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Perspective

Variable success in linking micro- and macroevolution

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ABSTRACT

Attempts to predict macroevolution from microevolution, and microevolution from macroevolution, when natural selection is the main cause have met with varying success. Explanations for failure are numerous, but the reasons are uncertain even when a link is found. Here, I discuss possible explanations for outcomes of three efforts and ways to test them. First, quantitative genetic variation within populations often predicts directions of species divergence with surprising accuracy. Natural selection probably contributes to this pattern, but the evidence suggests that even long-term phenotypic evolution is influenced by enduring genetic biases. Second, the rate of evolution of reproductive isolation repeatedly fails to predict species diversification rates for unknown reasons. Suspicion falls on the influence of ecological and population demographic processes that might play a dominant role in the net rate of accumulation of species, an idea as yet little tested. Third, macroevolutionary patterns in the distribution of phenotypes of species in clades can in principle predict selection coefficients in diverging populations. I use the concept of adaptive landscape to suggest why the macroevolutionary signal of divergent selection is strongest at the time of splitting and why little information about selection coefficients from phylogenetic methods remains in the long run. Estimating adaptive landscapes from first principles would facilitate further efforts to link microevolution and macroevolution.

Keywords: microevolution; macroevolution; natural selection; genetic constraints; diversification; adaptive landscape; correlated evolution; phylogeny; Ornstein–Uhlenbeck process

INTRODUCTION

The long-standing question of whether macroevolution can be explained by microevolution (Futuyma 2015) has given way to a more quantitative quest, namely to predict features of macroevolution from microevolutionary (population-level) processes and vice versa. Microevolution refers to the genetic and phenotypic changes that occur within and between populations by mutation, selection, migration, and drift. For simplicity, I include the demographic and ecological processes that affect population size, persistence, and evolution under the same term. By selection I mean the differential survival and reproductive success of individuals in populations. Macroevolution is the rise and fall of lineages of species (rates of species origination, species extinction, and diversification—the difference between speciation and extinction) and patterns of phenotypic divergence between populations and species (Mayr 1982). The modern effort to link microevolution and macroevolution focuses mainly on patterns and processes just above and below the species level, regarded as the boundary between scales of evolution (Rolland *et al.* 2023). Can what happens to lineages above the species level be predicted from events in populations beforehand, and can

population processes be predicted from macroevolutionary patterns?

Success in quantitatively predicting features of macroevolution from microevolution and the reverse has been variable so far. My first goal in this essay is to show that we lack an accepted explanation not only for failures, but even for successes. My second goal is to review and offer possible explanations and some ways to test them. I use selected examples rather than provide a comprehensive review. Much of my reasoning is based on the concept of the phenotypic adaptive landscape (Simpson 1953, Lande 1979, Schluter 2000), a key conceptual bridge between microevolution and macroevolution (Arnold *et al.* 2001, Hansen 2012, Rolland *et al.* 2023). This surface is derived from the individual fitness function (e.g. Martin and Wainwright 2013, Stroud *et al.* 2023) and is key to predicting selection in populations and the distribution of population means of co-occurring species (Lande 1976, Schluter and Grant 1984, Arnold *et al.* 2001, Beausoleil *et al.* 2023). Whereas a given population experiences the fitness contours of only a local peak of the landscape, a lineage can explore and spread across more of the adaptive landscape as it radiates. Though simplistic, the concept

has demonstrated theoretical and practical utility (Svensson and Calsbeek 2012).

I discuss three efforts to bridge micro- and macroevolutionary scales. The first is the surprisingly successful prediction of directions of phenotypic divergence between populations and species from measures of quantitative genetic variation within populations. However, the true explanation—whether caused by genetic constraints or by the shape of the adaptive landscape—still eludes us. The second example is the low success rate in predicting clade diversification rates (speciation and extinction) from measurements of population-level processes such as the rate of evolution of reproductive isolation. The third example is the uncertain inference of natural selection coefficients in populations from macroevolutionary random walk models fitted to species trait data and phylogenies. I investigate what predictions might and might not be possible and why.

WHY DOES GENETIC COVARIANCE PREDICT TRAIT DIVERGENCE?

A population under natural selection is not expected to evolve in the direction of greatest increase in mean fitness, but instead should follow a curved trajectory (Fig. 1). The reason is that quantitative traits covary genetically (Lande 1979), mainly because of pleiotropy. The simplest case is of a population evolving in the vicinity of a single adaptive peak (Fig. 1A). The direction of most rapid increase in fitness is straight toward the mean fitness peak, but the population instead evolves on a trajectory that is initially biased in the direction of maximum genetic variation, g_{max} (Schluter 1996). If genetic variation is present in all directions the bias will wane with time and a static adaptive peak will ultimately be climbed. If multiple peaks are present, however, then the bias might endure for longer if populations preferentially climb adaptive peaks in the direction of maximum genetic variation (Fig. 1B). A population tracking a fluctuating adaptive peak will yield a sequence of population means whose direction is also predicted by g_{max} (Holstad et al. 2024). For simplicity I assume that selection is frequency-independent, which although unlikely (e.g. frequency-dependent selection arising from species interactions is a major cause of adaptive peak shift) does not affect the points made herein.

