REVIEW

The net effect of functional traits on fitness

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Keywords

Comparative functional ecology, demographic trade-offs, density dependence, intrinsic growth rate, population growth rate, plant community assembly, vital rates

Abstract

Generalizing the effect of traits on performance across species may be achievable if traits explain variation in population fitness. However, testing relationships between traits and vital rates to infer effects on fitness can be misleading. Demographic trade-offs can generate variation in vital rates that yield equal population growth rates, thereby obscuring the net effect of traits on fitness. To address this problem, we describe a diversity of approaches to quantify intrinsic growth rates of plant populations, including experiments beyond range boundaries, density-dependent population models built from long-term demographic data, theoretical models, and methods that leverage widely available monitoring data. Linking plant traits directly to intrinsic growth rates is a fundamental step toward rigorous predictions of population dynamics and community assembly.

Glossary

Community assembly: process by which species arrive, establish, persist, increase or decrease in abundance over time, and go extinct within and across environmental gradients.

Components of fitness: measures of individual performance including survival, growth, and reproduction; also referred to as vital rates. The integration of fitness components yields an estimate of total fitness and integration of vital rates yields an estimate of population growth rate.

Demographic trade-offs: negative correlations between two or more vital rates.

Dynamic adaptive landscape: ecological framework that quantifies how the effects of traits on population fitness within and across species changes across environmental gradients. This framework extends evolutionary models of fitness landscapes where fitness is a function of traits in a fixed environment.

Evolutionarily stable strategy: strategy in a given environment that cannot be invaded by an alternative strategy.

Fitness: growth rate of a population, genotype, or phenotype. We focus on population growth rate as a measure of the fitness of a population.

Fitness landscape: conceptual or mathematical representation of individual or population-level fitness as a function of one or more phenotypic traits or genes.

Functional traits: morphological, physiological, or phenological attributes of species that impact fitness indirectly through their effects on individual survival, growth, and reproduction.

Fundamental niche: the environmental conditions and availability of resources where a species can maintain a viable population. In the presence of competitors, the species is further restricted to its realized niche.

Individual growth rate: rate of expansion or contraction in size of an individual organism over time.

Intrinsic growth rate: population growth rate at low density, in the absence of either intraspecific density-dependent effects or interspecific competition.

Invasion growth rates: population growth rate of the focal species at low density when growing with competing species that are at their stochastic equilibrium abundances.

Population fitness (λ): finite rate of increase of the population. This can be directly quantified for a single time step as N_{t+1}/N_t, where N is number of individuals and t is time. It can also be estimated using population models as the average or asymptotic population growth rate by computing the dominant eigenvalue of the transition matrix. In this paper, we emphasize the importance of quantifying intrinsic growth rates to standardize the measure of fitness at low densities to control for the confounding effects of competition.

Sensitivities: partial derivatives that quantify how vital rates effect population growth rate. Sensitivities can be relativized, which are called elasticities, to reflect proportional effects on fitness.

Vital rates: rates of birth, death, and growth of individuals, also called demographic rates and components of fitness.

Demographic trade-offs and population fitness

The alluring prospect that **functional traits** (see Glossary) can explain variation in species performance has invigorated comparative functional ecology, yet identifying the traits that determine **fitness** remains an important empirical challenge [1-6]. Inspired by classic evolutionary theory that linked morphology to performance and fitness [7], ecologists have recently intensified their search for relationships between functional traits and **vital rates**, but have avoided the more challenging links to fitness [8-15]. Analyzing **components of fitness** in isolation is an important step, but testing relationships between traits and vital rates to infer effects on fitness can be misleading without considering **demographic trade-offs** [16-18].

