

The ecological causes of evolution

Andrew D.C. MacColl

School of Biology, University of Nottingham, University Park, Nottingham, NG7 2RD, UK

Natural selection is the process that results in adaptive evolution, but it is not the cause of evolution. The cause of natural selection and, therefore, of adaptive evolution, is any environmental factor (agent of selection) that results in differential fitness among phenotypes. Surprisingly little is known about selective agents, how they interact or their relative importance across taxa. Here, I outline three approaches for their investigation: functional analysis, correlational analysis and experimental manipulation. By refocusing attention on the structure and consequences of ecological variation, a better characterisation of selective agents would improve understanding of natural selection and evolution, including adaptive radiation, coevolution, the niche, the evolutionary ecology of the ranges of species and their response to environmental change.

What causes natural selection?

When one contemplates how understanding of evolution has improved over the 150 years since Darwin first published his ideas about natural selection [1], it might come as a surprise to realise how little is understood about the causes of adaptive evolution in natural populations. Recent developments are causing evolutionary ecologists to think more explicitly about the nature of natural selection: how it varies spatiotemporally [2–5], the ecology that drives it [6–8], how adaptation, divergence and speciation result (or do not) [9–11], and consequences for, for example, macroecology [12], the niche [13] and adaptation to climate change [14]. Clearer thinking about, and more explicit investigation of, the causes of selection, so-called ‘agents of selection’ (Box 1) would greatly enhance understanding of natural selection.

Darwin obviously thought about such things. In *The Origin of Species* [1] he reflected on ‘checks to increase’: that is, the factors that curb population growth and result in the struggle for existence. Darwin was aware that ‘What checks the natural tendency of each species to increase in number is most obscure’, but he considered that biotic interactions were more important than were abiotic ones, and he regretted ‘our ignorance on the mutual relations of all organic beings’. Although there is now some understanding of the importance of individual selective agents in specific systems (see below), there is still a lack of systematic understanding of the gamut of agents for any one system, let alone the relative importance of agents across traits or taxa. Thus, Darwin’s assertion that ‘We know not exactly what the checks are in even one single instance’ is almost as true today as it was 150 years ago.

Following Darwin, early workers sometimes speculated about what drove natural selection on particular traits (e.g. [15]). However, a century passed before there was systematic thinking about the causes of natural selection. Clarke [16] and Wade and Kalisz [17] suggested similar approaches for identifying the causes of selection. These have seldom been followed through, so that rather little is still known about what causes natural selection. ‘The analysis of the causes of selection is in essence a problem in ecology’ [17], but it is an ecological problem of relevance to all evolutionary biologists. Here, I outline some ways in which the study of selective agents might shed light on research topics in evolutionary ecology, but I begin by considering three ways of identifying selective agents [16,17].

Functional analysis

The functional analysis of a trait or polymorphism, in which one infers selective agents from trait function, can be useful in the initial investigation of the causes of selection. For example, extravagant traits used in courtship are probably shaped by the aggression or choice of members of the same species. Clarke’s study [16] of the alcohol dehydrogenase (Adh) polymorphism in *Drosophila melanogaster* is archetypal. The two common alleles (‘F’ and ‘S’) differ in their efficiency of catalysing short-chain alcohols to aldehydes and ketones, as well as in substrate specificity for different alcohols and sensitivity to temperature [16]. This gives rise to an ‘eco-evolutionary landscape’ (see below), in which, even in this apparently simple example, the combinations of environmental conditions that favour different alleles are complex. The F allele is favoured by higher concentrations of ethanol, but this depends on the other alcohols present, as well as on temperature shock. This interaction between selective agents might be an important property of eco-evolutionary landscapes that determines the evolutionary outcome and maintains variation.

Functional analysis is most appropriate for those kinds of phenotype where an unambiguous functional characterisation is possible. However, it can still be misleading. The function of some traits might seem obvious, giving rise to potentially incorrect assumptions about the cause of the selection that shaped them (Box 2).

Observational data

Correlations between spatiotemporal variation in selection and putative environmental variables might help to identify selective agents [17]. Many studies have documented variation in the strength of selection through space and time. It is unfortunate that the ecological correlates of this have seldom been pursued in depth [5], because such studies afford a

Corresponding author: MacColl, A.D.C. (andrew.maccoll@nottingham.ac.uk).