This quantitative genetic theory leads to a genetic constraints or 'genetic lines of least resistance' hypothesis for the bias in directions of interspecific divergence under natural selection. If the location of adaptive peaks on the underlying mean fitness landscape is random with respect to genetic covariance, or the direction of fluctuating selection is random, then divergence of population means should be biased in the direction of g_{max}, at least for a time. In this case the major axis of phenotypic divergence among means of populations and species of a clade (d_{max}) is predicted to be more similar to g_{max} than expected by chance. With multiple traits, a lesser bias is also expected in the next most variable direction of genetic variance, and so on. Overall, the amount of evolution by natural selection observed in the principal directions (eigenvectors) of the within-population multivariate covariance matrix G should be overly similar to amounts of genetic variation in those principal directions. This prediction assumes that the principal directions of G remain roughly constant over the time frame investigated, and that
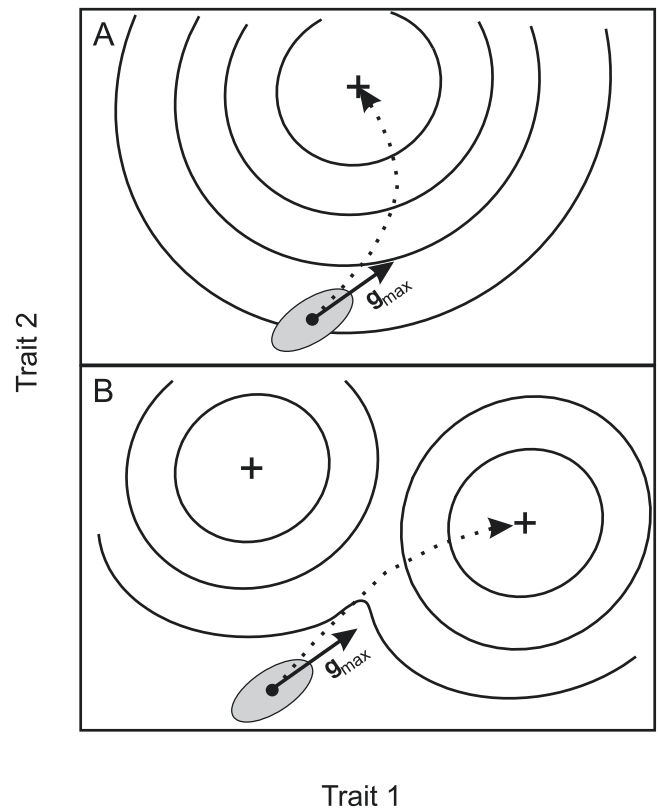

Figure 1. Trajectory of an evolving population on a static adaptive landscape. Contours represent population mean fitness, with peaks indicated by +. The shaded ellipse represents the population frequency distribution of additive genetic breeding values in two traits that covary genetically. With a single adaptive peak (A), the trajectory of the population mean is initially biased in the direction of maximal additive genetic variance (g_{max}) but the effect is temporary. With multiple peaks (B), the bias may endure for longer if peaks located in the direction of g_{max} are those most likely to be climbed.

genetic covariances measured today are similar to those at the time of divergence. Comparative studies suggest that although G evolves, its structure is relatively conserved over time (Houle et al. 2017, McGlothlin et al. 2022, Arnold 2023).

The genetic bias prediction has been verified numerous times, at least for morphological traits, in both recent and fossil lineages (Voje et al. 2023, Holstad et al. 2024). For example, phenotypic divergence among plant populations of the same species (Opedal et al. 2023) (Fig. 2), among vertebrate species separated by up to 4 Myr (Schluter 1996), among *Anolis* lizard species separated by up to 40 Myr (McGlothlin et al. 2018), and among Drosophilid fly species separated by up to 40 Myr (Houle et al. 2017) is greater in directions of highest genetic variation within populations than in directions having less intraspecific genetic variance. Also as expected if the bias is temporary, in one study the direction of divergence between species decayed to the random expectation after a few million years (Schluter 1996). This trend was also partly seen in pathway gene expression evolution in *Drosophila* (Innocenti and Chenoweth 2013) and in a large survey of morphological traits in contemporary and fossil lineages, where the pattern was weaker between species than among populations within species (Holstad et al. 2024).
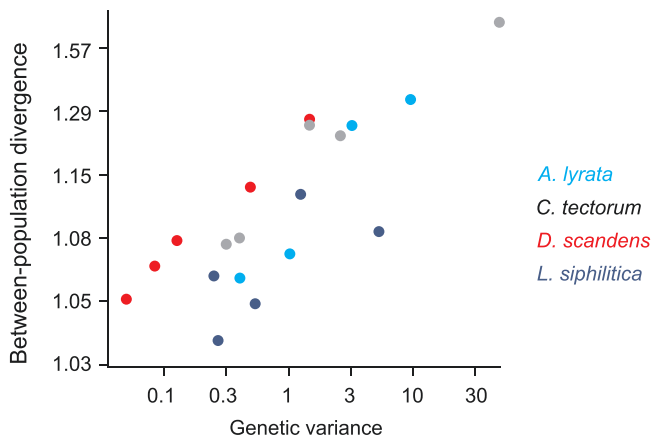
Figure 2. Positive association between the amount of additive genetic variance in the first four or five principal directions of the genetic covariance matrix **G** within populations and the magnitude of divergence between population means. The direction with the highest variance is g_{max}, which typically also shows the most divergence. Data are of leaf traits among 51 *Crepis tectorum* populations, floral traits among 16 populations of *Dalechampia scandens*, floral traits among 10 populations of *Lobelia siphilitica*, and floral and vegetative traits among four Scandinavian populations of *Arabidopsis lyrata*. Population divergence is measured as the proportional divergence of an average population from the grand mean. Modified from Opedal *et al.* (2023).

