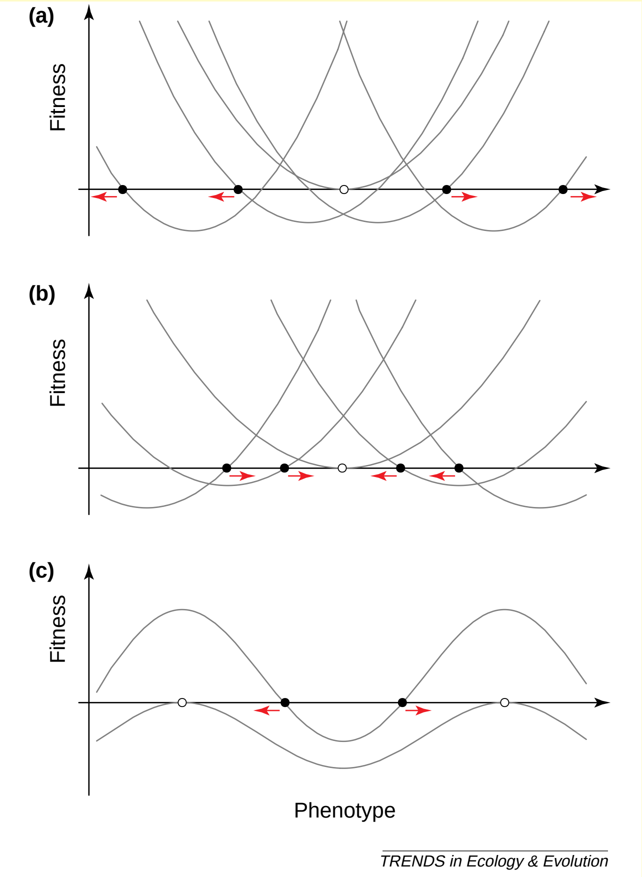

Figure I. The two types of disruptive selection. Grey lines give the fitness of mutant phenotypes that might invade the resident population, indicated by the filled and open dots. Mutant fitness is given as a deviation from the fitness of the resident and only mutants with higher fitness than the resident increase in frequency. **(a)** Fitness landscape in the neighborhood of an evolutionary repellor; **(b)** fitness landscape near an attracting fitness minimum. (evolutionary branching point); and **(c)** fitness landscape for a population of two coexisting phenotypes on either side of the branching point. Resident populations corresponding to filled dots experience directional selection in the direction of locally increasing fitness (indicated by red arrows). Open dots indicate strategies that do not experience directional selection.

advantage and the mean of the population will move towards this optimum (Figure 1a). Once most of the population is specialized on the most abundant resource, this part of the resource spectrum is depleted, and that phenotype is no longer favored (Figure 1b). As a result, phenotypes that deviate from the most common type have a fitness advantage and the population experiences disruptive selection. This is maintained until phenotypic variation increases to the point where the available resource spectrum is used more equally (Box 1 Figure Ic). This scenario is driven by negative frequency-dependent selection, emerging from competition for resources. Rare types enjoy an advantage because of decreased competition with the majority (Box 1).

Disruptive selection and then what?

For asexual populations, the advantage of rarity means that phenotypes on opposite sides of the fitness minimum can coexist in a protected polymorphism [11,12]. Disruptive selection acts to drive the coexisting types further apart, until they reside on different fitness peaks (Box 1, Figure Ic). In freely interbreeding sexual populations, however, the distribution of phenotypes is constrained by the processes of segregation and recombination, which cause many individuals to have the maladaptive intermediate phenotype [13,14]. As a consequence, processes that prevent the production of intermediates are favored, and it is these that we consider here. In addition to competition for resources, other ecological interactions can cause disruptive selection [10,15]. Common types can, for instance, be at a disadvantage by attracting the attention of their predators, experiencing increased incidence of disease, or having too few mutualists.

Empirical support for these theoretical insights is hard to come by owing to substantial experimental difficulties. However, it has recently been demonstrated that intraspecific competition for food in sticklebacks *Gasterosteus aculeatus* can favor both limnetic and benthic specialist phenotypes over generalists [16]. Other studies have shown that competition produces negative frequency dependence between phenotypes [17–20].