We focus our discussion at the population level and define **population fitness (λ)** as the growth rate of a population [19, 20]. This differs from the evolutionary focus on individual-level fitness [7, 21-24], but is analogous since we aim to compare growth rates across populations as one would compare growth rates across genotypes or phenotypes in evolutionary biology. The comparison of traits and fitness across species, not within species, is explicitly directed at ecological rather than evolutionary scales and processes. It has been argued that population growth rates are not the ideal performance currency to test trait-based theory, partly because they are difficult to measure [25]. However, we focus on population growth rates for three reasons: 1) we aim to understand the process of environmental filtering in **community assembly** where it is populations that persist or go extinct in a given environment [26, 27], 2) recent theory suggests that traits have stronger impacts at the population level because individual lifetime reproductive success is governed by random variation, *i.e.*, 'luck' [28], and 3) measuring lifetime reproductive success of individuals is difficult or impossible for most long-lived species.

Functional ecologists can advance community ecology by embracing population demography [2, 4, 29]. However, failure to account for trade-offs among vital rates has left a significant gap in our understanding of the adaptive value of functional traits (Fig. 1). Filling this knowledge gap is a fundamental step toward understanding the **fundamental niche** of species, and forecasting species and community responses to a rapidly changing world [1, 30, 31]. Our discussion draws primarily from examples of plant demography, but the core principles apply more broadly given that birth, growth, and death are affected by phenotypic variation and environmental contexts across the Tree of Life. In this Review, we 1) illustrate how individual vital rates can be misleading proxies for fitness, 2) describe a diversity of approaches to quantify intrinsic growth rates as a measure of population fitness, and 3) explain how to empirically identify the functional traits and environmental conditions that drive variation in population fitness.

Vital rates can be misleading proxies for fitness

Individual vital rates can be misleading proxies for fitness without considering demographic trade-offs. For example, species with fast individual growth rates may exhibit low rates of survival. If the growth-survival trade-off can generate co-variation in **individual growth rates** and survival rates that yield equal fitness, all else being equal (*e.g.*, equal reproduction rates), then individual growth rates tell us little about fitness [32, 33] (Fig 1). Similarly, populations with high survival and low reproduction could have the same fitness as populations with low survival and high reproduction [17, 34]. Consequently, if a trait is negatively related to survival, then it may be positively related to individual growth or reproduction [21, 35-37]. For example, wood density negatively effects individual growth rates but positively effects survival rates because faster tree diameter growth can be achieved by constructing low density wood, but this comes with a higher risk of damage and death from multiple causes [11, 15, 38]. Consequently, the net effect of traits on fitness is obscured when one vital rate is analyzed in isolation [21]. This knowledge gap can only be resolved by quantifying the net effect of traits on fitness (Fig. 1).

Fitness is challenging to measure. Annual plant communities have long been used as model systems for studying fitness in relation to traits because lifetime fitness and multiple generations are relatively easy to observe in annual plants. Physiological differences among annual species determine their fitness in response to inter-annual climatic variation [39-42], but concrete evidence that functional traits predict fitness differences among long-lived species is still lacking [24, 31]. It is far more challenging to quantify fitness for long-lived species, but the effort is justified given that they are the dominant life form on the planet.

There are several challenges posed by long-lived species. Fitness in long-lived species is driven by rates of individual growth, survival, and reproduction throughout the entire life cycle. These vital rates do not have equal effects on fitness and the relative importance of each may vary across environmental conditions [43-45]. Long-lived species may rely on rare recruitment events [46] and capturing these events can be challenging. However, fitness is often more sensitive to variation in survival and growth than in fecundity in many long-lived species [47-49]. Individuals of long-lived species may experience strong variation in conditions over their lifetime whereas annual species deal with environmental variation across generations. Trait effects on vital rates may also change with size [50] or ontogeny [2, 11, 51, 52]. Vital rate **sensitivities** quantify the contribution of each vital rate to population growth rate [16, 53] and can indicate the components of fitness on which natural selection can act (or has acted) the strongest [49, 54]. Some studies have focused on linking traits to the most important vital rate. For example, relating traits to survival rates for long-lived perennial plants [12] may be close to estimating effects on fitness because survival is the most important vital rate for perennials [8, 17]. But the hard truth of the matter is that we do not know unless fitness is measured directly (Fig 1).

A further well-known complication is that any effect of traits on fitness will depend on the environmental context because variation in traits is underpinned by ecological trade-offs [21, 23, 29, 55, 56]. As a result, relationships between traits and fitness change along environmental gradients [13, 14, 22, 39, 41, 57, 58]. Ignoring variation in trait-fitness relationships across environments has hindered progress toward using traits to make general predictions about how species respond to environmental change.

