

DEFINING FITNESS IN EVOLUTIONARY ECOLOGY

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Editor: Susan J. Mazer

An understanding of biological fitness is central to theory and practice in ecology and evolution, yet fitness remains an elusive concept to define and is challenging to measure accurately. Fitness reflects an individual's ability to pass its alleles on to subsequent generations. Researchers often quantify proxies for fitness, such as survival, growth, or reproductive success. However, it can be difficult to determine lifetime fitness, especially for species with long life spans. The abiotic and biotic environment strongly affects the expression of fitness, which means that fitness components can vary through both space and time. This spatial and temporal heterogeneity results in the impressive range of adaptations that we see in nature. Here, we review definitions of fitness and approaches to measuring fitness at the level of genes, individuals, genotypes, and populations and highlight that fitness is a key concept linking ecological and evolutionary thought.

Keywords: component of fitness, life history, population growth rate, selection coefficient, trade-off, vital rate.

Online enhancement: glossary.

Origins and Importance of Fitness as a Concept

The concept of fitness is typically attributed to Darwin, with the well-known phrase “survival of the fittest.” This phrase captures an important understanding of fitness by suggesting that some individuals—those with the most “fit” traits for a particular environment—would have higher survival than others. However, it was not until the fifth edition of *On the Origin of Species* in 1869 that Darwin used the phrase “survival of the fittest” in his treatment of natural selection (Darwin 1869). In earlier editions, the concept of fitness was defined more vaguely, in terms of how well an individual was suited to its environment. This iconic phrase was actually coined by Herbert Spencer. Spencer began to conceive of fitness in his book *The Principles of Biology* (Spencer 1864), where he outlined two key postulates of the evolution by natural selection. First, individuals or genotypes vary in their phenotypes (their observable traits) and fitness. Second, certain phenotypes may increase the fitness of individuals or genotypes. In other words, there is a causal relationship between trait values and fitness. Therefore, from the beginning, survival was inherently linked to successful reproduction, and the idea of the “fittest” returns us to the observation that some individuals are less fit than others within a population.

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Manuscript received October 2023; revised manuscript received December 2023; electronically published April 19, 2024.

Thus, the concept of fitness was born from the original notion of evolution by natural selection, and fitness is a critical component of how adaptive evolution proceeds. Yet biologists have disagreed about the formal definition of fitness since the term was first introduced (Dobzhansky 1968; Stearns 1976; Cooper 1984). Indeed, in his glossary, Stearns (1976, p. 4) defined fitness as “something that everyone understands but no one can define precisely.” Ultimately, fitness can be thought of as the ability of an individual to contribute offspring to the next generation. Fitness depends on the abiotic and biotic environment because, in a different setting, an individual may have dramatically different fitness. For example, an individual plant from a drought-prone inland habitat might have reduced fitness if moved to a coastal dune with salt spray from the ocean and high moisture levels (Hall and Willis 2006). Similarly, for perennial species that live for multiple years, the fitness of an individual can vary from year to year owing to interannual fluctuations in environmental conditions (Stearns 1976). Thus, fitness depends on the evolutionary history of a lineage, the genetic composition of an individual, and the specific conditions that individual currently experiences. Fitness cannot be considered outside of the larger context of an individual's genome, its evolutionary history, and its environment.

Although the concept of fitness was originally conceived at the individual level, fitness also manifests at lower and higher levels of biological organization. In this primer, we discuss fitness at the level of the individual organism, the gene, and entire populations. Furthermore, we highlight that fitness provides a

critical link between the ecological and evolutionary dynamics of species. Ultimately, in understanding fitness, we can make robust predictions about population stability through time and the process of adaptive evolution. These eco-evolutionary topics are of pressing concern, as industrialization and other human actions have dramatically altered the conditions that plants and animals experience in their native ecosystems as well as the fitness that these organisms are able to achieve.

Fitness at the Level of the Individual

Fitness: More than Meets the Eye

In the half century since Stearns (1976) criticized the lack of precision in definitions of fitness, organismal biologists have extensively characterized the growth, survival, and reproduction of individuals at different stages across their life cycles (Ehrlén 2003; Shaw et al. 2008; Horvitz et al. 2010; Miller and Compagnoni 2022). Researchers now acknowledge that an individual's or a genotype's fitness reflects its ability to pass its alleles on to subsequent generations. However, it is extremely challenging to define how fitness should be measured in practice. Would you count the number of offspring an individual produces? Would you also incorporate the survival or reproductive success of those offspring? For how many generations would you monitor descendants, knowing that each generation could (potentially) include exponentially more individuals than the last and that many seeds remain dormant in the soil for years, decades, or even centuries (Baskin and Baskin 2014)?

Further, many organisms are exceptionally long lived and produce variable numbers of offspring at different times in their life spans. Some species produce extremely small spores or seeds (the tiny flecks you see in real vanilla ice cream are seeds from the orchid *Vanilla planifolia*!) or disperse their offspring across large distances, making it challenging to quantify the total number of seeds produced. For instance, the airflow produced by vehicles driving down a road can disperse seeds of *Ailanthus altissima* (known as the tree of heaven) and *Clematis vitalba* (known as old man's beard) by over 45 m (von der Lippe et al. 2013), red foxes can disperse the seeds from fruits they eat up to 3 km away (González-Varo et al. 2013), and lowland streams can disperse seeds up to 1.8 km in the summer and 14.2 km during the winter (de Jager et al. 2019). Indeed, fruit-eating has even evolved in some clades of fish, with these clades becoming highly effective at dispersing seeds several kilometers away from the mother tree in extensive floodplain forests of tropical South America (Anderson et al. 2011). For many species, it would be logistically difficult to track seeds that are dispersed naturally simply to quantify fitness. In addition, some plant species, like aspen, strawberries, and ferns, reproduce clonally in addition to producing seeds or spores. Once established, clones often break apart and are no longer physically connected. How would you distinguish one individual or genotype from another and characterize fitness for a clonal species?

