The evolutionary ecology of interactive synchronism: the illusion of the optimal phenotype

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ABSTRACT

In this article, we discuss some ecological-evolutionary strategies that allow synchronization of organisms, resources, and conditions. Survival and reproduction require synchronization of life cycles of organisms with favourable environmental and ecological features and conditions. This interactive synchronization can occur directly, through pairwise or diffuse co-evolution, or indirectly, for example, as a result of actions of ecosystem engineers and facilitator species. Observations of specific interactions, especially those which have coevolved, may give the false impression that evolution results in optimal genotypes or phenotypes. However, some phenotypes may arise under evolutionary constraints, such as simultaneous evolution of multiple traits, lack of a chain of fit transitional forms leading to an optimal phenotype, or by limits inherent in the process of selection, set by the number of selective deaths and by interference between linked variants. Although there are no optimal phenotypes, optimization models applied to particular species may be useful for a better understanding of the nature of adaptations. The evolution of adaptive strategies results in variable life histories. These strategies can minimize adverse impacts on the fitness of extreme or severe environmental conditions on survival and reproduction, and may include reproductive strategies such as semelparity and iteroparity, or morphological, physiological, or behavioural traits such as diapause, seasonal polyphenism, migration, or bet-hedging. However, natural selection cannot indefinitely maintain intra-population variation, and lack of variation can ultimately extinguish populations.

INTRODUCTION

Synchronization is the matching of life cycle events with resource use among interacting organisms, and phenological evolutionary adjustments to favourable conditions for survival and reproduction. Species survival and reproduction depends on the synchronization of the life cycle with environmental conditions, including resource availability and other organisms with which they interact either directly or indirectly. Some organisms interact indirectly with others modifying the habitat in ways that can promote changes in community structure, as is the case with ecosystem engineers and facilitator species. In the first case, indirect interactions can be favourable to certain species and harmful to other species. In the latter, the facilitation may generally be favourable to each interacting species. Either way, the consequences of their behaviour are changing species number in a community (Jones et al. 1997; Stachowicz 2001; Martins et al. 2016; Laland et al. 2017).

The synchronization of organisms with local resources and conditions is a result of adaptations, which can evolve epigenetically (at least for a few generations) or through phenotypic natural selection in the long term. When we observe the suitability of organisms to specific conditions and resources in their respective habitats, we often find examples of adaptations that seem flawless. One striking example is the coevolution of Agaonidae wasps (obligatory mutualists) with *Ficus* species. As far as we know, each of the 800 known *Ficus* species (Judd 2008) is thought to have its own pollinating wasp species (Cook & Rasplus 2003). The adaptive modifications that characterize these interactions reveal sophisticated co-adaptations resulting from coevolution, including a considerable occurrence of co-speciation (Cook & Rasplus 2003). These examples of near-perfect co-evolutionary adjustment may give the impression that natural selection results in optimal phenotypes, that is, that selection leads to trait performance maximization,

sensu Fisher (1930). Contrasting Fisher's (1930) assertion, Wright (1932) demonstrated that different combinations of alleles can achieve equivalent levels of adaptation, represented by different adaptive peaks between valleys in an adaptive landscape. Hence, rather than always resulting in optimal phenotypes, selection acting in stable environments should result in multiple phenotypes with similar levels of adaptation.