Quantify intrinsic growth rates

Theory predicts that species are sorted along environmental gradients because species only occur in sites 1) to which they can disperse, 2) where their traits are adapted to the local conditions, and 3) where they maintain competitive advantage in multispecies communities [26]. We are focused on the second step in this Review, and so our emphasis is on the difficult task of quantifying the fundamental niche. Many statistical approaches test if traits predict species occurrences and abundances in a given environment [59-61], but analyses of observational abundance data cannot control for the confounding effects of competition [27, 40, 42].

The ideal metric of population response to the environment alone is estimated when the focal species is growing by itself at low density, which we define as the **intrinsic growth rate**, because it is least affected by either intraspecific negative density-dependence or interspecific competition. Modern coexistence theory emphasizes a similar but distinct quantity, the **invasion growth rate** [62-65], which is the population growth rate when competing species are at their equilibrium abundances. Invasion growth rates will ultimately be needed to integrate species interactions into predictions of community dynamics, but invasion growth rates are less practical to meet our objectives because they are computed using either 1) empirical multispecies models that are difficult to parameterize, or 2) experiments that run long enough for establishment of a resident community at equilibrium abundances, which could take many generations. Here we focus on the intrinsic growth rate as a key first step to identify the net effect of traits on fitness.

We have identified several approaches to quantify population fitness that span a trade-off of empirical rigor and logistical ease (Fig. 2). Confronting trait-based theory with empirical demographic data will yield the most transformative results. But, as pragmatists, we describe a variety of approaches that vary in the difficulty of data collection and the precision of empirically estimating intrinsic growth rates to galvanize progress in this field.

First, intrinsic growth rates can be observed experimentally (Fig. 2A). Multiple species can be introduced to multiple vacant sites across an environmental gradient. Demographic monitoring of these long-lived species over time can precisely estimate intrinsic growth rates because competition is experimentally controlled. Population models do not need extra parameters to account for density dependence; it is intrinsic to the data. Models of perennial plants will still require adequate annual transitions across the range of stages, which could be alleviated by planting a range of ages and stages (*e.g.*, seeds, seedlings, vegetative plants, flowering plants) from the beginning of the experiment to start multiple cohorts simultaneously. Planting species beyond their range boundaries provides especially robust assessments of the effects of traits on population fitness across environmental gradients [5, 66, 67] because it tests whether a species can recruit, grow, and survive outside its current range of environmental conditions. Importantly, syntheses of transplant studies beyond the range concluded that integrative measures of fitness were superior over individual vital rates at detecting reductions in performance beyond species ranges [67]. Forestry, in particular, has a long tradition of common garden experiments where multiple provenances of tree species are planted to evaluate genetic and environmental effects on species performance [68, 69]. Such common gardens are perhaps the gold standard

[40, 42, 70, 71], yet they are often prohibitively expensive in both time and money. We recommend that funding agencies develop international collaborative opportunities to fund the difficult work of establishing common gardens beyond range boundaries.

Second, intrinsic growth rates can be estimated using population models parameterized from observational data on individuals over time (Fig. 2B). Most published population models report asymptotic population growth rates, which ignore density-dependence [53, 72]. However, density-dependent models of vital rates that incorporate the effects of population size can be used to calculate intrinsic growth rates [53, 73, 74]. Integral Projection Models (IPMs) can be especially powerful in this context because they harness the strength of regression analysis to build models of vital rates as functions of organism size and any other covariate, including the density of neighbors [75]. This method requires that adequate variation in neighborhood density is observed. Once vital rate regression models are parameterized, intrinsic growth rates can be estimated by setting neighborhood density in the vital rate regressions to a fixed low value. This technique statistically controls for the effects of competition [12, 15], but it assumes that neighbor density is a good proxy for resource competition [76]. Moreover, observational datasets often lack measurements of population declines outside their natural range of environmental conditions precisely because the species cannot live in those conditions. Experiments are required to identify the environments in which populations decline. Demographic models of plants and animals have been synthesized for widespread use [77], but we encourage new demographic datasets to be measured across multiple species across environmental gradients.