Collecting seeds directly from individuals ensures that researchers know the identity of the seed parent (i.e., the parent that contributed the egg cells to each embryo). However, unless a species exclusively self-fertilizes, the identity of the pollen parent (i.e., the parent that contributed sperm via pollen) is typically unknown without genetic data. The challenge of ascribing paternity arises because pollen grains are dispersed away from individual

plants by various vectors, including water, wind, and animals, and are nearly impossible to monitor. Approximately 91% of flowering plants are cosexual (Villarreal and Renner 2013; Renner 2014), with individuals producing both seeds and pollen. For these species, we can directly measure the reproductive success of an individual as a seed parent, but we cannot directly measure success as a pollen parent without genetic tools to identify the pollen parents of seeds from surrounding individuals, generating an incomplete estimate of total fitness. Furthermore, all individual plants have access to limited resources, and studies that do not account for success as a pollen parent may be biased if investing resources in one sexual function comes at the cost of reduced resources for the other sexual function (a trade-off; see "Glossary"; e.g., Hodgins and Barrett 2008). There are similar challenges when estimating fitness for individuals that only produce pollen (as in dioecious species, which make up ~6% of flowering plants; Villarreal and Renner 2013; Renner 2014), and the difficulty is magnified for species that do not produce seeds (e.g., mosses and ferns) in which both egg and sperm are dispersed away from the parent individuals. Due to these logistical constraints, very few studies have quantified total fitness in plants (but for examples see Agrawal et al. 1999; Kulbaba and Shaw 2021).

Fitness often depends on both the environment in which a lineage evolved and the environment in which a genotype grows. Both biotic and abiotic conditions can change dramatically across space, and plants often evolve local adaptation (see "Glossary," available online) to different habitats (Leimu and Fischer 2008; Hereford 2009; Wadgyman et al. 2022). For example, the grass *Poa hiemata* grows in alpine habitats in Australia where local populations have adapted to the elevation in which they evolved (Byars et al. 2007). That is, in reciprocal transplant experiments (see "Glossary"), Byars and colleagues (2007) found that high-elevation genotypes survived best in high-elevation sites, and low-elevation genotypes had enhanced survival in low-elevation locations. This type of home site advantage is quite common in plants, which—unlike animals—cannot readily move away from unsuitable locations. Over evolutionary time, only genotypes capable of germinating and reproducing in a given location will persist. Maladapted genotypes will perish. Thus, plant populations can evolve in response to very localized natural selection, leading to extensive within-species adaptive genetic divergence across populations. That is, populations often evolve phenotypes that enhance fitness in their local environment and incur a cost in other environments. Wadgyman et al. (2022) recently reviewed local adaptation in depth. Here, we highlight that a genotype's fitness can differ substantially across environments. For example, high-elevation *P. hiemata* genotypes can survive at rates two to four times greater in high-elevation than low-elevation sites (Byars et al. 2007). Thus, when analyzing fitness, researchers must consider both (a) the evolutionary history of a genotype and (b) the environment in which a genotype is monitored.

Fitness across the Life Cycle of an Organism

Even though it is hard to measure fitness within or across generations, scientists often estimate fitness across the full life cycle of their study organisms. For example, we might quantify the probability that a seed germinates and that a seedling survives in a given location, the rate of growth of a juvenile individual, the probability that an individual flowers and produces seeds,

or the number of seeds an individual produces throughout its lifetime (fig. 1). All of these metrics reflect components of fitness (see “Glossary”), or separate measures of survival, growth, and reproduction that cumulatively influence fitness. Ultimately, we may be interested in an integrated measurement of fitness that accounts for these various components. For instance, defining fitness as an individual’s or a genotype’s contribution to subsequent generations (Reid et al. 2019) permits us to integrate survival and reproductive success into a single estimate of fitness (fig. 2). An individual that dies before reproduction—and therefore has a fitness of 0—is easily distinguished from a highly fecund individual that produces many offspring over the course of multiple years. For some species, however, we will never be able to quantify that idealized multigenerational version of fitness. In these cases, scientists will often measure proxies of lifetime fitness (fig. 1). For instance, *Welwitschia mirabilis* is a plant species endemic to Namibia and Angola that can reproduce for centuries, with individuals living for over 600 years and cone production beginning by age 20–40 (Herre 1961; Di Salvatore et al. 2013). It would be nearly impossible to estimate lifetime fitness accurately for such a long-lived organism. Estimating lifetime fitness can be challenging in animals too. Female *Loxodonta cyclotis* (African forest elephants) do not reach reproductive maturity until age 10–23 years, can remain reproductive for decades, and can live up to 75 years (Turkalo et al. 2018), which far exceeds the duration of most typical studies in evolutionary biology or ecology. That system is in stark contrast with the *Brassica rapa* (field mustard) or *Daphnia* species (water fleas), which can each complete a full generation within 2–3 mo (Dudycha and Tessier 1999; Franke et al. 2006), allowing researchers to collect robust data on lifetime fitness in a short period of time.