Populations inhabiting environments in which selection is fluctuating may evolve bet-hedging strategies, such as phenotypes with very different development times from egg to adult (Martins et al. 2001, see Figure 2 below). In environments where resources are plentiful and predictable, selection can lead to the evolution of specialists that can track resources over large geographic scales (Clark & Martins 1987). On the other hand, theoretical scenarios allow for equal resource intake by individuals subjected to intrapopulational competition, without resource monopolization (scramble competition) result either in persistence or stability in populations. Conversely, persistence and stability in populations, when competition with unequal intake of resource occurs with resource monopolization (contest competition), have a stronger effect on population persistence and stability (Łomnicki & Sedziwy 1989). There are at least two implications of these theoretical findings: (1) if the degree of inequality of resources intake increases, the contest competition could impair the stability and persistence of a population. Thus, the effect of directional natural selection on the evolution of resource intake specialization will be reached faster under contest than scramble competition. Nonetheless, the consequences to evolution of specialization in resources intake could be different if the authors allowed the amount of resources to change in spatial scale. (2) the contest competition could facilitate the evolution of an optimal phenotype due to its positive effect on population persistence and stability. However, we will show the impossibility of evolution of an optimal phenotype in nature. Besides, our goal is to review aspects of ecological and evolutionary strategies that allow synchronization of organisms, resources, and conditions.

1. POPULATION GENETICS AND EVOLUTIONARY FACTORS

Both Fisher and Wright models assume infinite numbers of population members, infinite resource abundance, and ignore demographic population features as an outcome of competition (Dietz 2005). Different from Fisher and Wright models, the model of evolutionary directionality factors is more realistic assuming the finite numbers of population members and the consequences of competition by scarce resources to population demography. Besides, the predictions of the model encompass both population genetics and demography. The cornerstone of this model is the statistical parameter evolutionary entropy. Introduced rather early by Arnold et al. (1994), the evolutionary entropy describes the rate at which a population uses the scarce resources; that is, the variance in ages of the

population reproductive members. The parameter specifies the robustness of a population or the return rate of a population to its original size after a perturbation (Dietz 2005). In a recent revision, Demetrius and Gundlach (2014) developed at length the range of evolutionary directionality theory and the entropic principle of natural selection. Anyway, under whoever model, the fittest phenotypes in a population will not be the optimal ones but the surviving phenotypes under the limitations imposed by competition and other inherent limitations from genetics, phenotypic plasticity and natural selection.

Despite Wright's assertion of the impossibility of selection resulting in optimal phenotypes, except under very particular circumstances, Fisher's idea persisted in the scientific community, even in researchers working in biological sciences. For instance, Travis (1989) defined 'optimizing selection as a type of natural selection that acts on metric traits, whereby individuals with intermediate trait values are more viable than individuals whose traits have relatively low and high values'. 'Stabilizing selection' also favours phenotypes whose traits have intermediate values, which may lead to the assumption of synonymy with optimizing selection. However, Travis (1989) distinguished these concepts by asserting that optimizing selection, which he calls viability or fertility selection, should act against the extremes of the trait distribution; stabilizing selection should instead protect normal morphogenesis against disturbances due to mild internal variation (e.g., mutations) or random variation in the external environment. However, this definition of stabilizing selection is more complicated and challenging to understand if one does not define these external and internal variations, nor describe the purported mutations. In practice, the result of both forms of selection is the same: phenotypes with traits of intermediate value are more viable than those of higher and lower metric values. Hence, some authors still equate optimizing selection and stabilizing selection (e.g., Streby et al. 2014), which demonstrates a degree of indifference for the distinction made by Travis (1989).

The concept of optimization in biology was borrowed from mathematical optimization theory. Its most frequent use is in mathematics, but it was also applied to economics, computation, civil and electrical engineering, geophysics, and molecular modelling in biology (Bandler et al. 1994). The term 'optimization' is used to describe the maximization of performance in scientific and technological processes and resulting products, and the minimization of energy expenditure employed to achieve the desired goal. Therefore, the expectation, implicit in the perspective of optimization models, is that the costs to manufacture these products must not exceed the potential benefits for performance of human activities.

