Opinion

Assessing rapid evolution in a changing environment

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Climate change poses a serious threat to species persistence. Effective modelling of evolutionary responses to rapid climate change is therefore essential. In this review we examine recent advances in phylogenetic comparative methods, techniques normally used to study adaptation over long periods, which allow them to be applied to the study of adaptation over shorter time scales. This increased applicability is largely due to the emergence of more flexible models of character evolution and the parallel development of molecular technologies that can be used to assess adaptive variation at loci scattered across the genome. The merging of phylogenetic and population genetic approaches to the study of adaptation has significant potential to advance our understanding of rapid responses to environmental change.

Evolutionary response to climate change

The speed and scope of ongoing anthropogenic climate change are potentially unmatched in Earth's history [1] and present biodiversity in general, and single species in particular, are likely to be faced with extraordinary circumstances [2]. The resulting ecological disruption and modification will likely be irreversible, with the most dramatic consequence being the extinction of species [3,4]. It is therefore essential to assess potential species responses. These responses can extend from range-limit alterations, which allow tracking of suitable habitat and thereby the promotion of species persistence at a global scale, to tolerance towards new conditions through either phenotypic plasticity or adaptation, which help species avoid local extinction. There is increasing evidence of species declining in abundance [3,5], which potentially underscores the constrained dispersal abilities of many organisms threatened by changing climate, altered land use and increasing anthropogenic habitat fragmentation [6]. These patterns highlight the importance of understanding the potential for species to adapt to climate change *in situ*.

Species characteristics, such as life history traits, as well as the magnitude and degree of exposure to environmental change will affect the relative importance of dispersal and adaptive mechanisms in species reaction to climate change [7–9]. Adaptation to rapidly changing environment has attracted considerable attention from, amongst others, those studying quantitative genetics [10], microevolutionary processes acting on phenology [11,12], and candidate loci that may confer adaptation [13]. These and other studies [14,15] make use of experimental approaches that determine the mechanisms of adaptation and the loci involved. This combined effort has led to some understanding of the limitations on adaptive response to climate change.

Identifying the capabilities of species for adaptation also has wider applications across ecological research and conservation, for example by changing how ecological niche models are built. In particular, species lacking the potential for rapid adaptation will require newly developed hybrid models that combine phenomenological and process-driven

Glossary

Adaptive landscape: a hypothetical response surface that expresses the relative fitness of individuals or populations as a non-linear function of genotype or genotype frequencies, respectively.
Brownian motion process: a random progression of character traits in which the character value for each species changes randomly in direction and magnitude in a temporally uncorrelated fashion.
Epistatic effects: these occur when the effect on phenotype by an allele at a locus is contingent upon the alleles present at a second locus.
Population genomics: the study of the genomes (in whole or part) of organisms from several populations within a single species that is becoming feasible due to new high-throughput sequencing techniques.
Mode of selection: this is characterised by the effect of selection in relation to the distribution of phenotypes that exists before selection occurs. Selection is directional when values on one side of the mean exceed, on average, values on the opposing side.
Ornstein–Uhlenbeck process: a stochastic evolutionary process that generalises Brownian motion by introducing an optimum value for the trait under consideration. Depending on selection strength, the trait is held near the optimum value such that the pull toward the optimum value is stronger as the trait drifts away.
Phenotypic plasticity: variation in a value of an observable character that occurs as an effect of environment and may or may not confer adaptation.
Phenotypic space: multivariate space of sufficient dimensions to accommodate the values of multiple traits measured on multiple individuals.
Phylogenetic constraint: the propensity of particular lineages to resist adaptation to a specific optimum.
Phylogenetic signal: the positive correlation between the degree of genetic relatedness of species and their phenotypic similarity.
Pleiotropy: the positive or negative correlation between two aspects of an individual's phenotype that results from the aspects both being influenced by one or more genes.
Tempo of evolution: the acceleration and deceleration of evolutionary rates and the description of the conditions for rates to be rapid or slow.