How do scientists pick the fitness components they measure? Their choices often reflect knowledge of the study species’ ecology and pattern of growth, survival, and reproduction (i.e., its life history; see “Glossary”). For instance, *Dianthus pavonius* (a carnation known as peacock-eye pink) is susceptible to

Microbatryum (anther smut), which is a sterilizing disease transmitted by pollinators (Bruns et al. 2017). Infections are acquired through open flowers, suggesting that traits such as the total flower number and the duration of time that individual flowers remain open could predict fitness for this species (Bruns et al. 2019). The choice of fitness component(s) can also be dictated by sampling considerations. Some fitness components need to be measured at specific periods of the life cycle, while others could be measured at multiple points and require the scientist to make decisions about sampling timing and frequency (fig. 1). Sampling efforts might be further constrained by the experimental design of the study, as there is a trade-off between the amount of fine-scale and coarse-scale data you can take. When estimating the fitness of individuals of a specific species, would you measure multiple fitness components in a single population or a single fitness component in multiple populations? In what contexts do you imagine one approach would be favored over the other? This quandary is further complicated by the fact that failing to measure an early-life fitness component (e.g., seedling survival) and focusing only on later-life fitness components (e.g., seed production) can produce misleading impressions of patterns of natural selection (a phenomenon known as the invisible fraction; Mojica and Kelly 2010; Wadgyamar et al. 2017). Importantly, the relevant fitness components to monitor are likely to shift, as patterns of natural selection can fluctuate over time and across space.

Selection will always act to increase mean fitness. Why, then, have all species not evolved to live a long life, begin reproducing at a young age, and produce a large number of offspring every year? Would this life history strategy not best maximize fitness? Why do we see extraordinary variation in life history strategies across species when seemingly small differences in life history traits can have a tremendous influence on their reproductive potential (fig. 3A)? Given that the resources available to an organism are finite, and thus limiting, then any investment of resources into one fitness component (e.g., seed production) must come at the cost of investment in another fitness component (e.g., survival;

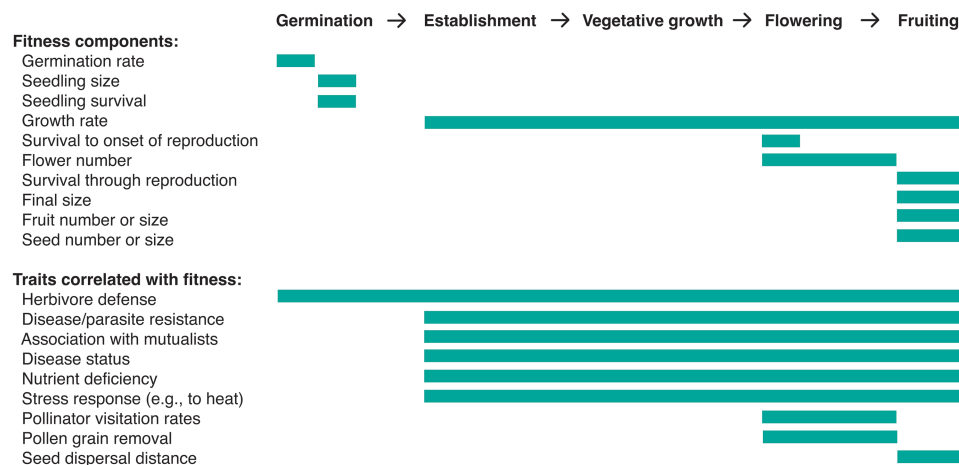


Fig. 1 Hypothetical timing of data collection for fitness components or traits correlated with fitness across the life cycle of a plant species in a field study. Some traits can be measured only during specific times of the year, while others could be measured at any point within the indicated time frame. The traits correlated with fitness are often subject to strong natural selection and should not be considered fitness components. Experiments can assess the extent of selection on these traits by quantifying the trait value and fitness on the same individuals or genotypes and then analyzing fitness as a function of trait variation.