Nevertheless, the long spans of divergence time involved in some studies correlating interspecific phenotypic divergence with the amount of genetic variance in directions of **G** is surprising given the nontrivial amount of standing genetic variation present in populations in most directions. Because the individual variants that make up standing genetic variation at any point in time are ephemeral, conservation of **G** over long time spans must depend on conservation of mutational covariance—the amount of phenotypic variance and covariance created by mutation each generation—which is strongly correlated with **G** (Houle *et al.* 2017). Mutational covariance emerges from the rates and mechanisms by which new mutations impact development—the genotype–phenotype map (Hansen 2006). These mechanisms are themselves subject to natural selection but appear to evolve relatively slowly (McGlothlin *et al.* 2022).

Yet, is the genetic line of least resistance the correct explanation for the observed correlation between **G** and phenotypic macroevolution? An alternative hypothesis is that the distribution of adaptive optima is not random, but rather they lie in a corridor that roughly parallels g_{max} (Fig. 3A). Under this hypothesis, termed 'selective lines of least resistance' by Arnold (2023), and similar to the idea of 'selective correlation' by Stebbins (1950), g_{max} in populations successfully predicts the direction of divergence between species because both genetic covariances and species divergence of traits are moulded by similar natural selection pressures (Schluter 1996, Arnold 2023).

A corridor of adaptive optima is highly plausible for functionally coupled traits. As an example, wing area and body mass are correlated among bird species (Alerstam *et al.* 2007), a relationship surely driven by selection favouring efficient aerodynamics and lift over a broad size range of species sizes. The relationship is not absolute—wing area varies among species of a given body
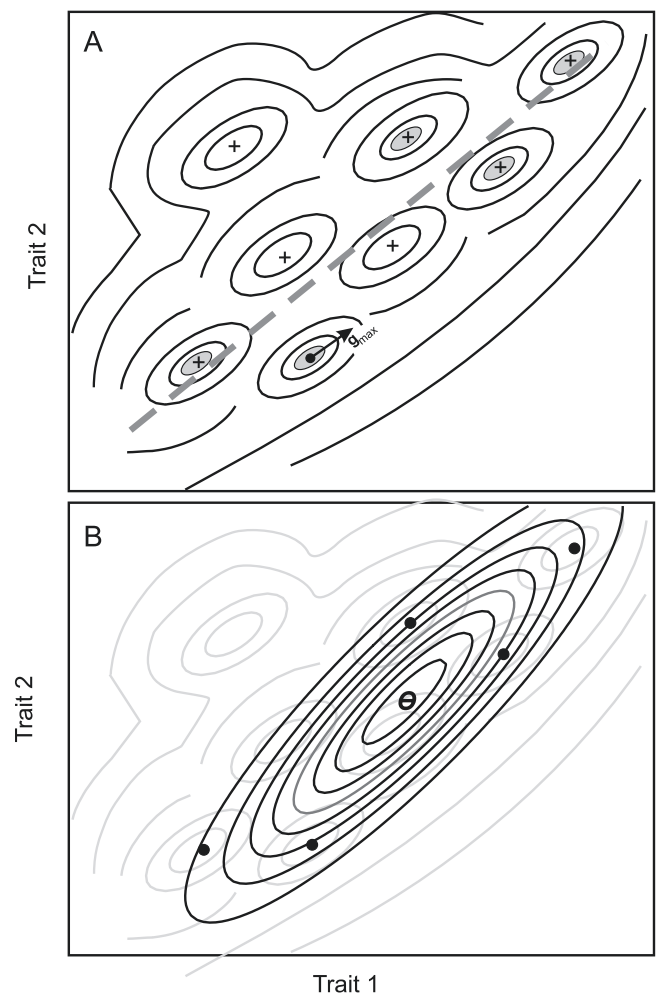

Figure 3. A, a hypothetical adaptive landscape with multiple adaptive peaks (+) oriented along a corridor, some of which are occupied by species (grey ellipses). Contours represent population mean fitness as a function of population mean in two traits. The direction of maximum genetic variation within species (g_{max}) is indicated by an arrow. The heavy dashed line indicates the major direction of the corridor of adaptive peaks. I assume the hypothetical species occupying the landscape are broadly sympatric (otherwise adaptive peaks from different regions would need to be superimposed somehow). B, the OU stationary distribution or 'surface' estimated from the means of the five species in A superimposed on the same adaptive landscape. Species means are indicated by filled circles. Contours indicate probability density of the fitted bivariate Gaussian OU distribution. The grand mean is indicated by θ. The stationary distribution was estimated using the mvMORPH package (Clavel *et al.* 2015) in R 4.3.2 assuming a random phylogeny for the five species.