Box 1. Agents of selection

Natural selection is not the cause of evolution, it is a process [56,57] in which the frequency of phenotypes within a population is changed, within a generation [58]. Their frequency is changed because their survival or their ability to reproduce is different from that of other phenotypes. The process happens when there is covariance between phenotype and fitness. This is often represented as a plot of the relationship between fitness and trait, which encourages one to think that the variation in fitness is caused by variation in the trait [59]. Instead, if one remembers that the relationship is a covariance (correlation), then one might be more likely to ask how the association arises.

Many studies have demonstrated the existence of covariance between trait and fitness [60], but few have asked why it exists. There are two possible answers: (i) the correlation arises during development [56,59]. This does not result in natural selection, and will not be considered here. (ii) Something in the environment causes the covariance. That ‘something’ has been called an agent of selection or a selective agent. Why do finches with bigger bills survive better during droughts? It is not because bigger bills are inherently better, but because that bill helps them to crack large, hard seeds [61]. It is the availability of different seeds that causes the covariance between bill size and survival. This is made plain by the fact that when the relative availability of different seeds changes (e.g. in wet years), the relationship between fitness and phenotype completely reverses [62]. Thus, the availability of different food sources is a major agent of selection in the evolution of finch bill size, but other agents, such as intraspecific competition, are also important [63].

Galapagos finch bills provide one of the few examples of a trait in a natural population where one can say, with any confidence, what the selective agents are. Others include cases of anthropogenic evolution, for example resistance to insecticides and drugs [64,65]. One can also be confident that factors such as competition, natural enemies and the abiotic environment are likely to be important selective agents, and one might even know that particular agents are important in certain situations. However, almost nothing is known about how different selective agents might interact or their relative importance across traits or taxa in the shaping of organisms by evolution.

real opportunity to identify selective agents. Simple plots of selection metrics against single environmental variables can be revealing about the workings of selection, but are surprisingly rare (e.g. [2,18,19]). However, the real utility of the correlational approach would come from examining how selection (β) varies with different environmental variables (e_i) using multiple regression, because only then can the relative importance of different variables and the extent of interaction be quantified (Equation 1):

$$\beta = c + m_1e_1 + m_2e_2 + \dots + m_n e_n + \varepsilon \quad (1)$$

where c is the intercept and ε is the residual error.

With this approach, much can be learned about selective agents by using data collection and statistical methods with which evolutionary ecologists are already familiar. One just has to remember to collect data on environmental variables when measuring selection. Yet such analyses are rare. A recent study [4] examined correlations between the strength of sexual selection and sex ratio, density and temperature, but was unable to do this in a multiple regression framework because of insufficient data.

Results of multiple regression analyses would be particularly informative if presented as a surface of the strength of selection plotted against pairs of selective agents (e.g. [2]). To avoid confusion with adaptive landscapes and other types of selection surface [20,21], I suggest that these representations are called eco-evolutionary surfaces or landscapes,

Box 2. The problems of functional analysis: an example

The problems of functional analysis are exemplified by the lateral plate polymorphism in three-spined sticklebacks (*Gasterosteus aculeatus*) [66]. Marine populations of this small temperate fish have a row of external, bony plates. Stoutly constructed, these have the feeling of a blunt file when handled. They give the fish the appearance of being encased in a suit of bony armour (note the implicit assumption about function) and, indeed, they are well designed so to function [67]. Many freshwater populations of sticklebacks are either devoid of these plates, or have them only in a much reduced form. Selection on the trait has been studied for more than 80 years [68], making this one of the best known polymorphisms in nature. Researchers now know the molecular genetic basis of the trait [69], that selection can be very strong [70] and can result in extremely rapid evolution [71]. Yet little is known of what causes the selection.