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elements that allow for both demographic and migratory responses [16]. Species that have the potential for rapid adaptation will also require a new generation of models. These will need to capture adaptive responses of populations that were in a suitable habitat before the environmental change and so are responding to a shift in favourable conditions as well as those populations which were originally in or have recently migrated to previously unsuitable sites [17]. Until now, theory was not sufficiently advanced to allow the combination of ecological niche concepts and ideas of species evolution into a unified approach to the study of adaptation in large number of species at once. Here, we address emerging attempts to combine phylogenetic and population genetic approaches to the study of evolutionary patterns and rates of adaptation to rapid environmental changes, emphasising the increasing flexibility of the phylogenetic framework.

Adaptive response: Scaling up from one species to many

The merging of population genetics theory with phylogenetics to study evolving ecological patterns could introduce an exciting new scientific approach for investigating how evolution shapes biodiversity. However, this can only be achieved by examining comprehensively large numbers of species at once. Rapid adaptation over a few generations is probably common in a wide range of taxa [11,14,15,18,19], and the phenomenon has been extensively studied using population genetics approaches. In particular, populations at range margins have been a productive research focus [20] because marginal populations are likely to be disproportionately more exposed to ongoing global changes compared to populations from areas central to a species' range [21]. In general, adaptation is a common and widespread microevolutionary phenomenon that is essential in the long term as a response to environmental change [22]. The current challenge is to understand how the potential for these responses is distributed among populations and, ultimately, among species.

One approach to scaling up the study of adaptive responses from specific populations to a whole set of species is based on the variation in rates and tempo of phenotypic evolution between species or clades. Evolutionary rates tend to vary with the strength and mode of selection and the capacity for adaptive divergence of populations due to their intrinsic demographic and genetic characteristics [23]. Under rapid change of the environment away from optimal fitness values of individuals, as expected under future climatic scenarios, a population will rapidly decline in size as maladaptive alleles are removed by selection [20]. This decline in population size is dependent on the amount of genetic variation available in populations [24] and the demographic process must support the spread and increased frequency of adaptive alleles for the population not to go extinct [25,26]. Following this rapid initial response to selection and accompanying population decline, the rate of adaptation slows as average fitness within the population approaches its maximum value and/or additive genetic variance is exhausted. Further, theoretical models predict that conditions that (i) flattened selective gradients, (ii) reduced gene flow towards local populations (that is, isolate populations from maladaptive alleles) and (iii) increased population size or growth, all enhance potential rates of adaptation [20,26]. These conditions are likely to vary between species and analysis of phenotypic evolution within populations of a broad range of species suggests that these predictions hold across divergent time scales and phylogenetic relationships [27].

However, genetic mechanisms that act to promote trait evolution and adaptation over long evolutionary times are probably different from those generating genetic variation and adaptation to changing environment at the intraspecific level. In particular, epistasis and negative pleiotropic effects reduce the probability that mutations become established in sequences coding for proteins [28]. In particular, a relatively small number of genes or even regions of genes accumulate mutations more easily than the average coding site. This can create phenotypic variation and allow rapid divergence of ecologically-significant traits that favour species divergence and radiation [29–31]. It is very probable that particular lineages have relatively higher capacity to harbour consequent adaptive changes and can therefore

Box 1. Evolution of C_4 photosynthesis

An example of the effect of global climatic changes on adaptation can be found in the grass family (Poaceae). This plant group, known for its economic and ecological importance, is host to one of the most striking examples of convergent genotypic evolution [62], which was triggered by an adaptive response to decreasing atmospheric CO_2 concentration [32]. The C_4 photosynthetic pathway is a suite of biochemical and anatomical adaptations that enhances photosynthetic performance in plants under high-temperature and low-CO_2 environments when compared to the standard C_3 pathway [63]. This suite of adaptations has appeared independently over 18 times in the diversification of the grass family [62,64]. Analyses of several genes that are responsible for key elements in the pathway [62,65,66] show that recurrent episodes of adaptive evolution at the genetic level occurred during each independent origin of the pathway. This evolutionary independence stands in contrast to the observed phenotypic convergence found in all C_4 plants [63].