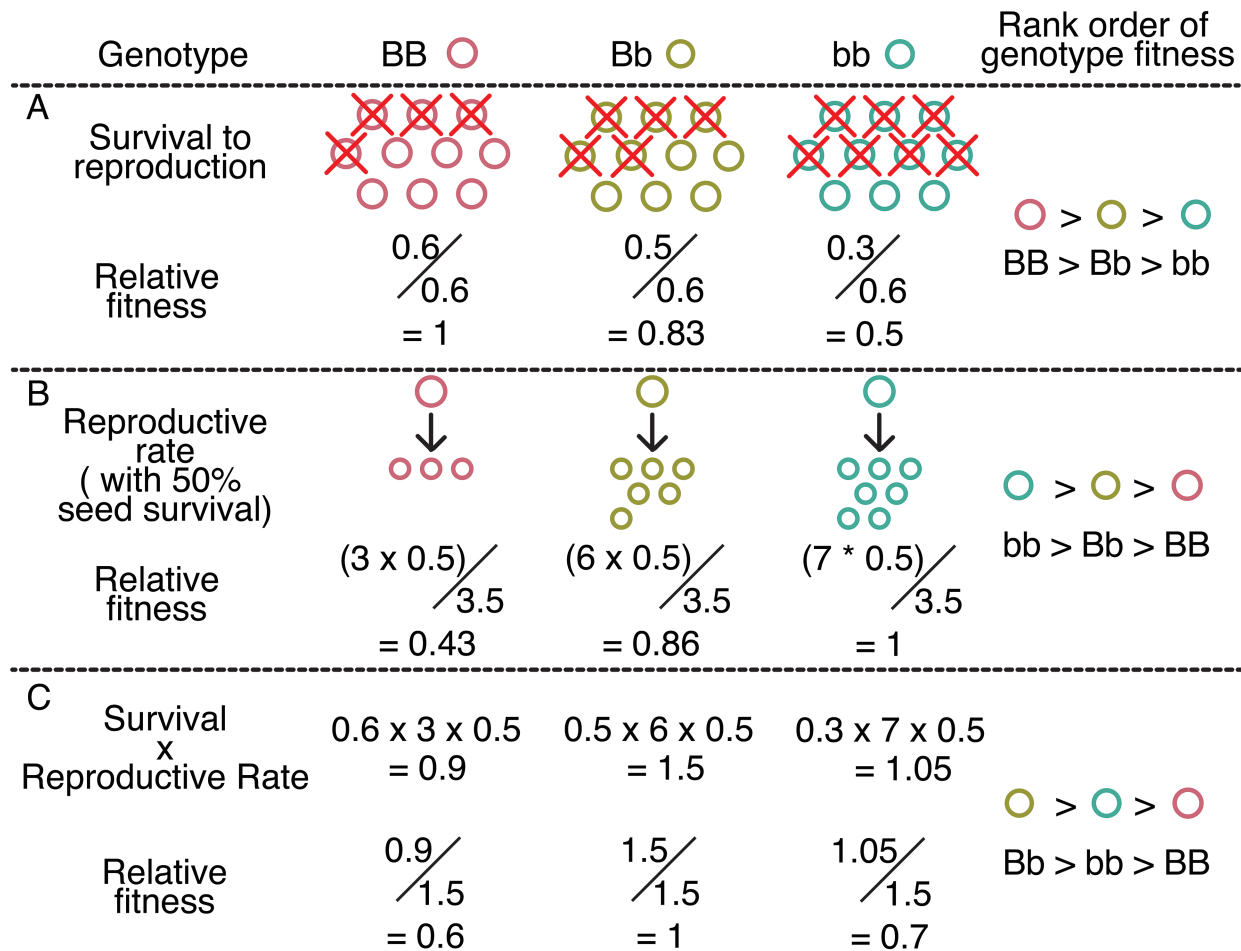


Fig. 2 Hypothetical fitness values for three genotypes measured as survival rate (A), reproductive rate (B; e.g., number of offspring, among individuals that survived, times the percent of seeds that survive), and a combined measure of survival and reproductive rate that can reflect lifetime fitness (C). In each case, absolute fitness (see “Glossary”) refers to the performance of each genotype (e.g., rate of survival, seed production, or lifetime fitness), unadjusted for the success of other genotypes. In contrast, relative fitness (see “Glossary”) is calculated by dividing each genotype’s fitness by the maximum fitness value across genotypes. Note that the rank order of genotype fitness changes depending on the fitness measure under consideration. Using the example in A, if the relative fitness of genotypes BB, Bb, and bb is 1, 0.86, and 0.71, respectively, then $s = 0.29$ (indicating that the fitness of the bb genotype is 29% lower than that of the BB genotype) and $h = 0.48$ (indicating that alleles B and b have nearly additive effects on fitness).

fig. 3B). Trade-offs among fitness components define a suite of common life history strategies that have evolved repeatedly across diverse taxa (Salguero-Gómez 2017; Friedman 2020). At one extreme, annual plants grow, reproduce, and die within one growing season and typically invest a large proportion of their resources toward reproduction (e.g., watermelon plants *Citrullus lanatus*). In contrast, perennial plants can live for decades or centuries and invest a substantial proportion of their resources into growth and defense, particularly early in life (e.g., pine trees of the genus *Pinus*). Life history strategies and the trade-offs that define them determine the way that separate fitness components contribute to total fitness and also predict fitness at the level of the population (Salguero-Gómez 2017).

Fitness at the Level of the Gene

An organism’s fitness reflects its capacity to transmit its genes to the next generation. It is easy to assume that the entire set of alleles

an organism has in its genome will be transmitted with equal success and frequency; after all, chromosomes are packaged randomly into gametes during independent assortment, giving each organism’s alleles an equal chance of being passed on. However, if the average effect of an allele across all individuals in which it is found increases the likelihood that an individual or its offspring will survive or reproduce, it will be favored by selection and may increase in frequency in the population. In contrast, if the average fitness of individuals carrying a specific allele is low, then the allele will decrease in frequency—at the extreme, if an allele is lethal, then all individuals carrying this allele will have a fitness of zero. The frequency trajectory of an allele will depend not only on its fitness effects but also on how it interacts with the environment, with other alleles at the same locus (dominance), and with alleles at other loci (epistasis) to shape fitness. Allele frequencies will also be affected by nonselective forces like genetic drift, migration, and linkage with other alleles under selection (Gillespie 1994).