Experimental evidence supports the idea that the plates confer mechanical protection against predation [72], and that predation causes selection on plate number within populations [73]. However, this does not mean that predation drives the variation between fully plated and unplated populations. Many low-plated populations subsist in the presence of substantial predation, suggesting that other agents must be involved. Numerous agents of selection have been suggested that might favour change in phenotype from the ancestral plated form: (i) invertebrate predators that catch by grasping can favour loss of plates [74]; (ii) pursuit predators might favour loss of plates by enabling enhanced speed and manoeuvrability [75]; (iii) lack of calcium in soft freshwater might drive selection on plates, because bone is partly calcium [76]; (iv) reduced nutrient availability or salinity might favour loss of plates because they are energetically expensive to grow and reduce buoyancy [77,78]; (v) parasites might contribute to selection, because the *Eda* locus, which controls the polymorphism, is in close physical linkage with a gene that has been implicated in resistance to nematodes [69]; and (vi) the hydrodynamic environment might affect selection, because plates might function in the transduction of water pressure changes to the lateral line [79]. Overall, the lesson is that it can be difficult to infer the cause of selection through functional analysis, even for simple traits with apparently obvious function.

because they explicitly display the connection between ecological or environmental variables and the potential for evolution, as indexed by the strength of selection. Eco-evolutionary surfaces are primarily heuristic: they make clear the way in which selection varies across ecological gradients, where maxima and minima occur, and the nature of interactions between agents. However, the regression parameters could also be used to predict the strength of selection in unmeasured environmental conditions. As an example, I constructed an eco-evolutionary surface for great tits (*Parus major*), using published data from Wytham Woods, Oxford. Figure 1 shows the relationship between selection on fledging mass [22], and two factors known to be important in overwinter survival: the temperature between December and February, and the amount of nuts (mast) produced by beech trees (*Fagus sylvatica*) [23]. When nuts are abundant, selection varies little and favours higher fledging weight; by contrast, when beech nuts are in short supply, selection varies greatly in strength and appears to favour lower fledging weights when winters are cold. The latter conclusion should be treated with caution. A lack of data for cold winters when beech nuts are scarce means that Figure 1 extrapolates into a poorly known region of ecological space.

Figure 1 was prepared with information from the literature and is not a serious representation of an eco-evolutionary landscape, such as could be constructed with

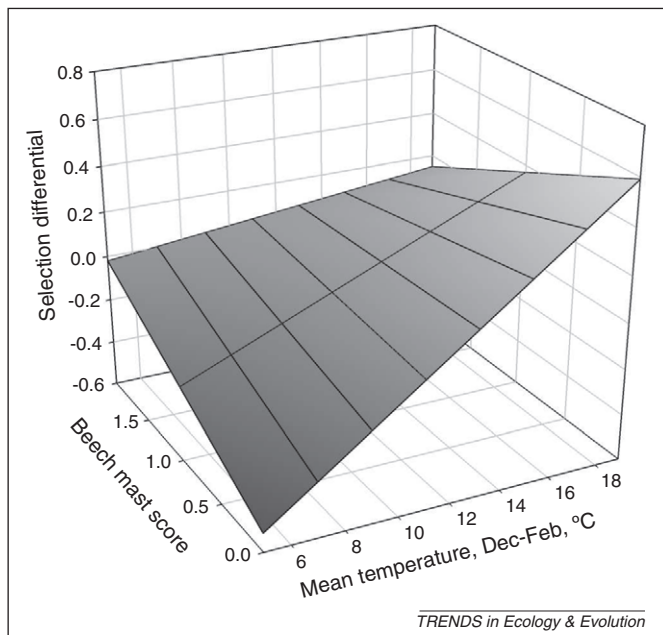


Figure 1. An example of an ‘eco-evolutionary landscape’ for fledging weight in great tits (*Parus major*). The figure shows the relationship, quantified by multiple regression, between the strength of selection (measured as survival over the first year of life), and two environmental variables: winter temperature (sum of monthly mean temperature from December to February) and availability of beech (*Fagus sylvatica*) nuts (‘beech crop index’) in the winter following fledging. The strength of selection appears to be determined by an interaction between the two environmental variables, and this might be a common property of eco-evolutionary landscapes.

purpose-collected data. Real attempts should use details of the natural history of a species to identify putative selective agents. Analyses will require data gathered either over many years or from different populations. Eco-evolutionary landscapes could reveal a good deal about natural selection in the wild, by forcing one to think about the ecological context of selection. Unfortunately they are not without significant weaknesses, as detailed below.