The evolution of the C_4 pathway in grass lineages occurred at different times, with the first appearance approximately 30 My ago. The appearance of the C_4 pathway in multiple clades within the grass family provides an opportunity for a statistical application of comparative methods. Christin *et al.* [32] incorporated the change in CO_2 concentration through time into a Markov model of character evolution. Rates of transition between C_3 and C_4 states, estimated by maximum likelihood, were allowed to be different before and after a time threshold defined as the CO_2 concentration that physiologically advantages C_4 plants. The impact of this climatic change on the rate of appearance of the C_4 character was then tested by comparing, using a likelihood ratio test, a null model forcing the rates to be identical before and after the threshold with the alternative model that did not restrict the rates. This study showed that the appearance of the C_4 pathway in grasses is associated with an abrupt decrease in atmospheric CO_2 levels in the Oligocene [32]. The accumulation of numerous biochemical and morphological modifications required for a functioning C_4 metabolism suggests that some lineages are predisposed to acquire these changes [67] in response to changing environmental conditions. This raises the question of whether such biochemical flexibility is generally associated with the potential for plants to adapt to changing environments. Other characteristics or traits may be regularly associated with adaptive potential (Box 2).

leave a trace of ‘residual evolvability’ in their descendant species (Box 1).

These arguments suggest that lineage specific characteristics must be considered if we want to jointly assess the potential for adaption over a broad set of species. The advantage of such an approach is the gain in statistical power achieved by analysing several independent events of adaptation at once (e.g. [32]). The approach we advocate here consists of studying historical and potential evolutionary rates in substantial numbers of species simultaneously and is embodied in a new phylogenetic approach to discover rapid evolution. Recent research demonstrates the utility of comparative methods for studying rates of trait evolution, for example during adaptive radiations and other diversifications [33–36]. These efforts are supported by an ever-widening taxonomic breadth, and rapidly expanding technology for high-throughput DNA sequencing, which will soon allow the routine reconstruction of highly resolved phylogenies of several hundreds of species. Large numbers of sequences from multiple populations and species suggests the feasibility of a better and deeper integration of population processes into phylogenetic comparative methods. Such a combined comparative approach might thus serve as a framework to bridge intra- and interspecific levels, which we see as an essential endeavour if we are to better understand the adaptive potential of species.

Evolutionary models in comparative analysis

With most comparative methods it is not possible to model the effect of directional or stabilising selection toward an optimal (adaptive) character state (Figure 1a) because these methods are based on the underlying assumption that Brownian Motion (BM) processes closely approximate character evolution [37]. The BM process is akin to genetic drift and can be used as a good null model, but is not an effective model for the processes of adaptive evolution. Furthermore, many current comparative studies compound this problem by only testing for presence or absence of a phylogenetic signal, without properly testing any suitable evolutionary model (whether adaptive or not). This is probably due to a common misconception that phylogenetic signal and evolutionary rate are necessarily related. Traits that confer adaptation can vary greatly in the levels of phylogenetic signal they display and, presumably, in their levels of resistance to further adaptation [38,39]. Simulations have shown that measures of phylogenetic signal cannot be used to distinguish different evolutionary processes because many evolutionary scenarios can generate similar levels of phylogenetic signal [40]. Measures of phylogenetic signal are thus not suited to test adaptive response between species [31].

To account for adaptation, modifications of the assumption of BM in comparative methods have centred on either weakening the strength of BM to the point that the analysis becomes non-phylogenetic [41] or transforming the branch lengths of a phylogenetic tree in an attempt to match the assumptions of the BM model [42]. The difficulty in the first approach is that BM is a pure drift process, and one does not obtain a model of selection from a random BM process by merely weakening it. Although the second approach of transforming phylogenetic trees results in statistically valid analyses, distortion of the phylogeny confuses interpretation and makes it difficult to infer the validity of the hypothesised evolutionary process and to estimate the rate and tempo of trait evolution. The listed limitations inherent in many current implementations of comparative methods suggest that other, more flexible approaches are required to identify and compare the adaptive potential of species (Box 2).