Third, theoretical demographic models explore the consequences of ecophysiological and demographic theory on trait optimization (Fig. 2C). Game-theoretic models of **fitness landscapes** implicitly account for density dependence to identify functional trait combinations that are **evolutionarily stable strategies** in a given environment. Game theory offers a rather different approach since the relationships between traits and vital rates are embedded in the model. Individual-based demographic models of competition for resources have been used to predict the coexistence of dominant functional strategies in forests [78, 79], and demographic models are also being integrated into global-scale dynamic vegetation models to improve trait-based predictions of ecosystem states and fluxes of carbon dioxide [80, 81]. These computationally rigorous approaches are located toward the middle of our trade-off of empirical rigor and logistical ease because they are neither empirical nor easy. Theoretical demographic models do not empirically estimate intrinsic growth rates of real species in real environments, but they generate testable hypotheses and demonstrate the relevance of demography in forest assembly and global scale vegetation dynamics.

Fourth, intrinsic growth rates can be estimated using widely available monitoring data (Fig. 2D). Rather than integrating vital rates across individuals, one can compute the annual growth rate of a population by dividing population size in one year by size in the previous year (*i.e.*, $\lambda = N_{t+1} / N_t$). When studying organisms where individual genets are rarely counted, as is often the case when monitoring plant or coral reef communities, then cover or biomass of the population could be substituted for population counts (*i.e.*, $\lambda = Cover_{t+1} / Cover_t$). Quantifying the ratio of cover in successive years to estimate λ has been applied to model dynamics of multiple coexisting species [82], and this population-level data can be used to estimate density dependence and project population growth rates at low densities [83]. Negative relationships that are fit to empirical measurements of $log(Cover_{t+1} / Cover_t)$ and density (*i.e.*, $log(Cover_t)$) are indicative of negative density-dependence [48]. Intrinsic growth rate can be computed as the exponentiated value of $log(\lambda)$ when total density is low (Fig. 2C). We urge caution when using this method for three reasons. First, this approach does not account for age or size structure, which are important drivers of population dynamics. Second, comparisons of population growth rates across species using changes in total cover may be affected by the fact that species vary in maximum size. Third, statistical artefacts can affect the estimates of density dependence given that $Cover_t$ is in the denominator of λ, and so it is important to account for census error when using this approach [76, 84].

The fifth method is distinct from the others because it ignores the dynamics of populations and examines the occurrence or abundance of species across environmental gradients (Fig. 2E). Occurrence is not fitness. Indeed, the link between intrinsic growth rate and probability of occurrence is not even strictly positive [85, 86]. Populations may be present at a site but they may be experiencing negative population growth rates, and absences of a population from a site could be driven by dispersal limitation or competition rather than abiotic environmental filtering [27]. However, we include the analysis of occurrence and abundance data here because we stand to gain tremendous insight by analyzing large datasets of thousands of species spanning global environmental gradients. In contrast, fitness data will be limited to local and landscape scales for the foreseeable future. Ecologists have been modeling species occurrence data for decades, but model-based frameworks can provide strong tests to determine if trait-environment interactions explain species occurrences beyond what the environment explains by itself [60, 87]. Moreover, this approach can generate hypotheses that can be empirically tested in common gardens and can potentially identify the most important traits to use in models of fitness. One drawback is that this approach cannot account for density dependence. New techniques that estimate metrics of colonization and survival from repeated measurements of occupancy along transects hold promise for leveraging long-term monitoring data to estimate demographic rates [88-90]. Modeling species occurrences will without a doubt continue to be a widely used method, but we especially encourage their application to large spatial scales that surpass those that are currently possible for demographic models.