Quality of data

Estimates of selection can be unreliable, data on putative selective agents might be unavailable, or the real agent of selection might not be among those factors that are examined. Simply collecting enough data to construct an eco-evolutionary surface is an enormous amount of work for any organism that does not have a very short generation time, especially if the form of the relationship between fitness and trait is complex [24].

Spatiotemporal correlation

Multiple regression should be efficient in identifying important selective agents, just as it is in identifying traits under selection when several are measured [25], but only when the real agents are among the environmental correlates considered. The ability of multiple regression to identify the true agent(s) will also depend on the extent to which putative agents are intercorrelated. If correlation is low, the approach could be quite robust, but a large amount of data will be required if correlations are strong, which is often likely to be the case [26]. A corollary of such correlations is that certain combinations of environmental conditions apparently occur rarely or not at all (such as cold

winters with scarce beech mast). The evolutionary consequences of correlations among environmental factors seem poorly explored, and this should be viewed as a research challenge.

The idea that genetic correlations [the genetic variance–covariance (G) matrix] can affect the outcome of evolution (through trade-offs and paths of least resistance) is well established [21,27]. There does not appear to have been explicit recognition of an equivalent role for correlations between selective agents (although see below, [9]). Yet they might help to understand widely recognised evolutionary phenomena, such as parallel and convergent evolution and the G matrix itself. Solving Equation 1 requires the generation of a variance–covariance matrix of environmental variables (which I denote ‘O’ after ‘oikos’, the ancient Greek for a household), because ‘m’, the vector of partial regression coefficients of selection on environmental variables, is obtained from Equation 2:

$$\mathbf{m} = \mathbf{O}^{-1} \cdot \text{cov}(\beta, e_i) \quad (2)$$

where $\text{cov}(\beta, e_i)$ is the covariance between selection and environment.

When the O matrix is estimated using field data, it quantifies the relationships between environmental variables: its entries are simply their variances and covariances through space and time for the species being considered. Box 3 indicates how research on the O matrix might illuminate understanding of evolutionary ecology.

Correlations between environment, traits and fitness

Correlative studies might fail to identify agents of selection robustly because of covariance between environment and trait expression, phenotype or fitness. The consequences for the measurement of selection have been reviewed elsewhere [28]. Wade and Kalisz ([17], their Figure 1) have already illustrated the difficulties that result for identifying agents of selection. These might be especially hard to overcome in the study of selective agents affecting plants, because of substantial phenotypic plasticity for quantitative traits. Animals are less phenotypically plastic, so the correlation between environment, traits and fitness might be less problematic (but see [29,30]).

Experimental manipulation of environment

The solution to most of the difficulties inherent in an observational approach to identifying agents of selection is to use an experimental one [17]. Although experimental approaches to the study of natural selection are not uncommon, many involve manipulations of traits or trait distributions [31,32]. These experiments tell little about selective agents, unless environmental factors are manipulated simultaneously. Such combination manipulations are powerful for gaining a full understanding of the target and cause of selection (e.g. [6,33]). Experiments that examine the change in selection following transplantation of organisms between environments are also common, but cannot unambiguously identify the selective agent for the reasons detailed above.

The most robust and straightforward way to identify selective agents is to manipulate putatively important aspects of the environment, and measure the consequences

Box 3. The O matrix and correlations between selective agents

Research on the guppy, *Poecilia reticulata* [80,81] has examined the evolution of different life histories upstream and downstream of waterfalls. The cause was initially assumed to be differences in predation [80]. However, the localities also differed in terms of their forest cover, light intensity, primary productivity [82,83], parasites [84] and guppy densities [85]. Patterns such as these, of correlations between environmental variables, are likely to be common in the eco-evolutionary landscape of organisms, but seem never to have been explicitly explored. They have several consequences.

Correlations make it difficult to establish the true cause of evolved differences between populations. The obvious solution is to manipulate environmental factors experimentally. This is relatively straightforward when correlations come about because 'that is how the world works', but more difficult if there are feedbacks between factors. Low predation and low light are associated because forests and waterfalls tend to occur on wet tropical mountains, but predators cause lower density [85]. Independent manipulation of predators and forest canopy cover might then be 'easier' in some sense than manipulation of predators and density, and result in interesting conclusions about the relative importance of selective agents [86].