In response to the fundamental limitation of BM-based methods, tools have been proposed that model selection directly. Following the suggestion of Felsenstein [43], Hansen [44] proposed to model adaptive evolution by means of the Ornstein–Uhlenbeck (OU) process. The model [45] was initially developed to assess how far a population mean phenotype could deviate from a selective optimum, given the strength of selection and the size of the population, but extension of this method has allowed the modelling of adaptation to be extended over larger evolutionary time scales [43,44,46,47]. While this extension renders the model incompatible with the presence of phylogenetic constraint for the trait under consideration [44], the development of

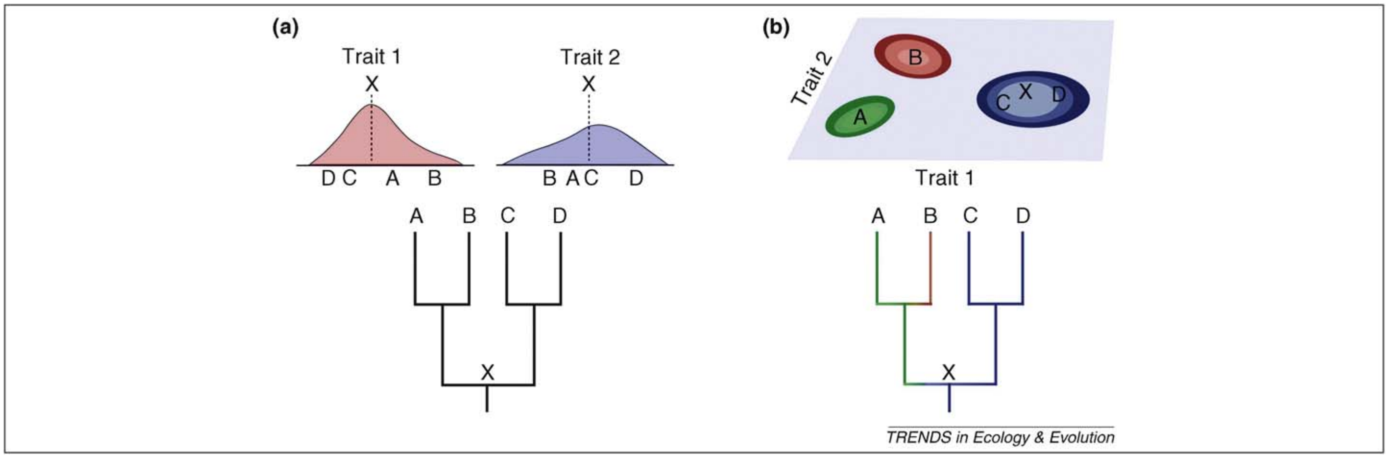

Figure 1. Shift in the study of trait evolution, here for two ecological traits and four species, A–D. The current approach to studying trait evolution **(a)** uses a single trait value per species and each trait is considered independently. A Brownian null model describes trait evolution from the most common ancestor (X), with the mean trait value of each species being the same as that of X. An alternate approach **(b)** is to model ecological traits as multivariate distributions in order to incorporate population-based measures of trait values (i.e. polymorphism within species), covariation (non-independence) between traits, and allow for different evolutionarily optimal trait values among lineages (e.g. for A and B).

Box 2. Comparative methods and niche evolution in a plant and a lizard

The factors influencing rates and distribution of phenotypic evolution have been a longstanding question. A recent study by Smith and Beaulieu [68] investigated how growth form and climate tolerance correlate in five angiosperm groups. The climate tolerances of species were estimated from data on species distributions. The mean values for 19 WorldClim [69] variables served as proxy tolerance estimates for each species. This approach assumed an adaptive component to among-species differences in these values. Phylogenetic multivariate analysis of variance assessed how among-species differences varied between species that were grouped by growth form (woody or herbaceous). The observed differences were compared to those expected based on a Brownian model of evolution.