Identify the traits that drive intrinsic growth rates

The next step is to model fitness as a function of trait-by-environment interactions [12, 55, 91]. This tests the **dynamic adaptive landscape** model to determine how the effects of traits on population fitness across species depends on the environment [92]. The question is not whether population fitness among species varies along environmental gradients; this has been known for centuries (Fig 3A). The question is whether traits explain variation in population fitness (or occurrence) among species through an interaction with the environment (Fig. 3B). One can compare the empirical support for a model where population fitness of multiple species is a function of the environment only, versus a second model that adds traits and a trait-by-environment interaction. The strongest ecological trade-offs will be seen when two conditions are met: the trait-by-environment interaction is both statistically supported and the effect of the environment on fitness changes sign along the range of the trait [12, 60, 87]. Computing the first partial derivative of fitness with respect to the environment isolates the fitness response to an environmental condition as a function of traits (Fig. 3C). This model can then be used to test predictions experimentally by using new species outside the training dataset, which is a necessary and powerful way to test the generality of traits.

This model often assumes that observed traits in a given environment reflect 1) adaptation to local conditions and 2) the existence of an optimum trait value. Ideally, intraspecific trait variation is measured to account for local adaptation rather than using only an average trait value [6, 29, 58]. However, it is important to be aware that many processes can influence the observed phenotype, perhaps even resulting in a maladapted phenotype. Rapidly changing environments could cause lags in the ability of a phenotype to adapt, leading to negative consequences for some fitness components. In these cases, the adaptive value of a trait can be over overestimated when focusing on single fitness components [6]. Moreover, multiple trait optimums may exist in environments where multiple functional strategies maintain species coexistence or where the trait distribution is multimodal [93]. Comparing models that include interactions with more than one trait to determine whether the effects of a trait on fitness in a given environment depends on other traits is a promising line of enquiry [14, 55, 92].

We have focused on the three core vital rates (individual growth, survival, and reproduction) as fundamental fitness components, though many other vital rates in the life cycle influence these components. For example, dispersal and germination rates influence reproduction, and dispersal limitation is a key constraint in community assembly. Traits such as seed mass and height are predictors of seed production and dispersal distance [94], which have been suggested to influence population persistence and species ranges by constraining geographic distributions but extending elevational limits [67, 95]. Greater understanding of the importance of immigration will improve our estimates of intrinsic growth rates and the links between traits and fitness, particularly across spatial environmental gradients (see Outstanding Questions).

Discovering how traits affect different vital rates and how these combine to drive fitness is a grand challenge in community ecology that bridges the fields of ecophysiology and evolutionary biology [7, 23, 24]. We anticipate that ecophysiological traits, such as embolism vulnerability, leaf turgor loss point, or chlorophyll *a* florescence, will exhibit the strongest mechanistic links to vital rates given their direct link to resource use [96-98]. Determining the physiological mechanisms that drive demographic trade-offs is an important Outstanding Question. We can decompose population fitness into contributions from underlying traits by calculating vital rate elasticities as functions of lower level parameters [99], which would allow us to quantify the extent to which demographic trade-offs obscure the indirect effect of traits on intrinsic growth rate [7]. This synthesis would lead to substantially new understanding of how functional traits affect survival, growth, and reproduction at the scale of individuals, and how these coalesce and propagate into net effects on population fitness [11, 20].

More work is needed to discover the physiological mechanisms that drive demographic trade-offs among species. For example, seed mass is positively related to seedling establishment but negatively related to seed production [11]. Specific leaf area is related to the 'fast-slow' continuum of life history strategies, where short-lived species construct cheap leaves and exhibit fast rates of photosynthesis [100]. Two independent demographic trade-offs among tropical forest trees were recently identified: the 'growth-survival' and 'stature-recruitment' trade-offs. The growth-survival trade-off was related to variation in wood density and leaf economics traits, whereas the stature-recruitment trade-off was related to height, seed mass, and leaf area [37]. Not only do traits explain demographic trade-offs, these demographic trade-offs can predict tropical forest dynamics [101].

We have emphasized the importance of quantifying intrinsic growth rates in the absence of competition, which is a necessary step for defining the species pool that can tolerate a given environment and for quantifying the fundamental niche of species. There is also an urgent need to develop frameworks for predicting interaction networks among species using functional traits (see Outstanding Questions). Traits can explain niche and fitness differences among interacting annual plant species [40, 42], but understanding how traits relate to invasion growth rates among long-lived species to quantify the realized niche of species is a research frontier [62-64]. Developing mathematical links between traits and interaction coefficients to predict coexistence dynamics for communities across environmental gradients will complement the research program proposed here.