Collinearity of selective agents might determine the way in which organisms evolve [55,87]. Figure 1a,b show the imagined eco-evolutionary landscape for a trait (resistance to parasites) in relation

to two selective agents: the abundances of parasites and predators. Superimposed in the x–y plane is an ellipse representing possible forms of the relationship between these two variables (their O matrix): positively correlated in Figure 1a, negatively in Figure 1b. In this example, the O matrix would be a 2×2 matrix, in which the diagonal elements give the variances of parasites and predators through space or time. The (symmetrical) off-diagonal elements give the covariance of parasites with predators, and would be positive for the O matrix represented in Figure 1a and negative for that in Figure 1b. The structure of the environment in Figure 1a might prevent the evolution of complete parasite resistance, for example, through resource trade-offs at the level of the individual, because abundant parasites only occur in the presence of many predators.

Relationships between selective agents could also shape relationships between traits. Figure 1c,d show hypothetical eco-evolutionary surfaces for two different traits: parasite resistance and anti-predator defence, in response to variation in corresponding environmental variables. If the O matrix of these variables is as in Figure 1b, then selection should result in a negative correlation between the traits, across populations. In the presence of large environmental fluctuations, or gene flow between populations in contrasting environments, this could contribute to the evolution of negative correlations between traits at the level of the organism (i.e. G matrix).

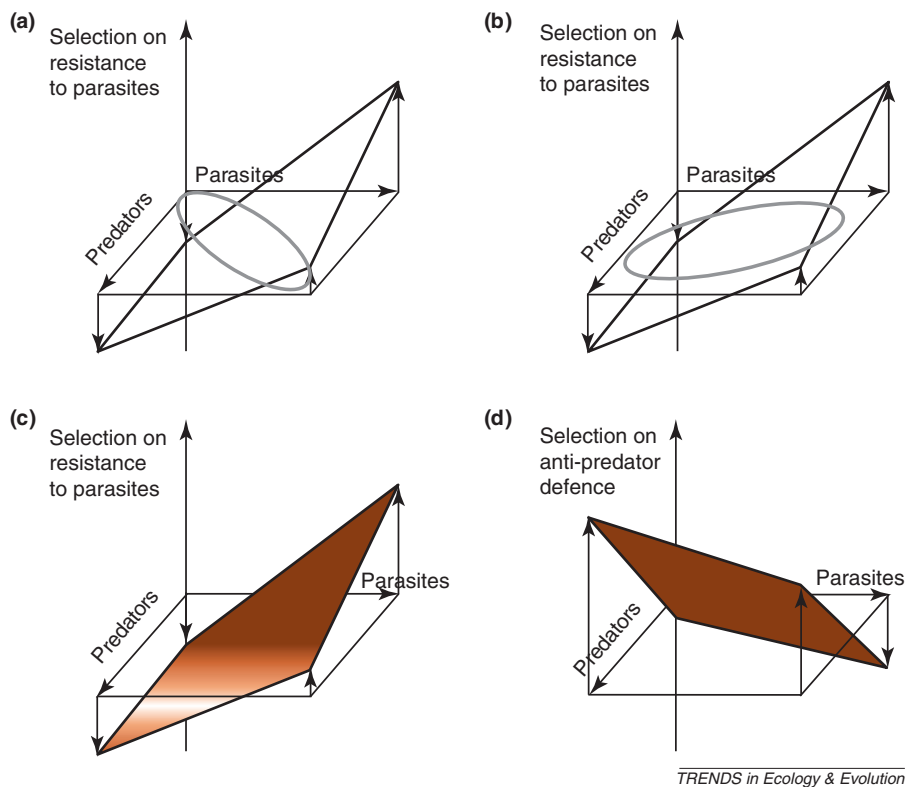


Figure 1. Hypothetical eco-evolutionary surfaces showing the relationship between abundance of parasites, abundance of predators and selection on parasite resistance (a, b, c) or anti-predator defence (d) in some imagined species. In (a) and (b), the grey ellipse indicates the correlation between the abundance of parasites and predators within the range of this species. The strength and direction of the correlation has consequences for how parasite resistance is likely to evolve. (c) and (d) suggest that the correlation between parasite resistance and predator defence will also depend on the correlation between selective agents.

for the strength of selection. Such studies are surprisingly uncommon, but Box 4 gives a flavour of them. Most experimental studies manipulate putative agents of selection directly. Where direct manipulation of selective agents is difficult (e.g. pollinators and herbivores), simulation of their effect can be as informative [6,34,35], but only if the manipulation simulates all the subtleties of the natural situation. For example, cutting leaves with scissors to

simulate herbivory might not reproduce the effect of real herbivores [36].