In particular, Smith and Beaulieu presented a flexible model that allowed rates of accumulation of evolutionary changes in climate tolerance to differ between woody and herbaceous species. The authors compared evolution of climate tolerance in this model to evolution in an alternative null model that forced an identical rate of adaptation in both growth forms. The accumulation of difference in climate tolerance depended on plant growth form. Woody lineages exhibited slower phenotypic and molecular evolution, which could constrain how woody species respond when faced with environmental changes. The result suggests that adaptation to future climate change will depend on the life-history characteristics of species. The implication is that other variability in life history may also be associated with the rate of adaptation to climate change.

In a comparable example, the effect of life-history on adaptation to the temperature variability among habitats was investigated by Labra *et al.* recently in *Liolaemus* lizards of South America [70]. These authors modified the approach of Hansen *et al.* [47] so that trait optima followed changes in habitat temperature. Labra *et al.* then tested whether physiological performances were similar between habitats. The results indicated that adaptation to thermal conditions evolved rapidly with little phylogenetic constraint, potentially indicating rapid adaptive shifts as lineages became specialised for specific habitats. In contrast, other characteristics, such as body size and critical thermal minimum did not indicate adaptation to thermal environment. However, permissible body temperature could also be constrained, resulting in congeneric species having similar habitat preferences. This points to the problem of interpreting trait variation that is strongly structured among lineages and the degree that this structure represents constraints on evolution. In summary, traits such as habitat preference, growth form and others can be evaluated across related clades to determine the association of particular character values with the extent of adaptation to both spatial and temporal environmental trends.

OU process models is a key step linking microevolutionary processes to macroevolutionary patterns though the incorporation of parameters that describe an adaptive landscape [48]. Indeed, this model has also been used to study trait evolution on population level phylogenies [49].

Further extensions of the OU process have allowed the optimum value of a phenotype to change through time using a BM model [47]. Maximum likelihood approaches have been developed to estimate evolutionary optima in different lineages [46] and to allow the optimum itself to change through time [47]. This reconciles tests of adaptive evolution that combine optimal trait values with phylogenetic constraint. If not considered, such constraints could lead to rejection of the hypothesis of adaptation simply because of spurious phylogenetic effects [31].

The actual BM and OU processes used in these studies constrain the rate of character evolution to be constant through time along the studied lineages (although in some formulations, OU models can lead to observed exponential divergence between lineages). The stochastic processes expressed in these models are, therefore, inadequate for modelling lineages which change between periods of stasis or rapid change in character values during lineage evolution [27]. This limitation will introduce biases that could, because of unmet model assumptions, result in a wrong rejection of the null hypothesis of neutral (i.e. BM) character evolution. There is ample room for more complex models of phenotypic character evolution and the time is ripe for these further developments. Changes in rates of evolution along a lineage have already been used in phylogenetics [32,50], and the development of Markov chain Monte Carlo techniques should lead to a refinement of available evolutionary models. Other types of stochastic processes, for example those based on compound stochastic processes or heterogeneous Markov chains, could permit the movement of trait values between adaptive optima that are scattered in phenotypic space [43]. Because they allow for rate changes through time and differences between lineages, the more rugged evolutionary courses of character values modelled by these stochastic processes could be more appropriate for modelling adaptive response to environmental changes.

Population level comparative methods

Scaling up from one species to many in studies of adaptive potential is important and the new evolutionary models that are emerging will play a key role. However, the information available in population level data, represented by polymorphism in the trait values measured, should not be excluded from such analyses. On the contrary, population-level data will provide additional information needed to assess the importance of the characteristics affecting species specific rates of adaptation. However, current implementations of comparative methods assume that traits means are measured without error for each species. In practice, the mean phenotype is usually estimated from small samples, with the assumption that intraspecific variation is negligible [44]. This assumption can lead to small sample artifacts and inflation of type I error rates [51,52]. These effects are especially important when comparing closely related species for which the amount of interspecific variance is small compared to intraspecific variation, and between there is a good deal of shared evolutionary history [53]. Accounting for intraspecific variation in comparative methods remains a significant challenge. However, meeting this challenge is essential for the future development of comparative methods. These developments are sure to be enhanced by next generation sequencing technologies as these will bring the necessary population genomic data necessary to use the developments foreseen.