The twin realizations that disruptive selection can persist for significant periods of time and that many ecological scenarios produce just this sort of selection

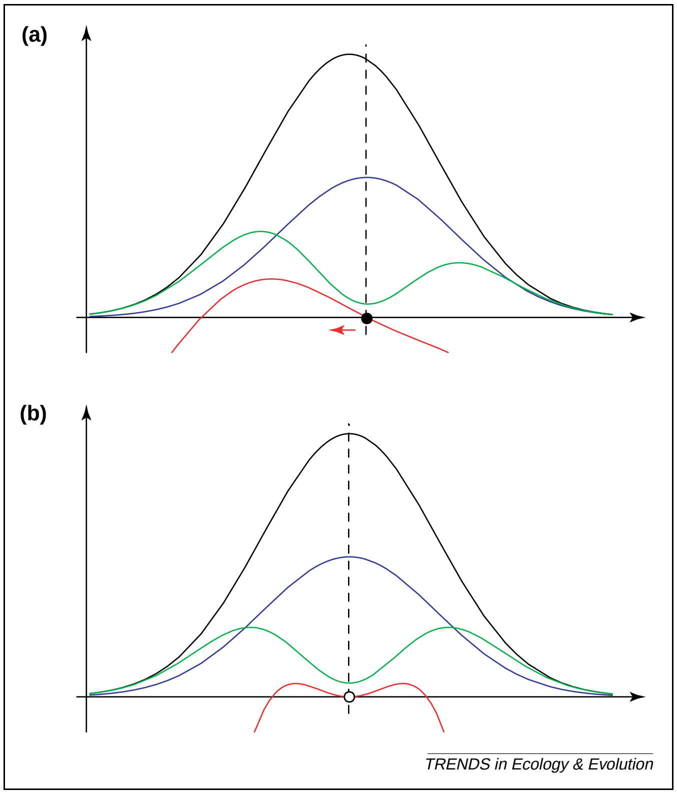

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Figure 1. Selection resulting from resource competition, according to the model by Ackermann and Doebeli [58]. The *x*-axis corresponds to a quantitative property (e.g. size) of a resource, which has a continuous and unimodal distribution in the absence of predation. Consumers are characterized by the mean of their utilization curve, giving the capture rate per unit time for each resource type. Black curves show the relative abundance of resources in the absence of consumers. Dots on the *x*-axis indicate the trait value of a consumer population and blue curves show the corresponding utilization curve. Green curves show the relative abundance of resources in the presence of the consumer population. Red curves indicate the fitness of mutant phenotypes given the resource abundances produced by the resident population. **(a)** The maximum capture rate for a resident phenotype (filled dot) is for resources larger than the most abundant resource (vertical dashed line), resulting in a higher abundance of smaller resources. This causes directional selection towards smaller trait values in the consumer (red arrow). **(b)** The resident phenotype (open dot) has a maximum capture rate for resources of the size that are most abundant in the absence of a consumer (vertical dashed line). This results in a symmetric resource distribution with a minimum for those resources utilized most intensively. Mutants with smaller or larger trait values than the resident phenotype benefit by escaping competition with the resident, causing disruptive selection.

regime has triggered a massive effort among theoreticians to explore the evolutionary consequences of such scenarios. To date, the consequence that has attracted the most attention is the phenomenon of evolutionary branching of a lineage [15,21,22], including the possibility of sympatric speciation [23–25]. However, splitting of a single lineage into genetically distinct lineages is not the only possible response to disruptive selection.

There is presently a limited awareness of the full spectrum of possible adaptive responses to disruptive selection and how to assess their relative likelihoods. All of the potential responses are characterized by a reduction or elimination of disruptive selection via some increase in the diversity of phenotypes and there are many ways in which this can be realized. Although much remains to be learned about the relative frequency of different responses to prolonged disruptive selection, it is unlikely that sympatric speciation will be the most common one. To appreciate the scope of disruptive selection as a creative evolutionary force, it is therefore important to understand the circumstances favoring the different potential responses to this form of natural selection.