Reasons to study selective agents

Natural selection and evolution

An understanding of natural selection cannot be complete without knowing its causes, their relative importance and how they interact to form the eco-evolutionary landscape.

Box 4. A summary of experimental studies of selective agents

I searched the abstracts of 205 papers on Web of Knowledge that cited Wade and Kalisz [17] to 24 March 2011, and examined those that measured selection after manipulating environmental variables (putative selective agents). In total, 41 studies of 34 taxa satisfied the criterion. Of those, 31 examined selection on plants, but only ten on animals. Abiotic variables were commonly manipulated (water, light, temperature, nutrients; 17 studies in plants e.g. [88], but only one in animals [89]). Manipulations of biotic variables were also common, including competition or density (four plant studies; six animal studies; e.g. [90,91]), herbivory and predation (nine plant studies; four animal studies; e.g. [92]) and pollination (eight studies; e.g. [34,35]). Apart from one manipulation of parasitoids [93], experiments involving parasites and disease were conspicuously absent. The effect on animals of directly manipulating resources appears never to have been investigated.

Only ten studies (all on plants) of the 41, manipulated more than one environmental variable in the same experiment (e.g. [92,94]). I could find only two studies on animals (neither cites [17]) that have manipulated two (or more) selective agents simultaneously [7,8]. These enable investigation of the effect of interactions among agents [8], which can be unexpected [95], and also the comparison of the importance of different selective agents [7], but this should be treated with caution. Ideally, manipulations of putative agents should be standardised, either by reflecting the variation in agents that occurs in

the wild, or keeping constant the variance in relative fitness that they create (e.g. if fitness is measured as survival, by ending experiments when mortality reaches 50%); otherwise incorrect conclusions might be reached.

For plants, the growing tradition of investigating selective agents for their own sake means that studies citing [17] are a good representation of all experimental studies (MacColl, unpublished data). For animals, this is less true. A significant literature that does not cite [17] reports experiments on selective agents that have been conducted to examine the causes of divergent selection. In this tradition, manipulations of the level of competition and, latterly, predation have been popular [96–98].

Another literature has examined how evolution in bacterial microcosms is affected by different experimental conditions. Although this approach measures the response to selection as the outcome, rather than selection itself, it identifies the relative importance of different selective agents in driving the evolution of particular phenotypes (e.g. [99,100]).

Most manipulations involve only two levels of a putative agent, often in the form of an all-or-nothing comparison (i.e. plus and minus some ecological factor). This is a simple starting point, but it runs the risk of overlooking subtleties in the eco-evolutionary landscape, and can make the comparison of the relative importance of selective agents difficult.

There is currently a resurgence of interest in natural selection, and how its strength varies both spatially and temporally [3,5,14]. Linking this directly to variation in selective agents would result in a more mechanistic understanding of selection. With an accompanying expectation of h^2 or G [37], this would also enable the prediction of evolutionary change in phenotypes in different ecological scenarios (e.g. high or low density, presence or absence of disease). A full understanding of many evolutionary phenomena is also contingent on understanding process as well as outcome. For example, testing different models of speciation requires distinction of separate types (natural vs sexual, divergent vs uniform) and causes of selection [21].

The ecology of adaptive radiation

Despite widespread recognition of the importance of ecology in driving divergence and speciation, little is known about which aspects of ecology are most important [21]. Understanding the selective agents affecting key traits would clarify this, but it is probably not enough only to know which agents cause divergent selection. McPeck [38] pointed out that ‘when more than one selective agent acts on the phenotype, the shape of the overall fitness surface depends critically on the relative strengths of the various selective agents’. Agents that vary between populations will only drive trait divergence if they cause selection of a similar magnitude to, or greater than the selection caused by agents that do not vary geographically. Given this difficulty, the eco-evolutionary landscape should be a useful tool when trying to identify the ecological cause of divergence.