size, according to feeding mode, air density, migration, sexual display, and other factors. Nevertheless, the two traits covary positively along the principal direction of interspecific variation. Viability selection against mismatched wing dimensions relative to body size in individuals within populations—correlational selection—has been demonstrated at least once (Schluter and Smith 1986), which could help to explain the maintenance of a positive genetic correlation between wing and body size traits (Boag 1983) over the long term. If so, then a correlation between the major axes of **G** and interspecies phenotypic evolution is

expected because both are shaped by similar selection pressures. Hybridization between phenotypically differentiated populations and closely related species might also contribute to similarity in the directions of $\mathbf{g}_{max}$ and $\mathbf{d}_{max}$ (Schluter 1996, Voje *et al.* 2023), but only in the case of populations and young species.

Testing whether adaptive peaks lie along a principal corridor of selection requires that the adaptive landscape be estimated from first principles using functional models of environment and estimates of trait performance and mean fitness, which has rarely been attempted even for single traits (Schluter and Grant 1984). The major axes of variation of the 'macroevolutionary adaptive landscape' might be used instead, calculated from models of phenotypic evolution fitted to species trait means and a phylogeny (typically the OU model, see below). However, such an estimate would be based on the observed joint frequency distribution of trait means rather than on independent information about the shape of the adaptive landscape, and so cannot detect the full distribution of adaptive peaks—for example those lying beyond. The same is true of adaptive landscapes estimated from field studies of selection (Beausoleil *et al.* 2023). Thus, such methods cannot distinguish between hypotheses to explain the observed correlation between **G** and the directions of phenotypic divergence.

A key prediction of the genetic bias hypothesis is that evolution in directions of low genetic variance (i.e. perpendicular to $\mathbf{g}_{max}$) should be slower than evolution in directions of high genetic variance (Schluter 1996). In other words, not only the amount of divergence but also its rate **R** should be related to the amount of genetic variance in the principal directions of **G**. The hypothesis of selective correlation makes no such prediction. For example, if a nonstandard wing to body mass ratio is favoured by selection in a unique environment, there is no reason to expect that its evolution should take more time than an equivalent amount of change in any other direction in the absence of genetic constraints. Existing evidence supports the rate prediction from the genetic bias hypothesis. Schluter (2000) found that evolution in vertebrate taxa was slower the more different was the direction of phenotypic evolution from the direction of maximal genetic variance. Houle *et al.* (2017) found that the multivariate rate of wing trait divergence between Drosophilid species in different directions, **R**, was correlated with **G** (see also Jiang and Zhang 2020). McGlothlin *et al.* (2018) found the same pattern for limb and other morphological traits in *Anolis* lizards. At higher macroevolutionary scales, evolution orthogonal to the major axis of phenotypic variation among species is generally associated with older taxa, implying slower rates (Guillerme *et al.* 2023). These findings suggest that genetic constraints, as summarized by **G**, play an enduring role in biasing directions of phenotypic divergence.

WHY DOES THE SPEED OF EVOLUTION NOT PREDICT DIVERSIFICATION RATE?

Macroevolutionary rates of diversification depend on the fates of ancestral populations (Mayr 1963, Allmon 1992, Schluter 1998, Price *et al.* 2014, Harvey *et al.* 2019). A burst of speciation should be preceded by a burst of populations forming, persisting, diverging genetically and phenotypically from one another, and evolving reproductive isolation. For these reasons we might

expect the rate of build-up of species diversity in a clade to be faster when the rates of any of these processes is increased. For example, the faster reproductive isolation evolves, the sooner populations are available again to speciate further. This is most likely to be true when sympatry is high, because rapid evolution of reproductive isolation will shorten the interval before spatially separated populations can come into secondary contact without merging. At this point the processes of new populations forming, diverging, and evolving reproductive isolation begins again (Price *et al.* 2014).

Yet, Rabosky and Matute (2013) found no correlation between estimated rate of clade diversification and the speed of evolution of pre- and postzygotic isolation in *Drosophila* or in the rate of evolution of postzygotic isolation in birds. Freeman *et al.* (2022a) obtained a similar result for the speed of evolution of song discrimination in New World passerine birds, a premating isolation metric. Populations in avian clades having high recent speciation (splitting) rates evolve song discrimination at a similar rate on average as populations in clades speciating at a slower rate. These results are unexpected because rapid evolution of reproductive isolation should shorten the waiting time to coexistence and thereby quicken the next round of new population establishment and divergence. The tests assume that the taxonomic species on which diversification rate estimates are based align with the biological species concept, based on reproductive isolation.

Several explanations are possible. One is that reproductive isolation evolves relatively quickly compared to the rate of establishment of sympatry, which then becomes the more rate-limiting step (Price *et al.* 2014). Another is that variation among lineages in the speed of evolution is low compared to the amount of variation in ecological factors that determine the number of populations, their rate of establishment, and the duration of their persistence. Tests of this 'persistence' hypothesis are hard to come by. Harvey *et al.* (2017) constructed a mitochondrial DNA (mtDNA) gene tree for multiple samples of each of 172 bird species and used it to identify 'population' splits nested within recognized biological species. Nodes at the population splits were identified as those demarcating a Yule branching process characteristic of species diversification (older than the node) from a coalescent branching process characteristic of within-species genetic diversity (younger than the node) (Pons *et al.* 2006). Such nodes were then used to estimate the rate of population origination within species, which was found to be correlated with the local clade speciation rate (Harvey *et al.* 2017). The 'populations' in this study were more like subspecies or phylogroups than contemporary populations. Nevertheless, the study showed that their rate of formation is correlated with clade speciation rates, supporting a prediction from the population persistence hypothesis.