Although it seems suggestive to characterize what could happen in nature, optimization is not appropriate in natural biological systems due to several reasons. First, for optimization to occur, configurations must be manipulated for some purpose. Evolutionary processes, instead, are nor teleological (Mayr 1992) and have a high component of stochastic behaviour. Second, phenotypes are not Cartesian machines that can

be manipulated to increase the functional efficiency or reduce energy expenditure. Organisms simply capture and transform light energy into biomass and heat. As we must recall, energy loss occurs via transfer between trophic levels, which limits the evolution of organisms that require more energy than is available in the upper trophic levels. Moreover, traits that develop at different rates across the ontogeny create more constraints in this process, driving the idea of optimality even more challenging to support. Natural selection against instability in long trophic chains diverges from linearity to a web-like configuration. Thus, long food chains do not exist in nature because they are unstable (Borrelli & Ginsburg 2014).

Parker & Maynard Smith (1990) advocate the use of optimization models in evolutionary biology to improve our understanding of the nature of adaptations but not to demonstrate that natural selection produces optimal phenotypes. They discard the idea that application of these models requires the assumption or 'proof' that organisms are optimal, and their use should be better understood in an instrumentalist (non-realist) epistemological context. They also recognize the difficulties in applying qualitative optimization models, because the biological parameters that constitute these models are difficult to measure. Quantitative optimization models applied to particular species whose biological parameters are more easily measured may help to reveal in greater detail the nature of adaptations. Nonetheless, in the 1980s and 90s, some theoretical and evolutionary biologists turned their attentions to exploring the advantages of optimization in order to better understand the eco-evolution of morphology and animal behaviour, particularly prey-predators' interactions. Pierce and Ollason (1987) were of the opposite opinion. They showed eight reasons why optimal foraging theory is irrelevant. Among these, they highlighted both the impossibility to expect animal behaviour to be optimal and to assess what optimal really means. They also denied the heuristic value of the theory because it encourages unjustified interpretations of animals behaviour. The value of qualitative optimization models in understanding adaptation could be useful in a few instances as aforementioned by Parker & Maynard Smith (1990), but not to understand the expected optimal phenotype and phenotypic plasticity evolution. There was also much effort by quantitative geneticists, starting in the 80s, towards optimizing genotypes to improve phenotypic traits in cash crops, for instance. These early efforts were not enough by themselves to improve the targeted traits. Nowadays, designing phenotypes requires multidisciplinary work by biologists, computer scientists, statisticians, engineers, breeders and biological engineers (see Cobb et al. 2013; Johnson 2013). Meanwhile, there are difficulties to obtain detailed knowledge of species genetic architecture, genes interactions, trait covariation, and to identify environmental factors underlying trait variation. It seems that the phenotypic plasticity approach is very important, for instance, to understand the effects of climate change on biodiversity (Noble et al. 2017). Plastic responses to environmental variation should be in general faster in ecological than evolutionary

time, making phenotypic plasticity a useful concept to predict phenotypic change in course of a few generations. Of course, as any biological phenomena, there are exceptions, because genetic adaptation may also happen in ecological time (see Charmantier et al., 2008; Genapp et al., 2008; Crozier & Hutchings 2014; Merilä & Hendry 2014; DeLong et al. 2016).

These practical difficulties due to natural system multidimensional dynamics, coupled with evolutionary constraints (Arnold 1992), lead to many problems for the optimization approach. Simultaneous evolutionary changes in a number of traits will hardly occur in an optimized way due to lack of a chain of fit transitional forms leading to an optimal phenotype or by limits inherent in the process of selection, which in turn is set by the number of selective deaths and by interference between linked variants (Haldane 1957; Hoffmann 2014). For instance, one of the main problems in dealing with selection in nature is exactly to account for missing information on traits that would drive evolution but were unmeasured, which can entirely disturb analyses of selection strengths in the multivariate space (Pigliucci 2006). All the above reasons make the evolution of optimal phenotypes highly improbable. A more realistic scenario is one in which the evolution of flexible adaptive strategies and phenotypic plasticity is favoured. Phenotypic plasticity is the ability of individual genotypes to produce different phenotypes (ecotypes) under different environmental conditions (Bradshaw 1965; Pigliucci et al. 2006), and can evolve through genetic or epigenetic transmission. As there are limitations restricting the evolution of optimal phenotypes, the evolution of adaptive phenotypic plasticity is also limited by the inability of an optimal trait to evolve (Murren et al. 2015). Adaptive strategies should thus be defined as the hereditary evolution of a set of traits that serves to counter the constraints imposed by trade-offs between growth, reproduction, and maintenance.