Lack of diversity in the evolutionary niche space (e.g. insufficient variation in selective agents within a species range) might explain why divergence between populations does not always progress to speciation (Box 3, [9,39]). This is akin to the idea that insufficient dimensions in trait space might hinder divergence [9,40], but refocuses the argument on the structure of the environment, rather than

of the phenotype, as the underlying determinant of the potential for diversification. For example, lacustrine fishes of many taxa diversify along a benthic–limnetic axis [41], suggesting that the cause should be sought in shared environmental features. The strong collinearity of selective agents across habitats in such lakes (i.e. resources, predators or parasites; e.g. [42–44]) might explain the limited diversity of species that have arisen, in contrast to, say, the startling morphological diversity of African cichlids. Repeated evolution along the benthic–limnetic axis within species has been attributed to evolution along genetic lines of least resistance in the G matrix [21], but this cannot explain convergent evolution across species, unless common environments shape the G matrix [45]. The O matrix might therefore be ultimately responsible for constraints in the direction of evolution (Box 3).

Adaptive radiation has been linked to ecological opportunity since the modern synthesis [11,20,21]. Ecological opportunity really arises from a change in selective agents (or from encountering conditions outside the existing O matrix), and thinking about it in this way might provide a mechanistic perspective that is useful in some circumstances. Key innovations were an important component of Simpson’s ideas [20] about ecological opportunity, to which he attributed a causal role in adaptive radiation. However, phenotypes must also be shaped by selection, which implies that, initially, key innovations might be key responses to a change in selective regimes. To attribute a causal role in adaptive radiations to key innovations requires that the adaptive radiation was not itself the result of a change in a key selective agent.

The adaptive landscape

The (phenotypic) adaptive landscape is central to understanding of the connection between micro- and macroevolution [20,21], but its depiction of fitness as arising from the phenotype is misleading. A common question concerns how speciation can lead to populations occupying different

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fitness peaks, because this appears to involve crossing parts of trait space with low fitness. A simple answer is that the landscape varies with environment, such that separate peaks in one physical (or temporal) location are linked by ridges of high fitness in other locations with different environments [46]. The relationship between the adaptive landscape and the selective agents that shape it can be envisioned by considering how the relationship between fitness and a trait varies with environment. The result is a half-way house between the adaptive and eco-evolutionary landscapes. Figure 2 shows what this surface might look like for the bills of Galapagos finches (*Geospiza* spp.). When conditions are dry, selection favours large bills; when they are wet, small bills are favoured. In between, selection is relaxed, enabling populations to move between peaks, especially if assisted by phenotypic plasticity [14].

The geographic mosaic of coevolution

Some of the ideas discussed here have a close affinity with the geographic mosaic theory of coevolution [47]. The strength of selection will often vary in a geographic mosaic, because underlying variation in selective agents might lead to hotspots of coevolution where interacting species cause reciprocal selection. The perspective introduced here differs from that of the geographic mosaic theory in explicitly seeking to understand the causes of the variation in the form and strength of selection (cf. [48]).

Linking population biology and evolutionary ecology

Identification of the demographic events that determine changes in population size, using techniques such as ‘key factor’ analysis (e.g. [49]), should be informative about the ‘checks’ on populations that Darwin discussed [1]. There is no necessary link between key factors (*sensu lato*) and the

strength of natural selection, because the former concerns the variation in population growth rates over time, and the latter their variation among individuals (genotypes). However, it seems probable that key factors should help to identify life-history events where the variance in fitness (‘opportunity for selection’ [50]) is greatest.

Some demographic studies have examined correlations between key factors and environmental variables (e.g. [51]), which make good candidates for selective agents. It would be interesting to know more about the relationships between demographic rate variance, variation in environmental factors and the actual strength of selection on phenotypic traits (see [52]). Theory suggests that selection should be strongest when population growth rates are low [53], which is likely to be when ecological conditions are poor. Empirical studies tend to support this [18,19], but the topic has attracted little explicit interest, in comparison to how heritability changes [37]. A knowledge of both is important to predict responses to selection in novel ecological circumstances.