Adaptive responses to disruptive selection

Here, we use ‘disruptive selection’ to refer to the second scenario above, where disruptive selection acts to increase phenotypic variation. The possible processes leading to such an increase can be roughly subdivided into three categories, consisting of those that lead to an increase in genetic variation within a species, those that lead to an increase in phenotypic variation without an increase in genetic variation, and those involving other species in the community (Table 1).

Increase in genetic variation

Disruptive selection affects the frequency distributions of alleles and genotypes within a population. For traits determined by several loci with additive effects, disruptive selection increases genetic variance by equalizing the frequencies of existing alleles at polymorphic loci [14,26–28]. If recombination rates are low, disruptive selection causes the build up of positive linkage disequilibria, such that haplotypes containing alleles that affect the phenotype in the same direction become disproportionately common [14,27]. These adjustments can occur relatively quickly because they exploit standing genetic variation and do not require new mutations to appear. However, in most cases, such changes only reduce the strength of disruptive selection [14,26,27].

Disruptive selection can have profound effects on the genetic architecture of polygenic traits. For example, it can reduce the number of polymorphic loci and favor an increase in effect size of those that remain polymorphic [21]. Whenever disruptive selection creates linkage disequilibria between alleles, modifier alleles that decrease recombination are favored [29].

In a one-locus two-allele model, a population close to an attracting fitness minimum (Box 1 Figure Ib) can be invaded by an allele that, when homozygous, corresponds to a phenotype on the opposite side of the fitness minimum [8]. Disruptive selection increases genetic variation by favoring alleles corresponding to more extreme phenotypes (Box 1 Figure Ic), resulting in a genetic polymorphism with heterozygote disadvantage. Selection will then favor mechanisms that prevent the production of inferior heterozygotes. Dominance modifiers can prevent the production of unfit heterozygotes by making their phenotype more similar to that of a homozygote [7,30–32]. Examples of resource polymorphisms that are believed to be controlled by mendelian switches include jaw asymmetry in the scale-eating cichlid *Perissodus microlepis* [17] and bill size in the black-bellied seedcracker *Pyrenestes ostrinus* [33]. In both cases, two distinct sympatric phenotypes are adapted to forage on distinct resources and it is believed that phenotypes are determined by a diallelic locus with dominance. Such systems could have evolved from an ancestral generalist that experienced disruptive selection by dominance

Table 1. Adaptive responses favored by disruptive selection

Responses	Favorable conditions	Refs
Changes in the ecological community		
Immigration by similar species	Availability of species and high migration rates	[69]
Destabilization of coevolutionary equilibrium into an evolutionary arms race	High variance of trait(s) in species under disruptive selection	[15,64–66]
Increase in genetic variation		
Frequencies of alleles at polymorphic loci are equalized	Additive polygenic inheritance	[14,26–28]
Positive linkage disequilibria	Low recombination rates	[14,27]
Increased effect size of alleles at polymorphic loci	No constraints on evolution of effect sizes	[21]
Decreased recombination rates	Linkage disequilibrium present	[29]
Dominance modification	Available genetic variation in shape of genotype-phenotype map	[30–32]
Assortative mate choice	Mating in the selective environment	[13,34–36]
Individual specialization with a genetic basis	(Not known at present)	[45]
Increase in phenotypic variation		
Sexual dimorphism	No developmental constraints on phenotypic divergence between sexes	[46–48]
Phenotypic plasticity	Reliable environmental cues, low cost of plasticity, high rates of gene flow	[53,54]
Bet-hedging strategies	No reliable cues and stochastic environments	[53,55]
Increase in individual niche width	Low costs of generalism	[58]
Specialization through learning	Behavioral flexibility through high learning and cognition abilities	[60]

modification and the magnification of allelic effects until each phenotype occupied a distinct fitness peak.

The evolution of assortative mate choice can also prevent the production of unfit offspring, with sympatric speciation as a possible outcome. Mate choice can be based either on the trait that experiences disruptive selection or on a closely linked marker trait. Theoretical studies have shown that sympatric speciation driven by disruptive selection is possible [13,24,34–36], but its actual occurrence and likelihood remain a cause for debate [22,23,37–39]. Cases where sympatric speciation might occur more easily are characterized by mating in the habitat that serves as selective environment for the ecological trait [23,40,41]. Prezygotic isolation can then be achieved through the spread of a single allele that causes either reduced migration between habitats [42] or strong habitat preference [43]. An intensively studied example where host fidelity is crucial for reproductive isolation is host-race formation in the apple maggot fly *Rhagoletis pomonella* [44].