A third possibility is that the effects of variation in the rate of evolution of reproductive isolation on variation in diversification rates wane over time as diversity builds and as environmental and geographical variables affect species diversity. Figure 4 plots the number of species against time in two hypothetical lineages undergoing an early burst after colonizing a remote archipelago. Measured speciation and diversification rates will be related to species numbers accumulated over a specific time period. Shortly after colonizing, a lineage may diversify rapidly if
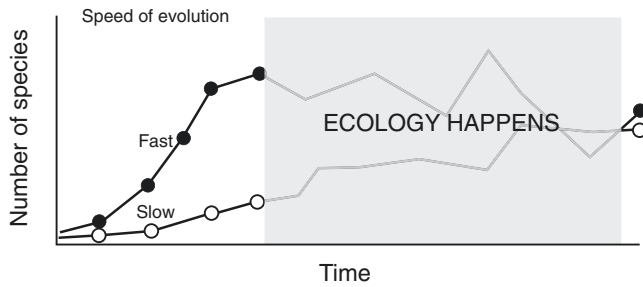
Figure 4. The number of species over time in two hypothetical lineages undergoing an early burst in diversification after colonizing a new environment. Initially, the rate of accumulation of species might be strongly influenced by the rate of evolution of reproductive isolation if resources are plentiful and enemies are few. In time, ecological factors that influence diversity of a clade intervene, including resources, enemies, and interactions between an increasing accumulation of species within the clade itself. Measured speciation and diversification rates at a given time point will be a function of the ratio of species numbers accumulated to that point and time. In the end, net diversification need not show a relationship with speed of evolution.

resources are plentiful and enemies are few. Possibly at this initial stage, the rate of accumulation of species is influenced by the rate of evolution of reproductive isolation. As an extreme example, the astonishing diversity of cichlid fishes in Lake Victoria could hardly have been achieved over the past 15 000 years (Meier *et al.* 2023) if the waiting time to evolve reproductive isolation was more typical—on the order of hundreds of thousands to several million years (e.g. Coyne and Orr 1997). Thus, the speciation rate in that clade owes a great deal to its rapid evolution of reproductive isolation. However, as species accumulate, other factors that influence the diversity of a clade will intervene, including chance, enemies, and possibly some regulation of faunal diversity within the clade itself. For example, despite the speed with which reproductive isolation evolves in the African cichlids, the number of species in lakes today is strongly associated with lake area (Wagner *et al.* 2014) and so too would the measured net rate of species accumulation.

Fourth, present-day rates might not be like those of the past. The population dynamics and evolutionary rates we measure today are not those of the ancestors of the clades whose diversification rates interest us, but rather are measured on the derived species that came after. For this reason, all tests of links between (past) macroevolution and (current) microevolution rely on the assumption that the present is the same as the past. Yet, the microevolutionary rates that caused diversification might be episodic and differ between then and now, breaking any correlation that once existed. For example, any tendency for the speed of reproductive isolation to decline over time and with changing ecological opportunity would weaken the association between contemporary and ancestral microevolutionary rates. Most key microevolutionary processes thought to determine clade diversification rates, such as number of populations, population persistence, effective population size, and genetic diversity might potentially be modified over time including by ecological interactions between an increasing diversity of species. Thus, feedbacks and other sources of environmental change (Schluter and Pennell 2017, Quintero and Jetz 2018, Harvey *et al.* 2020, Rana

et al. 2022, Drury *et al.* 2024) represent another explanation for the weak link between the rate of evolution of reproductive isolation and diversification.

Additional tests of the effect of variation in the rate of evolution have been achieved by comparing clade speciation or diversification rates with current levels of within-species genetic beta-diversity or isolation-by-distance—the steepness of the relationship between genetic divergence and space. The assumption behind such comparisons is that taxa whose species readily become genetically differentiated over a small spatial scale because of reduced dispersal or other factors should be more prone to generating new species rapidly. Yet, no relationship was found between diversification and genetic beta-diversity in Madagascar gemsnakes (Burbrink *et al.* 2023), in snake and lizard taxa from the Brazilian Cerrado (Singhal *et al.* 2022), in Australian skinks (Singhal *et al.* 2018), or in Costa Rican orchids (Kisel *et al.* 2012). Possibly, the chain of events connecting genetic beta-diversity at neutral markers to speciation rate is too indirect when reproductive isolation evolves by selection. Feedbacks might play a role here, because each speciation event causes the range of a former species to be split. Subsequent range expansion of the derived species might lower the slope of isolation by distance within each derived species, which would then take time to rebuild.

