

# Fitness of multidimensional phenotypes in dynamic adaptive landscapes

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**Phenotypic traits influence species distributions, but ecology lacks established links between multidimensional phenotypes and fitness for predicting species responses to environmental change. The common focus on single traits rather than multiple trait combinations limits our understanding of their adaptive value, and intraspecific trait covariation has been neglected in ecology despite its importance in evolutionary theory and its likely impact on species distributions. Here, we extend the adaptive landscape framework to ecological sorting of multidimensional phenotypes across environments and discuss how two analytical approaches can be used to quantify fitness as a function of the interaction between the phenotype and the environment. We encourage ecologists to consider how phenotypic integration will constrain species responses to environmental change.**

## Traits and fitness in ecology

A major current challenge for population and community ecologists is to produce accurate forecasts of species- and community-level responses to global change [1,2]. Phenotypic traits have recently been heralded as the key to making generalizable predictions of community dynamics [3–6] and have achieved some success at predicting community composition [7,8]. However, the rapidly growing field of trait-based ecology has emphasized the indirect link between traits and community dynamics without adequately resolving the important direct links between traits and fitness [96], which underpin the population dynamics that drive changes in community composition (Figure 1). Indeed, the integration of the fitness concept into species distribution models has only just begun [9–12] and clear empirical links between functional traits and fitness components are still rare [13,14].

Population- and species-level fitness differences are determined by differential rates of growth, survival, and reproduction (Figure 1) [15,16], which ultimately lead to

community dynamics on contemporary timescales and species sorting over environmental gradients [17,18]. Quantifying the adaptive value of traits has been at the core of evolutionary biology for decades [15,19,20] and the multidimensional nature of phenotypic adaptation has been a central component of this theory [21,22]. The overall aim of this review is to ground trait-based ecology in the foundational concept of fitness to improve predictions of species responses to the environment and to resolve the relationships between traits and fitness. This review is timely because the quantitative links between multidimensional phenotypes and fitness along many environmental gradients of importance to plants, animals, and microbes are still tenuous.

In this review, we (i) discuss the importance of the multidimensional phenotype and intraspecific trait covariation, (ii) introduce the ‘dynamic adaptive landscape’, and (iii) discuss two empirical approaches to quantitatively link traits to fitness components. The dynamic adaptive landscape is an extension of the adaptive landscape framework in evolutionary theory to ecological sorting on the multivariate phenotype on an ecological scale. This framework provides a conceptual and analytical bridge between ecology and evolution and has strong potential to improve trait-based predictions of species responses because it explicitly considers how phenotypic integration and intraspecific trait covariation can constrain organism fitness along environmental gradients. We illustrate the tangible benefits of this new approach with a trait-based model to

## Glossary

**Adaptive landscape:** a framework in evolutionary biology for mapping fitness onto multivariate trait or gene combinations to understand how a phenotype evolves under selection.

**Dynamic adaptive landscape:** an ecological framework proposed here for quantifying how the shape of the adaptive landscape changes across environmental gradients. Its explicit handling of intraspecific covariation aids our understanding of how complex phenotypes are sorted along the gradients.

**Environmental gradient:** continuous variation in the level of resources (e.g., light) or conditions (e.g., temperature).

**Intraspecific trait covariation:** unstandardized correlation structure of traits among individuals within a population.

**$P_{\max}$ :** the direction of maximum phenotypic trait covariance, directly analogous to  $g_{\max}$  in quantitative genetics.

**Phenotypic integration:** the pattern of functional, developmental, and/or genetic correlation among traits in a given organism.

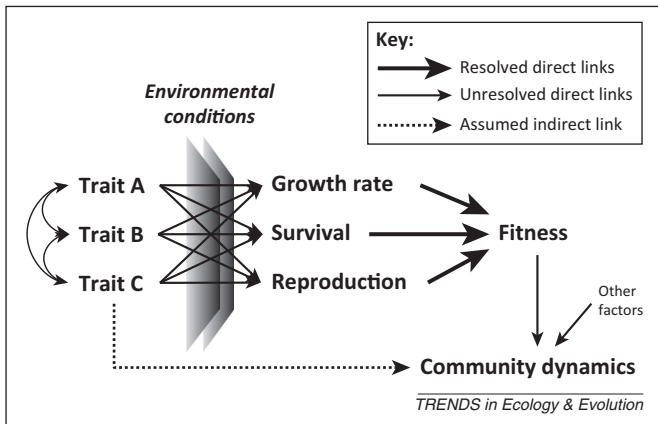
**Trait space:** mathematical representation of all possible or observed combinations of trait values.