There have been a number of attempts to use population-level data within comparative methods. The first involves partitioning the variance of character evolution into phylogenetic (i.e. interspecific) and error components [54]. The trait distribution within species can then be modelled by adding nonphylogenetic variation around the species means, assuming a nonphylogenetic burst of adaptation [55]. This burst can represent adaptive differences among populations, such as local adaptation due to climate variability and introduces an additional form of evolution independent of certain phylogenetic constraints. The effects of intraspecific variation can be modelled, following the work of Lynch [56], by allowing each character to have variation within species and for the measurements of different characters within species to be correlated (Figure 1b) [52]. These developments focus mainly on continuous characters, which is an appropriate approach for describing the climate tolerances of species or populations, but polymorphism in discrete traits at the species level can also be incorporated using Wright's [57] threshold model [58]. An appealing property of this model is that it allows for covariation among multiple characters (Figure 1b), which is difficult to accomplish with other types of models for discrete characters. Recent developments also suggest most comparative methods could benefit from research equating phylogenetic relationships with inbreeding coefficients between species [59]. Although interesting, it is not yet clear if this new approach will be useful for modelling rapid adaptation of natural populations to climate change.

Finally, accounting for within-species phenotypic variation within phylogenetic comparative analysis of evolutionary rates can be achieved by allowing multiple character values per species (Figure 1b). A straightforward strategy is to simply gather the population-level values into an empirical distribution for each species for the trait of interest. The comparative analysis is then repeated, using Monte Carlo techniques, by sampling from this empirical distribution [35,60]. This results in confidence intervals estimates for the parameter of interest, for example the rate of adaptation between species or the force of selection in a OU process, but does not explicitly account for intraspecific variation. A statistically more complex, but biologically more appropriate way, to account for within-species variation is to explicitly represent multiple populations per species and calculate both within- and between-species contrasts [53]. With this approach, intraspecific variation is first estimated for each species independently, assuming that individuals share all their evolutionary history. The contrasts between individuals within a species and between species are independent, because they are weighted differences in trait values. The novel and interesting aspect is that the contrasts between different traits have a covariance, which represents the phenotypic covariance of the original traits. The estimated trait covariation can, alongside genetic experiments, give an estimation of the selective covariances of traits [61]. Although this estimation is difficult [53], it is made possible by the use of Markov chain Monte Carlo techniques, whether in a full maximum likelihood setting using importance sampling or in a Bayesian framework. The general and widespread use of these approaches open a new avenue for bringing comparative methods into the era of population genomics. The additional information coming from population-level data will be very useful to model the tempo of adaptive rates within each species, which in turn could prove useful to examine differences in rates of adaptation between species more accurately.

Future directions and conclusions

Overall, the theoretical and statistical developments we have presented in this paper have the potential to move studies that use comparative methods into a new direction, by providing models that fit real biological data better than previous models. This is being accomplished by incorporating multiple correlated traits and intraspecific variability into comparative methods (Figure 1) and will take advantage of recent statistical and computational advances to estimate adaptive trait optima and phenotypic covariance [53]. This is particularly significant for studies of the evolving environmental niche, which is in essence a multidimensional construct with several correlated parameters (e.g. tolerance ranges of potential evapotranspiration and temperature). The recent developments of comparative methods open the possibility for a new set of approaches that will result from the fusion of phylogenetics and population genetics. This will allow biologists to test hypotheses about rates of adaptation by integrating data on ecological conditions, individual phenotypes and genotypes, and their frequencies in populations. This challenging endeavour is essential for a better understanding of the evolution of genes, phenotypes, populations and communities under rapidly changing environmental conditions. New approaches that combine population-based information with phylogenetic comparative methods could improve our understanding of the potential for rapid evolution and should help to identify lineages that are 'frozen' evolutionarily and which could be important foci for conservation efforts.

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