While further tests remain to be carried out, especially of speciation rate and population persistence, a complementary approach to bridging microevolution and macroevolution is to understand key environmental and geographical drivers of variation in rates at both scales. For example, differences in the geographical areas of 'continents' (defined here as a single land or water body generating most species within its borders) are predicted to influence both speciation rate and the build-up of species diversity. The underlying mechanisms would probably be a higher rate of establishment of new populations and by increased population size and hence persistence (lower population extinction rates) in larger areas, rather than via a large effect on the rate of evolution of reproductive isolation (Schluter 2016). Larger areas should thus increase speciation rates by allowing more populations to persist for long enough to undergo the evolution of reproductive isolation. Large areas should also maintain a higher species diversity via a lower species extinction rate, which will positively affect estimated net rates of diversification. A second driver for some taxa would be environments rich in resources and with few competitors or enemies. Depauperate environments are often associated with strong divergent selection on phenotypic traits (Grant and Grant 2002) which could lead to more rapid evolution of reproductive isolation and faster sympatry. Higher rates of evolution are known from remote archipelagoes and possibly the temperate zone relative to the tropics in association with its fewer species (Schluter and Pennell 2017). The presence of few competitors and predators would additionally lead to higher population persistence via higher population size, and increase speciation rates by allowing more populations to persist long enough to undergo the evolution of reproductive isolation, all else being equal. For a time, depauperate environments probably also favour higher species persistence (lower species extinction rates) which would also contribute to estimates of net diversification rates.

WHY DOES MACROEVOLUTION NOT PREDICT SELECTION?

Macroevolution of traits can sometimes predict microevolution when selection is the main cause. For example, patterns of long-term polymorphisms at major histocompatibility complex (MHC) and self-incompatibility genes (Klein *et al.* 1998) and in phenotypic traits (Parins-Fukuchi 2023) that are older than individual species can put bounds on estimates of the strength of frequency-dependent or balancing selection on these traits within populations. For quantitative traits, macroevolutionary models of trait evolution applied to phenotypic evolution in clades of species (Hansen 1997) are mathematically similar to microevolutionary models of evolution by natural selection on traits within populations (Lande 1976, Arnold 2023), leading to the question of whether coefficients from the two scales might in some cases correspond. Although the main applications of macroevolutionary and microevolutionary models are different (phylogenetic comparative methods vs evolutionary dynamics), both have been used to make inferences about natural selection (Bedford and Hartl 2009, Anderson and Weir 2022), opening a potential bridge between the two scales. Thus, it is worth asking what might be learned about selection coefficients on phenotypic traits from macroevolutionary analyses.

Most macroevolutionary insights into selection coefficients for quantitative traits are likely to come from trait divergence rate metrics obtained at the time an ancestral population gives rise to a new derived population, manifested as a splitting event in the phylogeny. As the newly derived population adapts, its evolution can be approximated by a Gaussian Ornstein–Uhlenbeck (OU) process (Lande 1976). The OU process is a mathematical random walk in which change at each step is the sum of both a nondirectional component and a mean-reverting tendency. The mean-reverting tendency here is directional natural selection, which pulls the population mean each generation toward the local adaptive peak. If population size is large, the change in the mean of a single trait each generation, $\Delta \bar{z}$, is proportional to the directional selection coefficient β, the gradient of the mean fitness function at the population mean (Lande 1976). β is determined by distance to the optimum and the width of the adaptive peak (the width of the mean fitness function around the local optimum, which is inversely related to the strength of stabilizing selection at the peak). Under this scenario, β also estimates the strength of directional selection away from the ancestral population, assumed to remain in its original environment (i.e. the strength of divergent selection). Evolution in the derived population eventually slows as it approaches the new adaptive peak. By fitting an OU model to a sequence of population means over time, such as in a long-term field study of a contemporary population (Lo Cascio Sætre *et al.* 2017, De Villemereuil *et al.* 2020) or a fine-scale fossil sequence (Hunt *et al.* 2008, Voje 2023), it should be possible to infer $\Delta \bar{z}$ per generation and from it the corresponding selection coefficient, $\beta = \Delta \bar{z}/g$, where g is the additive genetic variance in the trait (Lande 1976).

Similar population genetic inferences might be achieved by fitting an OU model to absolute phenotypic differences in a collection of sister species of varying ages all undergoing the same trajectory of divergence relative to an ancestral state. More typically, however, macroevolutionary data will consist of multiple sister species pairs each diverging at its own idiosyncratic rate and amount, requiring a different approach. In this case, a sister species OU model can be fitted to data on the squared or absolute difference between sisters as a function of their age (Bedford and Hartl 2009, Weir and Wheatcroft 2010). Such a model no longer describes the ascent of an adaptive peak by a derived species relative to its ancestor. Yet, the slope of the relationship at $t = 0$, which is the Brownian motion rate parameter and the step variance σ^2 of the fitted OU model (Butler and King 2004), should be related to the average $\Delta \bar{z}$ of sister species and its corresponding strength of divergent selection at the time of splitting. An OU model fitted to trait means of a whole clade of species, rather than only to differences between sister species, also contains information about divergence rates of sister species. It is reasonable to conjecture that the step variance σ^2 has a relationship to the average $\Delta \bar{z}$ at the time of splitting, and hence to the average divergent selection coefficient in the newly derived lineages.