Concluding remarks

Predicting fates of populations and communities using traits has often been called the 'holy grail' of ecology [1, 102], yet we often lack clear evidence that functional traits live up to the hype [24]. To advance this important research agenda, we encourage studies that link traits directly to intrinsic growth rates to test the generality of traits for predicting species performance. The complexity of population dynamics may have hindered an earlier integration of population demography into trait-based community ecology, but the time is right to bridge the divide. Demographic data are increasingly available [77, 103] and alternative methods for measuring population dynamics can leverage widely available monitoring data [82, 83]. Pursuing answers to these Outstanding Questions will advance our conceptual understanding of how the contours of fitness landscapes across multiple species shift along environmental gradients [92]. In closing, we hearken back to an analogous call for evolutionary biologists to become demographers [104]; we hope this Review provokes more community ecologists to become demographers to test the faculty of functional traits.

Acknowledgements

This work was funded by a grant to the authors from the National Science Foundation (DEB-1906243).

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Figure Captions

Figure 1. Relationships between traits and vital rates can be misleading proxies for estimating the effect of traits on fitness without considering demographic trade-offs [11, 16, 17, 21, 32, 43]. Different colored symbols represent species that exemplify different life histories: red triangles typify species such as annual plants that rely on high reproduction rates, blue circles typify species such as short-lived perennials that rely on rapid individual growth rates, and purple squares typify long-lived perennials that rely on high survival rates.

Figure 2. Four approaches to estimate population fitness span a trade-off of empirical rigor and logistical ease, and each approach exhibits different strengths and weaknesses. A) Illustration of experimental common gardens where each species is planted and monitored in its home range and in two additional sites beyond its range. This is the best way to observe population declines in ill-suited environments. B) Integral Projection Models can incorporate density dependence by using population size as a covariate in the vital rate regression models. C) Fitness landscape resulting from an individual-based model of forest dynamics where multiple combinations of height and leaf mass per area can stably coexist. Warm colors in this fitness landscape represent evolutionarily stable strategies [79] (reproduced with permission). D) Hypothetical time series of population-level data (e.g., counts, cover, or biomass) can be used to account for density dependence by regressing $log(Cover_{t+1} / Cover_t)$ on $log(Cover_t)$, which can be used to estimate population growth rate at low density (see blue dotted arrow). E) Multiple species distribution models can be used simultaneously to analyze how trait-by-environment interactions affect occurrence or abundance at global scales. This

method does not analyze fitness, but it can be used to generate hypotheses about which traits are most important at global scales.

Figure 3. Identifying the functional traits that drive environmental effects on population fitness will advance community ecology. (A) In this example of five hypothetical species, the red species is adapted to the high end of the environmental gradient. But why? (B) The trait-by-environment interaction across multiple species illustrates that the red species is adapted to the high end of the gradient because it has a low trait value. The grid of points on the horizontal surface of the 3D figure illustrates that each species has a different trait value and that each species was measured across the full range of environmental conditions. This rigorous sampling of species across the environmental gradient can only be perfectly accomplished in common garden experiments because species can be planted beyond their natural range. The unimodal fitness response is shown here to reflect the classic fitness function, but linear models are often used in practice given their greater simplicity for model estimation [12, 91]. (C) The first partial derivative of fitness with respect to the environment illustrates how species with different trait values respond to the environment differently. Note that because the trait-by-environment fitness function is unimodal in panel B, the fitness response will depend on both the trait and the environment [12], but the general relationship would still be negative overall in this example. The horizontal error bars reflect that species exhibit random trait variation among populations. To test whether traits can generalize to other species, this model can predict the fitness response for a 'new species' (represented by the diamond) that was not included in the original model. For example, if this new species had a high trait value, the model would predict a negative response to the environmental gradient, implying that, unlike the red species, it would exhibit high fitness at the low end of the environmental gradient.