

Understanding Maladaptation by Uniting Ecological and Evolutionary Perspectives*

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ABSTRACT: Evolutionary biologists have long trained their sights on adaptation, focusing on the power of natural selection to produce relative fitness advantages while often ignoring changes in absolute fitness. Ecologists generally have taken a different tack, focusing on changes in abundance and ranges that reflect absolute fitness while often ignoring relative fitness. Uniting these perspectives, we articulate various causes

of relative and absolute maladaptation and review numerous examples of their occurrence. This review indicates that maladaptation is reasonably common from both perspectives, yet often in contrasting ways. That is, maladaptation can appear strong from a relative fitness perspective, yet populations can be growing in abundance. Conversely, resident individuals can appear locally adapted (relative to nonresident individuals) yet be declining in abundance. Understanding and interpreting these disconnects between relative and absolute maladaptation, as well as the cases of agreement, is increasingly critical in the face of accelerating human-mediated environmental change. We therefore present a framework for studying maladaptation, focusing in particular on the relationship between absolute and relative fitness, thereby drawing together evolutionary and ecological perspectives. The unification of these ecological and evolutionary perspectives has the potential to bring together previously disjunct research areas while addressing key conceptual issues and specific practical problems.

Keywords: adaptation, fitness, global change, maladaptation.

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A Special Feature on Maladaptation

As the introductory article for this Special Feature on Maladaptation, we present a framework for understanding processes and patterns of maladaptation. We synthesize current

knowledge and unify ecological and evolutionary perspectives on maladaptation, focusing on a joint consideration of absolute and relative fitness. We hope that our synthesis and the articles that follow in this special feature catalyze productive study at a time when it is perhaps most crucial—in the face of rapid global change.

Why Do We Need a Focused Treatment of Maladaptation?

Evolutionary biologists tend to emphasize the power of natural selection in generating adaptation to local environments (Darwin 1859; Williams 1966; Endler 1986; Schluter 2000b; Bell 2008; Hendry 2016). Justification for this emphasis comes from multiple lines of empirical evidence. First, reciprocal transplant studies show that local adaptation is more common than not (Leimu and Fischer 2008; Hereford 2009). Second, estimates of selection in nature show that this force is typically weak, implying that most phenotypes in most populations are reasonably close to local adaptive peaks (Estes and Arnold 2007; Haller and Hendry 2014; Hendry 2017). Third, natural populations possess reasonable levels of additive genetic variance in traits (Mousseau and Roff 1987; Houle 1998; Hansen 2006) and fitness (Burt 1995; Hendry et al. 2018), implying the potential for adaptation to be rapid and effective. Fourth, many populations show rapid—and apparently adaptive—phenotypic responses to many forms of environmental change (Hendry and Kinnison 1999; Reznick and Ghalambor 2001; Hendry et al. 2008).

By contrast, ecologists and conservation biologists often emphasize the imperfection of adaptation (i.e., *maladaptation*) by focusing on the apparent unsuitability of organisms for local environments, especially in the modern world (Soule 1985; Primack 2006; Sodhi and Ehrlich 2010). This emphasis stems from innumerable cases of declining populations, contracting ranges, and local or global extinctions or extirpations (Carpenter et al. 2008; Urban et al. 2012; Dirzo et al. 2014; Ceballos et al. 2017; Ripple et al. 2017; Wolf and Ripple 2017), all occurring at a pace far greater than the background rate (Pimm et al. 2014; Ceballos et al. 2015).

How are we to reconcile these starkly contrasting evolutionary versus ecological perceptions of the prevalence and strength of adaptation versus maladaptation across the scope of life on Earth? We suggest that the disagreement mainly arises from the two groups using different fitness metrics when considering (mal)adaptation. Evolutionary biologists tend to focus on relative fitness: that is, an individual or population is maladapted when it has lower fitness than some other relevant reference individual or population (Fisher 1930; Wright 1931; Haldane 1932; table 1). This classic evolutionary view focuses on changing genotype frequencies or trait values but typically assumes constant population sizes (Wallace 1975;

Whitlock 2002; Bell 2008; Reznick 2015). Ecologists, by contrast, focus more on absolute fitness: that is, a growing or stable population is perceived to be well adapted to present conditions, whereas a population in decline suggests maladaptation. This classic ecological view focuses on changing population size but typically ignores changes in genotype frequencies or trait values (Elton and Nicholson 1942; Birch 1948; Hutchinson 1959; Levins 1969; MacArthur 1972; Anderson and May 1978).