Although distinct genetically determined morphs or species represent a possible outcome of disruptive selection, other distributions of genotypes could be favored. In the case of a continuous distribution of phenotypes, disruptive selection could be eliminated without splitting the population into discrete clusters, by the appearance of a range of genotypes. Bolnick *et al.* [45] list 16 empirical studies that report within-population genetic variance with individual specialization of different genotypes, giving some support to this scenario (Box 2).

Increase in phenotypic variation

Disruptive selection acts on phenotypes and several mechanisms can increase phenotypic variance without affecting genetic variance. The evolution of sexual dimorphism can reduce the strength of disruptive selection, for instance when the sexes specialize on different ecological niches [46–48]. A prerequisite is that developmental constraints do not limit the divergence between the sexes. Unambiguous evidence that sexual dimorphism results from disruptive natural selection rather than sexual selection is hard to come by and both forces are likely to operate jointly. There is evidence of an ecological cause in the hummingbird *Eulampia jugularis*, the sole pollinator of two *Heliconia* species. Males and females differ in their bill size and each sex feeds most quickly at the flowers of the species approximating its bill dimensions [49].

Disruptive selection can emerge from both spatial and temporal environmental variability and, under these circumstances, phenotypic plasticity and genetic diversification are alternative responses. A traditional idea [4], still considered important [50], is that plants often evolve plasticity when living in habitats with pronounced spatial variation. Being sessile, plants must cope with environmental variability over such short spatial distances that local adaptation is counteracted by gene flow. An example is plastic variation in leaf morphology in aquatic buttercups *Ranunculus* spp. [4,51,52], where submerged and emerged individuals have markedly different leaf types. A conclusion, supported by theoretical modeling [53,54], is that, in the face of spatial heterogeneity, reliable environmental cues, low costs of plasticity and high rates of gene flow all favor plasticity over genotypic specialization.

Unlike spatial variation, the purest form of temporal variation, with non-overlapping generations experiencing different environments, does not select for genetic diversification [5,55,56]. Instead, phenotypic plasticity and bet-hedging are possible outcomes. Plasticity is probable in regularly alternating environments associated with reliable cues, exemplified by the seasonal morphs of many insects such as butterflies [57]. Bet-hedging is favored in the absence of reliable cues, that is, when the environment where selection occurs is unpredictable at the time of phenotype determination. With overlapping

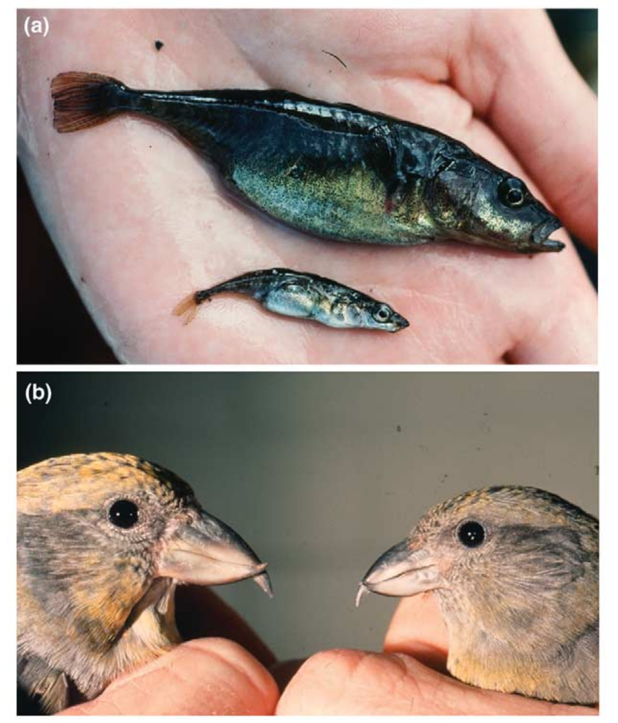
Box 2. Disruptive selection in the wild

Here, we discuss two intensively studied examples where phenotypic diversification is likely to be driven by disruptive selection.