The eco-evolutionary landscape and the niche

The eco-evolutionary landscape has an intuitive relationship with the niche, as a description of the ecological parameter space within which an organism exists. They differ because, the response variable for the niche is the population growth rate [54], whereas for the eco-evolutionary landscape it is some measure of natural selection for a trait. The eco-evolutionary landscape for key ecological traits can provide a way to think about the evolutionary niche: regions of the space with zero average directional selection over long time periods will be evolutionarily stable. Elsewhere, selection will favour change in the phenotype of the population so that (genetic constraints willing) the organism becomes a better ‘fit’ to its niche. Note that this perspective shifts the emphasis from the Hutchinsonian interpretation of the niche as a property of the organism, back to a Grinnellian interpretation of it being a property of the environment [13,55], or at least a property of an organism by environment interaction. This has implications for niche conservatism [10], because it requires researchers to think more about why the environment, rather than the organism, does not change, in those cases where lineages show evolutionary stasis. The opposite of niche conservatism, diversification, should occur where environmental change moves an organism outside its evolutionary niche, but allows population growth rate to remain positive.

The macroecology of species distributions

Little is known about the role that variation in the strength of selection plays in a failure of adaptation at species’ range margins ([12], but see [26]). The perspective presented here might inform macroecology by encouraging explicit investigation of: (i) the range of environmental factors (selective agents) that are associated with range margins, and how they are correlated with each other; and (ii) variation in the strength of selection on key traits throughout the range of a species.

Evolutionary responses to environmental change

Predicting such responses will be difficult if the strength of selection is not a simple monotonic function of variation

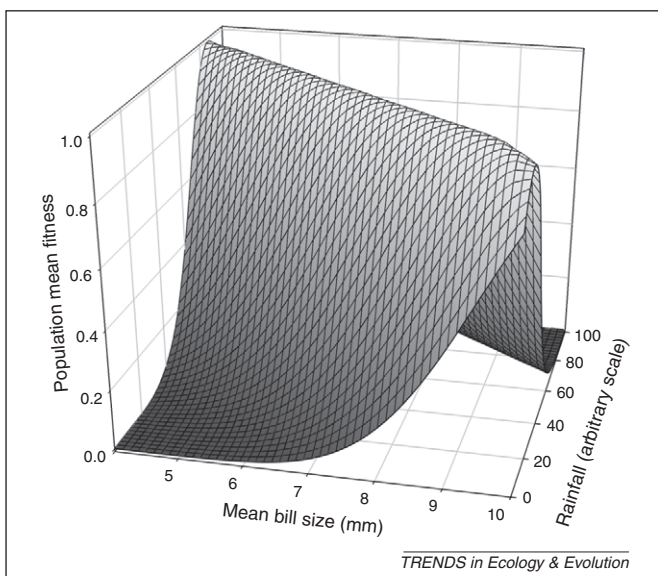


Figure 2. Hypothetical depiction of the relationship between population mean fitness, population average bill length and rainfall for the medium ground finch (*Geospiza fortis*). Selection favours large-billed birds following drought years, because available seeds are large and hard, but favours small-billed birds following wet years, when seeds are small. This kind of surface is a half-way house between the eco-evolutionary landscape and the adaptive landscape (*sensu* Simpson [20]), which makes explicit the fact that the shape of the adaptive landscape varies with ecological circumstances.

in environmental factors. The examples used here suggest that different environmental factors interact to determine the strength of selection and, hence, that evolutionary response in future environments are different from those in current environments. More explicit consideration of variation in the strength of selection and of the eco-evolutionary landscape could help to predict the evolutionary response of species to environmental change [14].

Concluding remarks

Current understanding of the causes of natural selection and, therefore, of evolution, is poor but could easily be improved by the appropriate analysis of existing data, and new experimental studies that explicitly measure the impact of environmental manipulations on the strength of selection. In particular, there is much to be learned from: (i) exploration of eco-evolutionary landscapes, especially using existing data from long-term evolutionary studies; (ii) meta-analysis of existing experimental and observational studies of natural selection where selective agents are known or can be inferred; and (iii) experiments that manipulate putative selective agents and measure the corresponding change in the strength of selection on adaptive traits. Such experiments would be especially useful if they simultaneously manipulated more than one selective agent, while controlling for variation in the opportunity for selection.

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