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**Figure 1.** Path model, adapted from and inspired by Arnold [15], illustrating the hypothesized causal relationships among phenotypic traits, measures of performance, fitness, and community dynamics. Importantly, environmental conditions mediate the link between trait values and performance because one phenotype cannot be adapted to all environmental conditions. For clarity, this path model does not explicitly show how the environment can influence the expression of phenotypic traits in a given genotype. The curved arrows indicate the covariances among the traits, which further constrain how individuals perform in a given environment. Measuring fitness as lifelong reproductive output is ideal but is rarely possible, especially with long-lived organisms. Measures of individual organism performance, such as growth rate, survival, and reproduction, are the proximate drivers of fitness. These performance measures can be scaled up to the population level by calculating vital rates: population growth rate, survival rate, and reproductive rate. The rapidly growing field of trait-based ecology has emphasized the indirect link between traits and community dynamics without adequately resolving the important direct links between traits and fitness components that underpin many aspects of community dynamics.

demonstrate how intraspecific trait covariance can constrain species distributions depending on how the phenotype maps onto the dynamic adaptive landscape.

### The multidimensional phenotype and intraspecific trait covariation

Average trait values among species provide valuable information about where species are most likely to successfully grow, survive, and reproduce [23,24]. Mean trait values are useful for many applications in ecology, but have inherent limitations for others. For example, when traits are used to quantify the niche of a species [25,26], comparisons of simple vectors of mean trait values among species do not provide any information about niche breadth nor on how much niche overlap occurs among coexisting species [27–30]. This can be problematic because niche overlap is at the core of our understanding of species interactions, coexistence, community assembly, and species sorting [27,31–34].

Recently revived interest in intraspecific trait variation has greatly complemented our understanding of average functional differences among species [28,35–38]. The location (mean) of species in trait space (see Glossary) is arguably a critical moment in the trait distribution, but trait variation is also important because it affects both how a species responds to immediate changes to environmental conditions [39], as well as its evolutionary trajectory over time [40]. Two species with identical mean trait values will occupy different regions of a 2D trait space if their trait variances differ (compare blue and orange species in Figure 2A). If species differ in their trait variances, this can indicate that one species has a greater diversity of genotypes or a stronger plastic response to the environment,

and if the trait under study impacts the fitness of this species, then both genetic diversity and environmental plasticity will impact its potential distribution along an environmental gradient [41]. While trait means and variances are clearly important, we argue that these two ingredients alone are insufficient to quantify functional differences among species and cannot inform their dynamic evolutionary or ecological responses over time or across environmental gradients.

The third necessary ingredient is intraspecific trait covariation. Interspecific trait covariation has underpinned the quantification of trait spectrums that reflect trade-offs among functions and strategy dimensions [42–45]. However, intraspecific trait covariation has received little attention despite its fundamental importance in determining fitness differences among species [46–49]. Individuals belonging to two species that have identical trait means and variances, but have opposite covariance, might occupy different regions of trait space (compare the green and red species in Figure 2A). Understanding intraspecific trait covariance is therefore just as important as estimating trait means and variances to describe the shape and space occupied by species within the available trait space [25]. Performance and fitness are best quantified by multiple integrated phenotypic traits [4,50–52] because adaptation is a multivariate process [22] (Figure 1). While this has long been acknowledged by ecologists [53–56], it has not yet become an inherent part of the community ecologist's toolbox in the same way that it has pervaded the toolbox of the evolutionary biologist [20,21]. Quantitative genetics has developed tools to study trait covariance within species because it can influence directional selection and hence the evolutionary trajectory of a species [15,20,22,40,57]. For example, the multivariate breeder's equation predicts how population trait means will change over generations according to the heritability of the traits and the relationships between traits and fitness. A similar emphasis on intraspecific covariance is necessary for ecology to make accurate predictions of species responses to environmental change because environmental filtering is inherently a multivariate process.

The whole-organism phenotype is an integrated expression of multiple traits that are jointly influenced by developmental, genetic, and environmental effects [58,59]. Matrices of average functional traits among species are analogous to the interspecific genetic variance–covariance matrix ( $\mathbf{L}$ ) versus the intraspecific genetic variance–covariance matrix ( $\mathbf{G}$ ) in evolutionary biology [21,58]. The ensemble of the  $\mathbf{L}$  and  $\mathbf{G}$  matrix, or their individual elements, does not necessarily need to be positively correlated because the forces shaping the genotypes among species can be different from those at play within species (Figure 2B) [60]. Generally, significant differences between interspecific and intraspecific genetic covariances ( $\mathbf{L}$  and  $\mathbf{G}$ , respectively) indicate the action of natural selection [58].  $\mathbf{L}$  and  $\mathbf{G}$  are more likely to be similar if species have diverged solely by genetic drift [57,61]. If we assume that interspecific trait covariance matrices ( $\mathbf{Q}$ ) and intraspecific phenotypic trait covariance matrices ( $\mathbf{P}$ ) are determined mostly by genes and less by the environment, which is a common simplifying assumption in

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