Thus, in principle, field measurements made on populations at the time of divergence and divergent selection inferred from an OU model fit to sister species data should agree. Challenges to accomplishing this nevertheless abound, not least because field estimates of selection in populations fluctuate spatially and temporally (Grant and Grant 2002, Siepielski *et al.* 2017). Most new populations are also probably ephemeral and need not evolve at the same rate as those giving rise to persistent new lineages (Futuyma 2010, Rosenblum *et al.* 2012). Fitting OU curves to the difference between sister species as a function of their age is also not straightforward because of common artefacts in comparative data. For example, in birds, measurable phenotypic divergence between sisters is usually already present at $t = 0$, according to age estimates based on mtDNA sequences, implying that early divergence times tend to be underestimated. This can lead to artificially high estimates of divergence rates at the apparent time of splitting, because an OU curve must be forced through the origin and so fit an initial slope that is unrealistically steep (Freeman *et al.* 2022b).

By contrast, little information about selection coefficients is contained in the long-run frequency distribution of species means—the so-called stationary distribution (Cressler et al. 2015) yielded from fitting an OU model to sister species or a clade of species. Under these applications of the OU process, the squared difference between species means is assumed to increase initially in proportion to divergence time. As divergence proceeds, the effect of divergence time gradually weakens, and species means or sister species differences increasingly behave as though randomly sampled from a fixed underlying frequency distribution (the stationary distribution). The mean-reverting component of the model, the tendency for species means to evolve toward the grand mean θ, yields this effect. The strength of the tendency toward θ is described by the parameter α, which is sometimes interpreted as 'stabilizing selection around an optimum'. However, this analogy with natural selection is not apt because no fitness difference is implied. Real species traits commonly show a weakening of the effect of time on the difference between species trait means with increasing time since divergence, but whether the evolutionary trajectories of clades are otherwise well approximated by the mathematical OU process

is understudied (Pennell et al. 2015). Average absolute beak size difference between avian sister species fits a power function (which has no stationary distribution) somewhat better than an OU curve fitted to absolute sister species differences as a function of age (Freeman et al. 2022b), but OU might still be useful as an approximation.

An assumption of the OU clade model is that the stationary distribution is Gaussian (normal). The stationary distribution for absolute value of the difference between sister species is half-normal (Anderson and Weir 2022). Deviations from a Gaussian distribution, such as when trait distributions are better fitted by a mixture of Gaussians ('multipeak' models), are sometimes interpreted as evidence for 'divergent adaptation'. Differences between clades in their fitted grand means are often interpreted as indicating multiple 'selection regimes'. However, these patterns have no ready microevolutionary interpretation. Population genetic theory for divergence under natural selection predicts no particular shape for the long-run frequency distribution of species means. The distribution of species means is expected to depend on features of the adaptive landscape that are usually unknown.

Evaluation of inference about selection from the OU clade model benefits from a comparison with the adaptive landscape, which describes mean fitness of populations as a function of mean phenotype (Fig. 3). The OU stationary distribution corresponding to the hypothetical species data in Figure 3A is depicted in Figure 3B. This stationary distribution represents a useful visualization of the fit of the OU clade model to the species data. It represents an approximation to the frequency distribution of species means while correcting for phylogeny. The mean of the stationary distribution for trait i is θ_i. The width is largely determined by the inverse of the mean-reverting tendency α_i in the fitted OU model.

The comparison between Figure 3A and Figure 3B helps to explain why the modelled stationary distribution for species data, sometimes referred to as the OU 'macroevolutionary adaptive landscape' (see Pennell and Jiang 2024), might be unrelated to natural selection coefficients within species. If different species occupy different peaks in the adaptive landscape, then the width of the stationary distribution, the long-run frequency distribution of species means, will be far greater than the width of individual adaptive peaks. In agreement, estimates of the strength of the mean-reverting tendency α in macroevolutionary model fits to univariate species data are orders of magnitude weaker than the estimated strength of stabilizing selection in populations (Arnold 2023).

The comparison in Figure 3 identifies additional differences between the OU stationary distribution from the clade model and the adaptive landscape. Whereas adaptive landscapes at any point in time are typically rugged (Schluter and Grant 1984, Beausoleil et al. 2023), the OU 'surface' is smooth and does not resolve local fitness optima. This is because it is not computed from the contours of the adaptive landscape. While this seems obvious, it implies that the OU stationary distribution contains no more information about natural selection than the species means themselves and their phylogenetic relationships. On the other hand, individual adaptive peaks move (Grant and Grant 2002, De Villemereuil et al. 2020) and one perspective is that in the long term they travel stochastically across the full phenotype space (Arnold et al. 2001). Although unlikely to be literally true (peaks may oscillate more than they travel, and small-beaked finches should always be able to find small seeds), fluctuations in peak position combined with shifts between peaks may be similarly described. In this case one might hypothesize that the OU surface based on current species data represents a smoothed estimate of the long-term frequency distribution of adaptive peak locations. This hypothesis assumes that a clade randomly samples the full adaptive landscape during evolution. Yet, the ruggedness of adaptive landscapes, the stochasticity inherent in peak shifts, and genetic biases to the direction of peak shifts make it likely that a given clade will occupy only a portion of the adaptive landscape (Fig. 3B) and that many adaptive peaks will lie beyond those currently occupied. If so, then the OU 'landscape' will deviate from the adaptive landscape and separate clades evolving on the same adaptive landscape will have distinct OU model fits.