Sticklebacks

Several coastal lakes in British Columbia, Canada, were colonized by marine threespine sticklebacks *Gasterosteus aculeatus* (Figure Ia; reproduced with permission from Todd Hatfield) after the last glaciation [69]. In some of these lakes, for example, Paxton Lake, a species pair evolved in which the smaller species is a specialized plankton feeder (bottom fish in Figure Ia), whereas the larger species is specialized on benthic prey (top fish in Figure Ia). Two explanations for the origin of this species pair exist. First, the two species could have evolved in sympatry in each lake from a marine ancestor. Second, they could have originated from two consecutive invasion events made possible by repeated sea-level changes. In this scenario, the first invaders evolved from a planktivorous marine ancestor into an intermediate feeding type. After the second invasion of planktivorous marine sticklebacks, the former invader evolved into the present-day benthivorous form owing to character displacement. Currently, the second scenario appears to be better supported [69].

Most lakes in British Columbia, however, harbor only a single stickleback species, which have a mean phenotype that lies between the two peaks of the bimodal distribution of the two-species lakes [70]. Evidence exists that at least some of these intermediate populations experience disruptive selection [16]. As a possible response, intermediate sticklebacks show a high degree of behavioral specialization: individuals that more closely resemble either the planktivorous or benthivorous populations of the two-species lakes in terms of morphology prey selectively on the corresponding resource [70].



Crossbills

The asymmetric lower mandible of the bill of red crossbills *Loxia curvirostra* (Figure Ib; reproduced with permission from Craig Benkman) is an adaptation to extract seeds from conifer cones. A putative ancestor with a 'straight' bill could have experienced disruptive selection, given that a lower mandible crossed to either direction enables a more efficient exploitation of conifer cones [71]. When harvesting seeds from a given cone, birds always orient so that the lower mandible is directed toward the axis of the cone. Different perches are favorable for left- or right-directed lower mandibles (Figure Ib), depending on the orientation of the nearby cone(s). If perch sites are limited, then conifer cones contain two different resources, each of them requiring a different bill crossing. In crossbill populations that rely on cones that cannot easily be removed from branches, the frequency of individuals of each crossing morph is one-half, and it has been suggested that this bill polymorphism is maintained by negative frequency-dependent selection [18]. The crossing type is associated with neither sex nor species and the phenotype determining mechanism is currently unknown [72].

generations, genetic diversification is a possible outcome of temporal heterogeneity, but will be selected less strongly than will bet-hedging [55,56].

In environments where a variety of resources are available, disruptive selection on resource acquisition traits decreases when individuals use a broader spectrum of resources [58]. Experiments with *Drosophila* have shown that strong intraspecific competition can select for the use of a wider range of resources [59]. Costs in terms of reduced utilization intensity to generalists can prevent the evolution of increased niche width [58].

Effectively different phenotypes can be realized by learning, resulting in a rapid phenotypic response to selection. For instance, individuals of Cocos Island finches *Pinaroloxias inornata* specialize on different resources, independent of age, sex, morphology, or location; these individuals might be specializing through observational learning [60]. Such spreading of behavioral phenotypes will decrease intraspecific competition and thereby decrease the strength of disruptive selection. Learning and cognition can be important for the ability of species to exploit a wide spectrum of resources and to survive in a range of environments [61], suggesting that behavioral flexibility influences the strength of disruptive selection.

The community perspective

Mathematical models suggest that disruptive selection on a species arises from interactions with its prey, predators or competitors [10,15]. Thus, changes in the populations or characteristics of those interacting species can affect the selection regime experienced by the focal species. Examples could be the addition of one or more interacting species or coevolutionary change in an already present interacting species. In fact, these changes are made more likely by the ecological circumstances that produce disruptive selection on the focal species, and can also act to remove existing disruptive selection.

In a resident species undergoing disruptive selection, mutant genotypes with more extreme trait values would be favored if they arose and could breed true. Thus, immigrants of an ecologically similar species having more extreme trait values could experience a similar advantage.