Although the revolution caused by Mendel's discoveries drove rapid development of the field of genetics from the beginning of the twentieth century onward, the Mendelian simple approach was never well established as a basis for the inheritance of complex phenotypes, as explicitly discussed in the debate between Mendelists and biometricists up to early 1930's (Provine 2001). This is now obvious, considering the advances in genomics that clearly show that the notion of a single gene encoding a unique characteristic does not hold true in the era of current molecular genetics (see Buiatti & Buiatti 2008 for a detailed history). The modern evolutionary synthesis incorporated the Mendelian inheritance (in a Fisherian basis) in the hard conceptual core of the theory, but this is exclusively valid for an allelic (in a Mendelian sense) transmission of traits across generations (Bondurianske 2012). Advances in molecular biology have demonstrated that the hereditary transmission of phenotypic characteristics is clearly more complex than proposed in the 'one gene encoding one attribute' model. For example, the configuration of phenotypes resulting from natural selection and evolution of complex animals depends on genotypic selection of clusters of interacting genes and covariates

that function systematically (Pardini & Guimarães 1992). The outcome of evolution is several possible genotypes that encode possible phenotypes (rather than optimal phenotypes), due to random errors and constraints imposed by the mutations, as well as the inherent imperfections of genetic inheritance transmission processes. Further, the direct transmission of traits via cytoplasm and chromatin, regardless of genetic inheritance, may also influence certain phenotypic characteristics (Jablonka & Lamb 1998; Gilbert & Epel 2008). Taken together, all these additional constraints and possible outcomes prohibit the existence of optimal phenotypes in nature. The constrains and limits to natural selection and evolution also prevent enhancing variability in natural populations. Bottlenecked populations, for instance, carry less variability than size stable populations (Amos & Hardwood 1998).

Genetic populations also suffer fitness losses due to the accumulation of deleterious mutations. This is referred to as the 'genetic load', in which the presence of harmful genes decreases fitness for the average individual in a population relative to the fittest genotype. That is, the difference between the fitness of an average phenotype and the fittest phenotype of a population is relative to that average one, and not to the theoretical optimal phenotype. A population with high genetic load could be in danger of extinction, if directional natural selection intensity is not enough to drive the population to a safe zone. Furthermore, as Crespi (2000) claimed, the fit of selected traits can never be perfect because organisms are adapted in some degree at least to one generation in the past.

On the other hand, within the distribution boundaries of a population, there will always be phenotypes with relatively lower fitness (marginal isolates), which tend to be eliminated by natural selection. When these phenotypes remain close to the distribution limit, it is by means of migrations. If mutations in these marginal genotypes have adaptive value outside of the geographic distribution area of the population, complex genetic rearrangements are possible (e.g., including reproductive isolation and parapatric speciation) leading to quick shifts and much faster speciation process than initially proposed under a simple 'founder effect' (Mayr 1954; see Templeton 2008 for a review on importance and reality of founder effect in evolution).

Under stable environmental conditions, stabilizing selection acts to maintain the adaptive characteristics of organisms (Vladar & Barton 2014) (Figure 1). 'Purifying', or negative selection (Charlesworth & Jain 2014) eliminates individuals with lower fitness than average for the population. Purifying selection reduces the negative effect of harmful mutations when the environment is relatively stable, whereas 'directional', or positive selection (Endler 1988), is manifested when conditions change, favouring the phenotypes whose mutations are beneficial for increasing fitness (Figure 1). 'Disruptive', or diversifying selection (Landi et al. 2015) also occurs when changed conditions do not favour the most common phenotypes; the less common phenotypes on the extremes of the trait distribution curve (Figure 1) then achieve better relative performances regarding fitness.