Recognition of these contrasting emphases on absolute versus relative fitness is not new. For instance, Dobzhansky (1968a, 1968b) wrestled with applying these distinctions, as did Endler (1986), and attempts at reconciliation have been made (e.g., Holt and Gomulkiewicz 1997; Hendry and Gonzalez 2008). Moreover, explicit attempts to conceptually and quantitatively integrate the two perspectives are emerging. For instance, the Price equation (Price 1970) has been modified and expanded to link evolutionary and ecological effects on absolute and relative fitness (e.g., Coulson and Tuljapukar 2008; Ozgul et al. 2009; Lion 2018; Ellner et al. 2019; Govaert et al. 2019). A related body of work integrates evolutionary and population dynamics through the lens of “evolutionary rescue” (Gonzalez and Bell 2013; Gonzalez et al. 2013; Carlson et al. 2014). Despite such progress, many evolutionary biologists and ecologists remain unfamiliar with the contrast between these views of adaptation and maladaptation and how they are interrelated.

Our goal in the present article is to bridge the ecological and evolutionary perspectives on maladaptation. We start by contrasting disparate definitions. We do not advocate a single unified definition or metric because, as noted above, different fields of biology already have well-established divergent traditions and perspectives. These differences have value, reflecting different research priorities. For instance, the first concern of conservation practitioners is often whether population absolute mean fitness is sufficient to prevent population declines regardless of trait optimization that might preoccupy an evolutionary biologist.

We then summarize existing evidence concerning the prevalence and strength of maladaptation in nature. We emphasize how inference depends on one’s choice of metrics concerning fitness (absolute vs. relative), phenomenon (process vs. state), and assessment (qualitative vs. quantitative). As a result, populations can appear maladapted from an evolutionary perspective (e.g., local types do not have higher fitness than immigrant types) yet nevertheless appear well adapted from a demographic perspective (e.g., they are widespread, abundant, and not declining; table 2). On the other hand, populations can appear locally adapted from an evolutionary perspective yet be declining in abundance (e.g., app. A, sec. A1; apps. A, B are available online). We conclude by outlining the key processes that can give rise to—and maintain—maladaptation from these different perspectives.

Table 1: Various forms of genetic load interpreted in the context of a framework for considering maladaptation