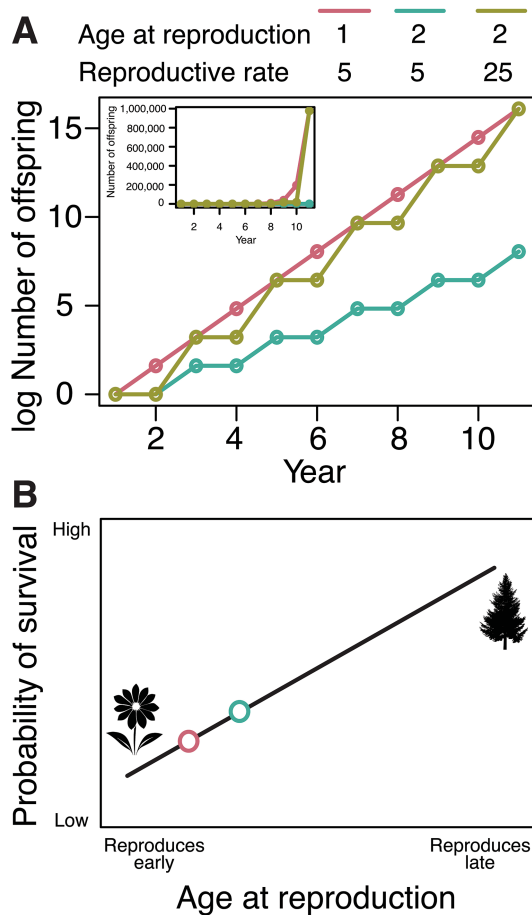


Fig. 3 A, Individuals or genotypes that reproduce earlier in life have higher reproductive potential than those that reproduce late (all else being equal). The pink line reflects the reproductive potential of a single individual or genotype that can produce five offspring at an age of 1 yr (as can all of its offspring). Ten years later, it will have produced nearly a million descendents, as seen in the inset. The teal line represents an individual or genotype with the same reproductive rate but that delays reproduction until 2 yr of age (as do all of its offspring), producing only 3125 descendents in 10 yr. The gold line demonstrates that the teal individual or genotype would have to produce 25 offspring at age 2 to compensate for the disparity in reproductive output that delayed reproduction can generate. B, Trade-off between age at reproduction and survival, showing that the high reproductive potential gained by reproducing early is associated with a higher mortality rate. The two circles along the line reflect where the two species introduced in A would fall along this continuum.

Can we make predictions about allele frequency changes based on what we know about selection? Yes! In particular, two variables, the selection coefficient (s ; see “Glossary”) and the dominance coefficient (h) can be used to predict changes in allele frequency due to selection. The selection coefficient s describes the magnitude of fitness difference between individuals with the most fit and least fit genotypes. So, for example, the most fit homozygous genotype has a fitness of 1, the least fit homozygote has a fitness of $1 - s$. The dominance coefficient, h , modulates how selection affects fitness in heterozygotes so that the heterozygote fitness is $1 - hs$ (for a worked example, see fig. 2). This model

can also account for overdominance wherein the heterozygote genotype is the most fit ($h < 0$), and underdominance, wherein the heterozygote is least fit ($h > 1$).

If the traits that influence individual fitness are associated with alleles at a single locus, it can be straightforward to estimate fitness effects and predict changes in allele frequencies over time. However, most complex traits are polygenic (see “Glossary”), which means that they are influenced by many loci with small effects and/or effects that vary across environments. If individual fitness is polygenic, learning about the fitness effects of specific alleles requires teasing apart variation at thousands or tens of thousands of sites in the genome. How can we make sense of so many selection coefficients?

There are two main strategies for estimating s when fitness is polygenic. Selection component analysis measures allele frequency differences across life stages or generations and uses these frequency differences to estimate s . This approach has been used in *Mimulus guttatus* (monkeyflowers) to show that the allele frequencies of hundreds of single nucleotide polymorphisms (SNPs; see “Glossary”) differ between individuals that successfully germinate and the subset that survive to flower, which suggests that alleles at these SNPs are under selection due to differential survival, that is, viability selection (Monnahan et al. 2015). Similarly, over 1500 SNPs had allele frequency differences between individuals that flowered and those that were successful pollen parents, suggesting that potentially these alleles are under fecundity selection (i.e., selection to produce offspring as a pollen parent). In an alternative approach, we can directly estimate associations between genotypes and survival or fecundity. These methods are similar to genome-wide association studies (GWAS), except that the trait under consideration is a fitness component. For example, in *Arabidopsis thaliana* (a widely studied model organism in plant biology), over 6000 SNPs have detectable, sometimes quite large, values of s because allele frequency correlates with fitness in at least some environments (Exposito-Alonso et al. 2019).

Why is it helpful to know how many alleles affect individual fitness? Understanding the number of alleles that affect fitness and the strengths of their effects is important for a number of basic questions in evolutionary biology (Mitchell-Olds et al. 2007). Here, we will focus on estimating the number and distribution of selection coefficients on specific SNPs to tease apart how selection can differ across environments or among populations (Figure 4). For example, *A. thaliana* alleles that were positively associated with fitness in specific common gardens were also more common in populations located near those gardens, suggesting that local adaptation had increased the frequency of alleles in environments where they improve fitness (Fournier-Level et al. 2011). Similarly, the estimate of s for many *A. thaliana* alleles differs across locations and environmental conditions, consistent with genetic trade-offs in which the alleles that increase fitness in one environment are likely to decrease it in another (Agren et al. 2013; Exposito-Alonso et al. 2019; Oakley et al. 2023). In addition, *Silene latifolia* (white campion) alleles that increase male fitness through paternity often have deleterious effects on female survival, consistent with a trade-off in fitness effects across sexes (Delph et al. 2022). In these examples, estimating selection on specific alleles broadened our understanding of the nature of trade-offs across contexts.