Moreover, it is essential to consider that natural phenotypic selection per se does not imply automatically in evolution (Fisher 1930). It occurs in a single generation of individuals through the action of natural selective agents, which simply eliminates phenotypes whose performance is insufficient for survival and reproduction (and thus, maintenance in the population). Even organisms that can reproduce may have inadequate performance under restrictive environmental conditions that directly impact fitness, for example, if adults make poor choices for nesting sites (Ost & Steele 2010). It is also important to consider that, under classical breeding equation, evolution will be equated as a response to selection if trait variation responsible for survival or higher fitness is heritable and if there is, of course, variation in this trait.

Variation in characteristics maintains differential fitness distributions, thus ensuring maintenance of populations both temporally and spatially. We can refer to this as ecological and evolutionary continuity. The concept of ecological continuity has been used in the past to evaluate habitat quality through bioindicators in old forests (Norden & Appelqvist 2001). Adding evolutionary continuity to the overall concept allows us to generalize patterns for species occurring in any habitat type. Ecological and evolutionary continuity, like speciation, occurs by means of spatio-temporal variation in resources and environmental factors (in habitats occupied by individuals capable of surviving and reproducing under those conditions). This continuity also results in relatively stable community structure over time (Turcotte et al. 2012). On the other hand, evolutionary continuity can be described by directionality theory. As pointed out above, the concept of evolutionary entropy besides integrating genetics and ecology can be a useful descriptor of how the energy flow could maintain community structure.

Another factor that may affect individual performance is the occurrence of sterile individuals in a population.
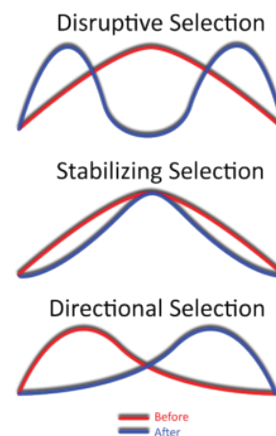

Figure 1. Schematic representation of the three theoretical models of natural selection (disruptive, stabilizing and directional) showing a. increase trait variance, b. reducing trait variance and c. no variation in trait variance after selection. The optimal phenotypes in a. are the extreme modes of the distribution in blue, arrived at by changing trait variance, b. the unchanged mode of the resulting trait distribution, albeit with larger variance and c. the new mode of the resulting trait distribution, with no change in trait variance.

Sterilization can occur through various means, including incidents during ontogeny (e.g., Cooke et al. 2013), or as a result of parasitism (e.g., Abbate et al. 2015). These events can reduce the probability of reproduction to zero for affected individuals. However, despite lack of contribution of attributes to the genotypic and phenotypic composition of the next generation, some may survive and compete for resources with other members of their population, or with individuals from populations of coexisting species with which their diets partially overlap. These individuals, through resource competition, may diminish the potential fitness of reproductive members of their own or other populations. There are also cases in which reproductively fit individuals do not reproduce if they are excluded from the social group (e.g., Russell 1981), as well as helpers (e.g., in a nest) that do not reproduce but remain with parents to help brood offspring (Riehl 2013). According to the hard life hypothesis, helpers may stay at the nest to provide for their offspring when the food supply is restricted, favouring an increase in inclusive fitness (see Koenig et al. 2011 for a discussion of these hypotheses).

Despite the unpredictability of random events, changes in variation and inheritance of traits and more complex possibilities of performance of organisms in shifting natural environments, phenotypic selection may be predictable as a general process. However, which characteristics of ancestors and progenitors will be found in offspring phenotypes remains unpredictable due to statistical issues. The theory of 'descent with modification' predicts that the offspring will possess phenotypic characteristics of the parents, however, it is hard to predict which characteristics will be similar to which of the parents in a complex system with changing environments. Although traits in progeny may be predominantly similar to one parent, there will always be some combination of phenotypic attributes of both, as well as the possibility of expression of ancestral traits.