An interesting feature of the OU clade model fit is the implication that there are soft clade-specific 'bounds' on species trait values over fairly long time spans. Such bounds might derive from biophysical constraints, lack of genetic variation, or edges of the resource distribution, depending on the traits being modelled. These hypotheses might be harnessed to make predictions about mechanisms of selection in populations at edges versus the middle of the trait distribution. The actual selection coefficients experienced by edge populations are otherwise unlikely to be noticeably distinctive, however.

CONCLUSIONS

Attempts to predict macroevolution from microevolution, and vice versa, when selection is the main cause, can claim some successes. Here I have focused on our understanding of the basis for at least one successful link and for cases in which a predicted link was not detected. My goal was to probe some of the reasons for varying outcomes, and to suggest possible explanations and tests in hopes of strengthening the foundational connections between the two grand temporal scales of evolution.

The major directions of phenotypic differences among populations are often well predicted by genetic and mutational covariance, at least for morphological traits. Both natural selection and genetic biases are likely to play a role, but it is difficult to make contrasting predictions. Do adaptive peaks mainly lie along a corridor or do they extend in all directions? Testing this would require estimates of the adaptive landscape derived from first principles, so that we might estimate mean fitness within and beyond the frequency distribution of observed species means. The task might require a more complete understanding of environments and trait performance than we currently possess, though performance surfaces from biomechanical principles are a beneficial start (Tseng 2013, Holzman et al. 2022). Selection is almost certain to influence codivergence of functionally interacting traits across species. At the same time, a hypothetical corridor of adaptive peaks is unlikely to be a complete explanation for the correlation between genetic covariance and directions of interspecific divergence because it does not by itself explain why adaptive evolution in directions of lower genetic variance appears to take longer than the same amount of phenotypic

evolution in the direction of $\mathbf{g}_{max}$. Thus, mutational and standing genetic covariance probably play a role in biasing the directions of phenotypic divergence at the macroevolutionary scale.

A second mystery is why the apparent genetic bias lasts so long. Quantitative genetic theory predicts that the bias caused by genetic covariance should decay with time, at least for a population climbing a single nearby adaptive peak (Fig. 1). The bias might last longer if there are multiple adaptive peaks or if peaks fluctuate, but it is still expected eventually to weaken (Schluter 1996, Holstad et al. 2024). Tests of this prediction are still few, but there is some evidence of decay with time. However, it is still surprising that the observed association between mutational, genetic, and between-species covariation holds in some lineages for tens of millions of years. It seems that although evolution in different phenotypic directions is correlated with within-population amounts of standing genetic variation and mutational variance in those directions, these standard metrics of quantitative genetic variation are not sufficient measures of true 'evolvability' (Hansen 2006) in the long run. Selection, including constraining selection on unmeasured, genetically correlated traits (Holstad et al. 2024), probably plays a role, even though we are not well positioned to predict it. Future progress might be made via a molecular dissection of standing genetic covariation and its link to the genetic differences between species.

Although only a few tests have been carried out, the generally low success in linking speciation, extinction, and diversification rate of clades to the speed of evolution in populations suggests either that the present is not like the past (in part because past diversification might have modified present-day rates of evolution via feedbacks) or that diversification rate responds most to variation in demographic processes instead, such as in the number and duration of populations undergoing the evolution of reproductive isolation. Such demographic processes, rather than rates of evolution, are likely to underlie the observed relationship between diversification rate and area (Losos and Schluter 2000, Kisel and Barraclough 2010, Wagner et al. 2014), which may be a major contributor to variation in diversification rate. The demographic processes themselves are challenging to measure, and are probably noisy and fluctuating over time. A complementary approach to testing their role is to focus on the role of main drivers at both microevolutionary and macroevolutionary scales, such as area and ecological opportunity.

The reverse is also true—that macroevolution might predict microevolution, and I have focused on whether it can predict selection coefficients for quantitative phenotypic traits in populations. Others have already noted that the OU parameter governing estimates of the strength of the mean-reverting tendency in species data is greatly different in magnitude than known stabilizing selection coefficients in populations (Arnold 2023), highlighting the contrast between micro- and macroevolutionary parameters. I have attempted to provide some intuition as to why this is the case, based on differences between the adaptive landscape and the stationary distribution, or 'macroevolutionary surface', yielded by the OU clade model. I argue that features of the OU stationary distribution—which are often described in terms of one or more 'selection regimes'—contain little information about selection. This is in contrast to tests of adaptation based on comparative methods employing the OU clade model (Felsenstein 1988). OU surfaces provide limited information about selection because they lack access to fitness, are based on species means of clades that each occupy only a portion of the adaptive landscape rather than the contours of the landscape itself, and because population genetic theory of selection has little to say about the frequency distribution of means for clades of species evolving under natural selection. In contrast, the estimated rate of divergence at the time of splitting might contain information about the strength of directional selection between populations (e.g. in a derived population away from its ancestor), information that is gradually lost as time passes.

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