Estimating selection coefficients on loci across the genome can have some limitations. These studies require very large sample sizes to generate enough statistical power to make estimates

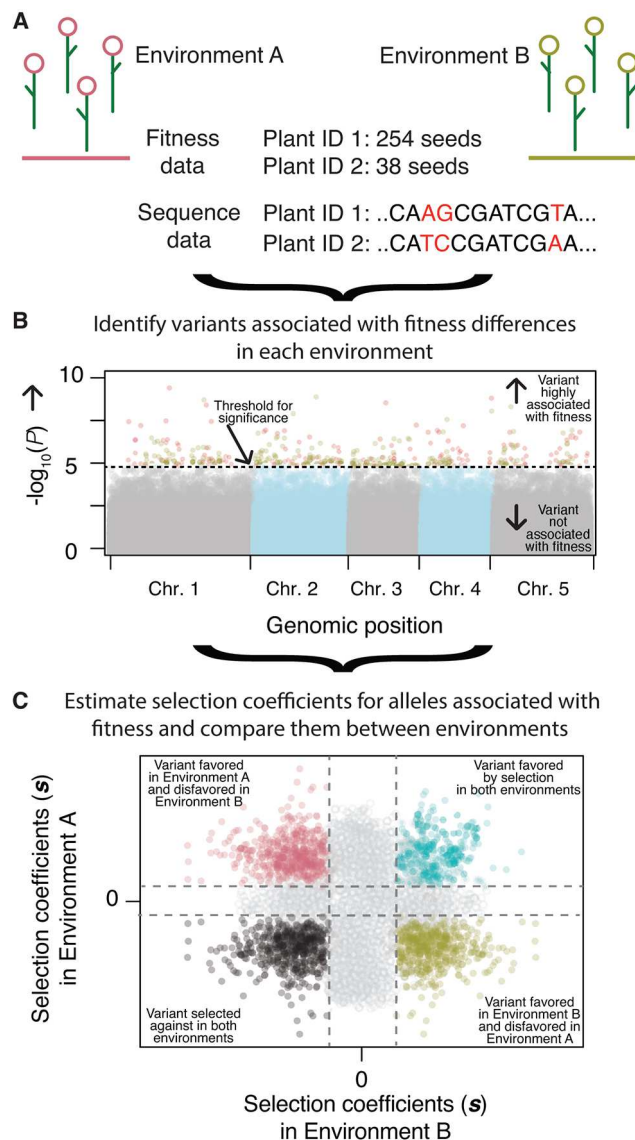


Fig. 4 An approach for identifying alleles associated with fitness in natural populations of a single species that occur in different environments. **A**, Fitness estimates and sequence data are acquired for plant populations experiencing two different environments. **B**, The association between genotype at each locus and fitness estimates is examined, shown here in a Manhattan plot. Statistically significant associations are those that are strong enough to surpass the significance threshold. **C**, Selection coefficients (s) for all variants in each environment are plotted against each other to investigate trade-offs in fitness across environments.

of s . Even so, there will always be some error in estimating s , and statistical analyses are often more prone to overestimate than underestimate s , biasing our perception of selection (Josephs et al. 2017; Kelly 2021).

Fitness of a Population of Individuals

So far we have discussed the fitness of individual organisms and alleles at genes across the genome, but biologists are often

interested in whole populations, which are groups of individuals of a given species that grow together in the same place. The average fitness across all individuals of a population is equivalent to that population's growth rate. The population growth rate, λ (see "Glossary"), is simply the number of individuals in a population after 1 yr (N_{t+1}) divided by the starting number of individuals (N_t); if this ratio is exactly 1, then that means the population is stable over time. Population growth rates >1 indicate that the number of individuals is increasing over time, and population growth rates <1 indicate that the population is shrinking. Biologists frequently want to know whether a given population is stable, growing in size, or declining in size over time. For example, it is important to quantify how quickly a population of an invasive weed is growing in order to predict its rate of spread or whether a population of a threatened species is stable or declining in order to enact conservation measures. But what determines a population's growth rate?

Populations are made up of many individuals differing in age, size, fitness, and (only in some plant species) sex, and their aggregate fitness is what determines the growth rate of the population as a whole. As we discussed above, an individual's fitness involves many aspects of success across its life cycle, from seed germination to early survival and growth and, ultimately, the number and quality of offspring it produces. These fitness components, aggregated across many individuals, make up the vital rates of a population. Vital rates (see "Glossary") are the average life history traits, such as average seed germination or average survival, that determine the overall number of deaths and births occurring within a population over a given time period (and therefore the population growth rate). Demographic models (see "Glossary"), such as matrix models, combine vital rates for the entire life cycle of an organism to calculate an overall population growth rate without needing to directly count changes in the number of individuals over time (fig. 5). In this way, information on individual fitness is used to understand the health of the population as a whole.