Finally, in the organic world, life results from interactions (Coutinho et al. 2011). There is no living being that does not interact with the environment, attempting to obtain sufficient energy for survival and reproduction. To this end, the activities of organisms must be synchronized with the resources they use, and with the conditions that allow the existence of resources and those that use them. Besides, behavioural interactions of organisms with the environment is an important factor both in genotype and phenotypic evolution. Life diversification can be increased by the behaviour of individuals creating new ecological niches and therefore new evolutionary opportunities for other organisms (Laland et al. 2017).

2. ECO-EVOLUTIONARY STRATEGIES AND SYNCHRONY AMONG ORGANISMS, RESOURCES, AND ENVIRONMENTAL CONDITIONS

Every organism interacts in many ways modifying environmental conditions. A portion of these interactions results from (co) evolution by natural selection and speciation, and a portion

from the evolution of epigenetic phenotypic plasticity (Duncan et al. 2014). These interactions are responsible for the evolution of various life histories, which are characterized by ecological-evolutionary strategies. Ecological-evolutionary strategies are sets of integrated adaptive features (suites) that compose organismal life histories. Conflicting energy demands (trade-offs), specifically about survival and reproduction, can lead to the evolution of variable life strategies (e.g., iteroparous species, which can have several reproductive episodes during their lifetime, and semelparous species, characterized by a single reproductive episode before death). Because the ecological and evolutionary impacts of these two strategies differ, it is useful to distinguish between interindividual trade-offs, which are related to female reproductive effort and the likelihood of her survival to the next reproductive season, and intergenerational trade-offs, which are related to female reproductive effort and the probability of survival for her offspring (Stearns 1979).

Genotypic variability produces phenotypes that differ in performance potential, sensitivity to environmental variation, and notably, the degree of vulnerability to competition and predation. However, natural selection may maintain balance among traits, depending on the relative frequencies of occurrence of those traits in a population (e.g., Dawkins & Brockmann 1979). This frequency-dependent strategy cannot be replaced by other competing strategies (Maynard Smith & Price 1973). An evolutionarily stable strategy (ESS) is a strategy which, if adopted by a population in a given environment, cannot be invaded by any alternative strategy that is initially rare. It is relevant in game theory. In the case of the Dawkins and Brockmann (1979) study, the ESS is perhaps the most straightforward strategy adopted, but more complex mixed strategies may also evolve in the same populations (Martins et al. 2001). In unpredictable environments, the ESS enables future survival and reproduction for parents and offspring. These strategies may include diapause, dormancy of immature stages of insects and seeds, migration, seasonal polyphenism, and bet-hedging (Martins & Barbeitos 2000). In all cases, the response of the organism depends on environmental triggers that initiate physiological, morphological, or behavioural changes. For example, environmental triggers can either initiate diapause or dormancy or end it, in which case adults emerge simultaneously when resources are available.

Extreme conditions can considerably affect resource availability and hence performance, decreasing the likelihood of survival and reproduction. Less extreme conditions have lower impacts on performance but do not ensure continuous survival and reproduction *per se*, as they also depend on the temporal and spatial availability of resources. Even for iteroparous species, if resources are in poor supply, survival and reproduction will be seriously jeopardized for parents and offspring. Semelparous species, as the Pacific salmon (Crespi & Teo 2002), can invest in biomass for several years before reaching reproductive maturity, when they reproduce only once and die. However, under specific conditions such as high predation risk for offspring, facultative iteroparity may evolve (Futami & Akimoto

2005). The evolution of strategies for synchronism among organisms and environmental conditions reduces their extinction risk.