The invasion of such immigrants reduces the fitness of phenotypes of the original species that are similar to the immigrant and produces directional selection for divergence. The immigrant essentially has the same ecological role as one of the two phenotypes shown in Figure Ic (Box 1). Subsequent character displacement of the two coexisting species can eliminate disruptive selection in the same way as illustrated for the two phenotypes in Figure Ic (Box 1). Ecologically, the final state following immigration and displacement is similar to what would be predicted if sympatric speciation and divergent evolution had occurred within the resident species, except that variance in the trait under selection increases across a group of, rather than within a, species (Box 2).

It is also possible that two or more new species immigrate into the ecological system containing a resident population experiencing disruptive selection. If these species have phenotypes on either side of the resident phenotype, both could be more fit than the resident. The original resident will then be driven to extinction and the two new species will evolve to the peaks of the fitness landscape shown in Figure Ic (Box 1).

Isolated and species-poor systems are most likely to undergo intraspecific diversification before an immigration event. Thus, it is not surprising that examples of extreme intraspecific niche width come from isolated islands (e.g. the Cocos Island finch [60]), or that the most convincing examples of sympatric speciation (e.g. the Arctic char *Salvelinus alpinus* from Icelandic glacial lakes [62] and crater lake cichlids [63]) come from habitats where invasion of a closely related or ecologically similar species is at best a rare event.

Disruptive selection frequently arises in mathematical models of predator–prey coevolution [15,64–66] in which the capture rate of the predator is maximal for prey that have a corresponding phenotype; for example, large predators are best at catching large prey, whereas small predators are best at catching small prey. In models of this scenario, the only potentially stable coevolutionary equilibrium is one where the mean predator phenotype is optimally adapted to the mean prey phenotype. The prey species occupies a fitness minimum at this point, and whether evolution approaches this equilibrium depends on the genetic variances of the two species. Low genetic variance in the prey enables the predator to adapt to its prey, resulting in subsequent disruptive selection on that prey. However, a sufficiently large genetic variance in the prey relative to that of the predator enables the prey to evolve faster and escape the evolutionary control of the predator. Disruptive selection then becomes directional, and the result is either runaway selection to extreme phenotypes in both species, or evolutionary cycles in the trait values with predators chasing prey. Because disruptive selection in the prey increases its genetic variation and stabilizing selection on the predator reduces its variation, disruptive selection in the prey might often turn into directional selection during evolution. How frequently these outcomes occur in nature is currently unknown.

Which response should we expect?

As we have illustrated, various processes can be triggered by disruptive selection. To evaluate the importance of disruptive selection for biological evolution, one needs to be aware of this spectrum and of the circumstances favoring one process over the others. Much recent interest in disruptive selection has focused on sympatric speciation. Although an interesting topic, it should be compared with other outcomes that might be more common, given the broad spectrum of possibilities. It is also possible that disruptive selection triggers more than one response. For instance, in many resource polymorphisms in fish, phenotypic differences are determined by genes and by the type of resource consumed early in development [67]; a combination of genetic differentiation, plasticity and sexual dimorphism also seems feasible [68].

What determines the likelihood for each process to occur? We propose that the type of variation that is most readily available at the onset of disruptive selection has a head start and can respond first, possibly preempting other responses. If genetic variation is already available to the population, disruptive selection will quickly act to alter the genotype frequencies in the population. If phenotypic variation can increase rapidly through an input of ecologically similar immigrants of other species, or because the organism experiencing disruptive selection has a high capacity to learn new behaviors, these processes are likely to decrease the strength of disruptive selection.

Without the immediate availability of variation, genetic and developmental constraints are likely to have a role in determining the evolutionary response to disruptive selection. We suggest that a fruitful theoretical research program should enable the simultaneous evolution of different responses, systematically exploring the effects of constraints and the strength of selection on different responses. A series of recent mathematical studies has used this approach [47,48,54,56,58].

Conclusion

Disruptive selection has regained a prominent role in evolutionary thinking, especially in speciation research. The revival of interest in this category of natural selection seems justified, based on the large number of ecological scenarios that could lead to frequency-dependent disruptive selection. We suggest that, to better understand the effects of such selection on biological diversity, future work must develop a more systematic understanding of the full spectrum of responses that can create phenotypic diversity.

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