Demographic models can also tell us which vital rates are most important for population growth, by comparing how a small change in one vital rate would change the population growth rate (also called a vital rate's sensitivity). Sensitivity analysis has been used to uncover fundamental life history principles. For example, species that can reproduce multiple times over longer life spans, such as many trees, are usually more sensitive to changes in survival than to changes in reproduction (Silvertown et al. 1993). This suggests that viability selection may be stronger than fecundity or sexual selection in species with this type of life history (Crone 2001). Sensitivity analysis is also useful for identifying vital rates that can be targeted to either increase or decrease the growth rates of populations under management. For example, population growth of a rare wetland annual, *Aeschynomene virginica*, is most sensitive to increases in seedling establishment, suggesting that conservation efforts should focus on creating the open habitats that promote seed germination and seedling survival (Griffith and Forseth 2005). On the other hand, population growth of invasive ragwort (*Jacobaea vulgaris*) is most sensitive to changes in adult maturation and fecundity. Management strategies that increase competition with native plant species along with biocontrol agents like the flea beetle were highly effective at reducing these

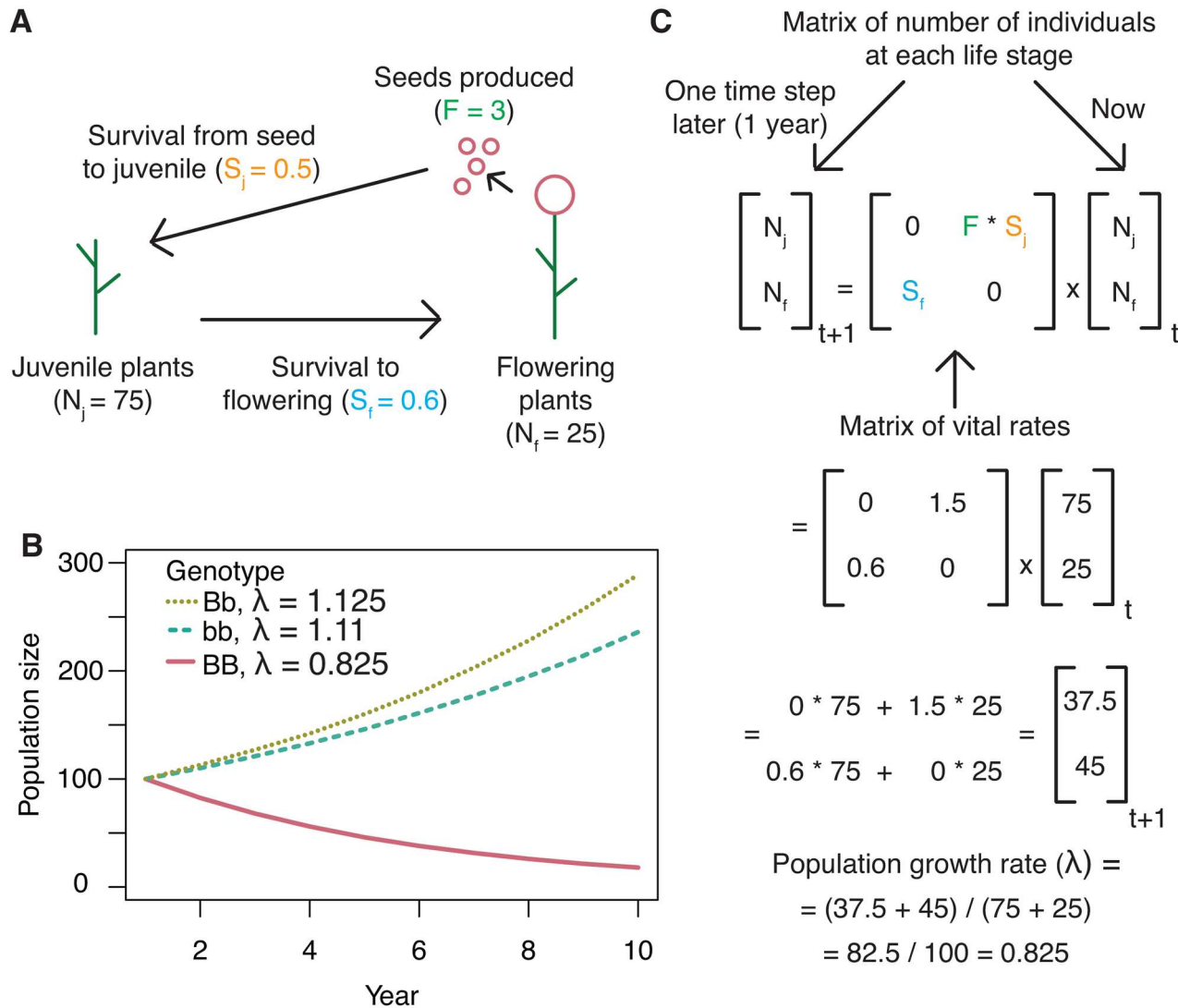


Fig. 5 A, Life cycle diagram for a hypothetical biennial species that germinates and grows vegetatively in one year and flowers and produces seeds in a second year. Biennial species take 2 yr to complete their life cycles. Repeated surveys of the population allow researchers to estimate the number of juvenile plants (N_j) and flowering plants (N_f) at each time point and to model three vital rates: the survival rate for seeds transitioning into juveniles (S_j), the survival rate for juvenile plants transitioning into flowering plants (S_f), and the number of seeds produced by flowering plants (F). B, The population growth rates predicted for the three genotypes are depicted in figure 2, assuming that all genotypes have 25 juveniles and 75 flowering plants in year 1 and that all three vital rates stay the same over time. C, Calculation of the population growth rate for genotype BB using a Leslie matrix model. This approach estimates the number of individuals at each life stage in the population at time $t + 1$ by multiplying stage-specific survival and reproductive rates by the number of individuals at each life stage in year t . That is, the future number of juvenile plants depends on the current number of adults, the rate of seed production (F), and the survival of seeds to the juvenile stage (S_j). The future number of adult plants depends on the current number of juveniles and the rate of survival of juveniles (S_f). The population growth rate (λ) is estimated as the projected population size at time $t + 1$ divided by the population size at time t . Given that $\lambda < 1$ for the BB genotype, we can infer that its population is declining.

vital rates and causing invasive populations to decline (Dauer et al. 2012).