Holometabolous insects require extensive feeding to complete their life cycle, and under conditions of resource shortage, dormancy guarantees the survival of immatures until adult eclosion in the following season (when presumably there is enough resource availability). This is the case for the solitary digger wasp *Editha magnifica*, who progressively provisions her nests. Each larva, which reaches the size and biomass almost equivalent to that of adults, needs to consume about 100 butterflies to reach adulthood (Martins 1993). Dormancy and bet-hedging occur simultaneously (Martins et al. 2001; see Hopper 1999 for a review) and can produce multimodal time distributions for immature development, increasing the probability of survival and future reproduction of the population. The same occurs in parasites, whose developmental times are synchronized to that of their respective hosts (e.g., as occurs in the solitary digger bee *Ptilothrix plumata* and its parasites (Figure 2).

Certain species, which reproduce in the location of birth (philopatry), develop pre-pupae that, under adverse conditions, can remain dormant until the resources for self (adults) and offspring provisioning are again available when they eclode. If the ecological conditions remain relatively stable, a succession of several generations may occur at the same site where the parents were born (e.g., Antonini et al. 2000). Even in regions with relatively mild temperatures, some organisms (e.g., lungfishes) may bury themselves in sludge for up to several years until sufficient water flow returns (Greenwood 1986). Metabolic rates may also be reduced at very low temperatures, a condition associated with fat storage from periods when the food availability was higher. Several animal species reduce physical and metabolic activity and remain in hibernation during the stressful seasons.

Alternatively, when resource supply decreases and reduces the probability of survival and reproduction, a subset of the population may disperse and find more favourable conditions for survival and reproduction elsewhere. It is well known that certain adult vertebrates (e.g., birds, fish, and aquatic mammals) migrate to avoid unfavourable seasonal climate for survival or reproduction, but arthropods also use this strategy. In some gall midges (Diptera, Cecidomyiidae), for example, reproduction can occur by larval parthenogenesis: the early developed eggs hatch internally, and the larvae consume the body of the mother-larva before leaving to feed on the surrounding resource. The well-studied gall midge *Heteropeza pygmaea* can synchronize the environment because it is facultatively paedogenetic: female larvae may become adults or repeat the larval pedogenetic cycle, whereas male larvae must develop to adulthood. When resources are abundant, female larvae produce more larvae and the population increases very fast. When food resources become scarce, they grow into adults (males and females) who are able to reproduce sexually and migrate in search of other sources of resource (Went 1979).

In relatively stable environments, interactive synchronism can be maintained for up to millions of years. This is the case for the interaction between the pollinating wasp Agaonidae and *Ficus* species, a prominent example of coevolution whose oldest fossil evidence is 34 MYA (Compton et al. 2010). Despite this long history of interaction, extinction of some wasp species and thus, associated *Ficus* species, is inevitable. The interaction is maintained over time through speciation. Over evolutionary time, several species of the interacting pairs undergo mutations, and selection continually directs mutual survival and reproduction of the coevolved pairs (see also Turcotte et al. 2012). However, this is not the whole story. Diffuse coevolution, which involves several species interacting simultaneously, seems to be more frequent than pairwise coevolution, especially in plants (Strauss et al. 2004).