Fitness as the Bridge between Ecology and Evolution

Fitness bridges the fields of evolutionary biology and ecology by examining the demography of populations and the degree to which populations are adapted to their local environments

(Dobzhansky 1968; Endler 1986). Fitness is a key concept in ecological theories about coexistence (Chesson 2000), competition (Lotka 1925; Volterra 1926; MacArthur 1972; Tilman 1980; Tilman 1982), and ecological niches (Hutchinson 1957). For instance, a key definition of the ecological niche is the range of environments across which populations are stable or growing (i.e., have a mean fitness greater than or equal to 1; Hutchinson 1957). Ecologists and conservation biologists often focus on vital rates

and absolute fitness (Brady et al. 2019; fig. 2) to ask questions such as: Are vulnerable populations at risk of extinction (i.e., $\lambda < 1$)? Can management efforts succeed in restricting the spread of invasive species? In contrast, evolutionary biologists tend to focus on relative fitness (fig. 2), where the fitness of a given allele, individual, genotype, or population is compared to some reference level (such as the maximum or mean fitness across alleles, genotypes, or individuals in a population) to address questions such as, How does natural selection operate on phenotypes in a given environment? Are populations adapted to their local environments? A complication from these contrasting perspectives of absolute and relative fitness is that the two metrics can yield different conclusions about the same question. For instance, a population could be maladapted to its local environment in the absolute sense if its growth rate is less than 1. In contrast, if the test for local adaptation is based on relative fitness (a local population's growth rate relative to the growth rates of nonlocal populations), then a higher growth rate of that same population in its local environment compared to nonlocal populations would lead to the conclusion of local adaptation (Brady et al. 2019). For this reason, evolutionary ecologists should report both absolute and relative fitness measures, since they complement one another and each tells us something unique (Brady et al. 2019).

Both ecologists and evolutionary biologists seek to understand and predict a population's ability to persist in the face of environmental change and recover from environmental degradation. Integrating fitness concepts across biological scales can yield novel theoretical insights and applications because the fitness dynamics of alleles, individuals, and/or populations are often associated (Reed 2005; Leimu et al. 2006). The complementarity of these approaches can perhaps best be illustrated by conservation management practices that merge conservation genetics with population ecology. When an environmental stress such as drought causes a population to decline, the population could eventually recover if the frequency of an allele that confers a fitness advantage under drought increases. This process is known as evolutionary rescue (see "Glossary"; Gomulkiewicz and Holt 1995). Evolutionary rescue is most likely to occur when populations are large and have sufficient genetic variation to adapt to environmental change. Conservation practitioners can develop management plans that enhance the likelihood of evolutionary rescue in small populations or declining populations that contain reduced genetic variation, suffer

from inbreeding depression, and/or experience reduced evolutionary potential as a result of genetic drift. Evolutionary rescue theory unites the evolutionary process of adaptation and the ecological process of demography across biological scales, but there are few empirical studies in natural plant and animal populations (Carlson et al. 2014).

Conclusions

Fundamental theory and applications in ecology and evolutionary biology rely heavily on the concept of fitness at multiple levels of organization, including genes, genotypes, individuals, and populations. Nevertheless, defining and quantifying fitness remains challenging. Biologists tend to choose one or a few measurable phenotypes as proxies for fitness, but such fitness components may poorly reflect long-term eco-evolutionary dynamics. To select appropriate fitness measures, researchers should carefully consider information on a species' life history, a population's demographic composition, and the potential for trade-offs among fitness components. Evolutionary biologists often rely on relative fitness to infer patterns of natural selection and adaptation, while ecologists tend to focus on absolute fitness to determine whether populations are stable, growing, or declining. Thus, fitness is a unifying concept in biology because it bridges evolutionary processes such as adaptation and natural selection with ecological processes such as demography.

Acknowledgments

We are grateful to Caroline Beuscher, Emma Chandler, Clayton Hale, Emma Horne, Riley Thoen, Elizabeth Thomas, and Anna Wyngaarden for providing helpful comments on the manuscript. This project was funded by the National Science Foundation (IOS-2220927 to J. Anderson and M. DeMarche, DEB-1553408 to J. Anderson, DEB-2131815 and IOS-2220928 to S. Sheth, DEB-1753954 to M. DeMarche, IOS-2220930 to S. M. Wadgyrmar, IOS-2220929 to E. Josephs), National Institutes of Health (R35-GM142829 to E. Josephs), and USDA National Institute of Food and Agriculture Hatch (project 7002993 to S. Sheth). All authors contributed to the conception and writing of the Primer, with S. M. Wadgyrmar playing a lead role in organization and figure development.

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