In environments where the climate is relatively constant, strong variation in resource availability in successive years, for example, due to unpredictability in rainfall regime, may induce high mortality and low offspring production. This may negatively affect individual fitness and population performance, especially for specialists with restricted phenotypic plasticity (see Griffith & Sultan 2012). Synchronism between organism life cycles, favourable climatic conditions, and resources is essential for both generalists and specialists, although the latter may suffer significant consequences if the resources in which they specialize are restricted. Generalists are not subject to such restrictions because they can switch food items according to availability and abundance (Abrams
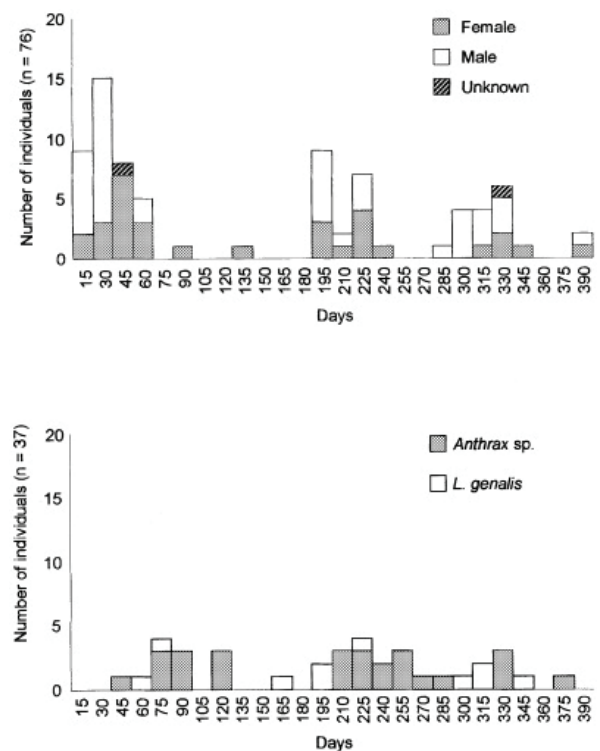

Figure 2. Distribution of egg-to-adult development times for Ptilothrix plumata and its parasitoids, grouped into 15-day classes. (Figure 4 from Martins et al. 2001)

2006). Populations of specialists and generalists also contain individuals that are specialized in sub-sections of the total resources used by the species (Araújo et al. 2011; Costa et al. 2015). On the other hand, obligate specialists of certain types of resources may be able to track preferred items, regardless of the conditions they experience along the broad distribution of those resources. This is the case for the dipteran *Arcivena kielmeyerae* (Cecidomyiidae) (Gagné 1984) and the Coleopteran *Anthonomus biplagiatus* Redentbach (Curculionidae) (Clark and Martins 1987) that are the endoparasites of floral buds of 12 species of *Kielmeyera* in several areas of four Brazilian states where environmental conditions are variable.

The abundance and predictability of specific resources are prerequisites for the evolution of specialists (MacArthur & Levins 1967). If the favourable conditions are maintained, or as in the example of the floral bud parasites described above, the predictability and availability of the resources can be tracked by the individuals regardless of the conditions where the resource is found. The result, in this case, is the superposition of the geographical distributions of the specialists and their resources.

3. CONCLUSIONS

Natural selection favours continuous exponentially growing populations under unbounded resources availability, favourable conditions and absence of natural enemies. Populations actually should circumvent a variety of biotic and abiotic constraints, changing adaptively in ecological and evolutionary times, in order to achieve maximum growth rates. These changes, however, do not lead to optimal phenotypes in nature.

Although the use of qualitative or quantitative optimization models may aid in our understanding of the nature of adaptations in certain cases, the idea that natural selection produces optimal phenotypes should be abandoned in evolutionary biology. Since there are only possible genotypes and phenotypes, we expect that natural selection will eliminate phenotypes that are unlikely to survive and reproduce in a generation, and favour those that are able to survive and reproduce

to the next generation. This performance aspect of selection should not be confused with evolution. Selection occurs over the course of a generation, while evolution is the hereditary transmission of traits for the next generation by deterministic or stochastic mechanisms.

The adaptive suite of traits is characterized by evolutionarily stable strategies that allow organisms to overcome the effects of chance. These strategies operate both locally and on broad scales, allowing overlapping geographic distributions of specialists and their resources. In these cases, specialists can track resources over geographic scales irrespective of variation of environmental conditions. However, the occurrence of interactive synchrony does not prevent extinction when there is insufficient variability in a population to respond to random variations in resource availability and environmental conditions. Natural selection cannot indefinitely maintain such variability in a population. Thus, the population can be extinguished without sufficient variability or genotypic and phenotypic diversification through speciation. Limits to natural, errors in the evolutionary processes of trait transmission, as well as constraints on these complex and imperfect processes, result simply in possible genotypes, which encode possible phenotypes, over a limited time horizon.

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