Type of genetic load	Key reference(s)	Description	Relationship to maladaptation framework
Genetic load (encompasses all types of load specified below)	Haldane 1937; Muller 1950; Crow 1970; Wallace 1970	Typically formulated as $(W_{\max} - \bar{W})/\bar{W}_{\max}$ and often thought of as “substitutional” load, which indicates that W_{\max} occurs due to segregating genotypes already present in population. Contrasts with lag load below.	All forms of genetic load indicate relative maladaptation and are ambiguous with regard to absolute maladaptation. In figure 1, genetic load would be proportional to the distance on the Y-axis between the local optimum and mean population fitness, scaled by the former.
Lag load	Smith 1976; Burger and Lynch 1995; Chevin et al. 2017	Typically $(\bar{W} - \bar{W})/\bar{W}$. Similar to genetic load, but \bar{W} refers to most fit genotype based on potential mutations not yet present. It is often used to infer potential rates of evolution in a population waiting for optimal mutations. Also refers to population decline following selection, with trait values lagging behind shifting optimum.	In figure 1, lag load would be proportional to the distance on the Y-axis between the global optimum and mean population fitness, scaled by the former. A likely cause of relative and absolute maladaptation in many contemporary studies of climate change (table 3).
Segregation load (or balanced load)	Kimura and Crow 1964; Crow 1970; Haag and Roze 2007	Segregation of deleterious recessive alleles into homozygotes, occurring in some but not all individuals in the population.	Likely a common source of relative and absolute maladaptation in wild populations, especially in the case of heterozygote advantages.
Drift load	Lynch et al. 1995; Whitlock et al. 2000; Willi et al. 2013	Segregating load that has become fixed in the population due to drift.	A potential source of relative and absolute maladaptation in small populations.
Migration load	García-Ramos and Kirkpatrick 1997; Bolnick and Nosil 2007	Inflow of maladapted alleles from populations not adapted to the local environment.	A likely cause of maladaptation in many classic and contemporary (table 3) instances of relative maladaptation.
Mutation load	Muller 1950; Kimura et al. 1963; Lynch and Gabriel 1990; Agrawal and Whitlock 2012	Due to ongoing inputs of deleterious mutations.	Background mutation or mutagenic exposure resulting in deleterious alleles. Invoked as a potential source of maladaptation in several studies of adaptation to pollution (table 3).
Recombination load	Charlesworth and Barton 1996; Haag and Roze 2007	Genetic recombination resulting in the disassociation of favorable combinations of loci. Loss of linkage disequilibrium (across loci) favored by selection.	Presumably a common source of relative and absolute maladaptation, but also (like mutation or migration) a likely contributor to future adaptation.
Meiotic drive load (or selfish chromosomal transmission)	Sandler and Novitski 1957; Hiraizumi 1964; Zimmering et al. 1970; Lindholm et al. 2016	Biased segregation of alleles during, or shortly after, meiosis that results in a distribution of alleles in gametes that does not correspond to frequencies expected by random segregation. Maladaptation can evolve because selection favors “driven” alleles that produce phenotypes with lower fitness.	Not well described in wild populations but theoretically capable of causing both relative and absolute maladaptation.
Nonlocal load	Mee and Yeaman 2019	Neutral mutations are deleterious in nonlocal environments, causing “nonlocal maladaptation.”	Nonlocal maladaptation (i.e., of imported genotypes) can falsely indicate local adaptation via selection rather than via conditionally maladaptive drift of the imported reference population.

Note: Generically, genetic load is a relative measure of fitness disadvantage in a population (Crow 1970), with the point of reference and source of load varying among different versions of load. Our framework deviates from the literature on load, which are all evolutionary, whereas we see the state of maladaptation as a broader phenomenon that can result from evolutionary environmental change.

Table 2: Examples of relative maladaptation without apparent negative population dynamic consequences

System	Relative perspective	Absolute observation	Hypothesized explanation	Key reference(s)
Trinidadian guppies	Guppies from oil polluted environments show no evidence of adaptation to oil pollution in laboratory experiments. They are maladapted in a home-versus-away comparison.	Guppies are extremely abundant in oil-polluted environments, perhaps more so than in many pristine environments.	Even though guppies cannot adapt (at least not strongly) to oil pollution, their competitors/predators/parasites have an even harder time persisting in oil-polluted environments. Hence, biotic “enemy release” compensates for lack of abiotic adaptation.	Rolshausen et al. 2015
Trinidadian guppies	When guppies from highly parasitized populations are introduced into parasite-free environments, they rapidly evolve increased parasite resistance.	The introduced guppies showed rapid increases in population size following the experimental introduction.	Rapid adaptation by the introduced guppies to other environmental changes (e.g., predators and productivity) had the pleiotropic effect of causing maladaptation with respect to parasite resistance. Adaptation to those other environmental changes was presumably more important than the resulting correlated maladaptation to changes in parasites.	Dargent et al. 2013, 2016
Roadside frogs	Wood frogs exposed to high-salt environments beside roads perform poorly in all environments, whether salty or not.	Wood frogs are very abundant in roadside ponds, perhaps more so than in many woodland ponds away from roads.	Populations fail to evolve higher fitness in roadside ponds due to persistent mutation, negative transgenerational plasticity, or assortative migration (with roadside ponds attracting less fit individuals). Alternatively, incomplete fitness measures obscure local adaptation.	Brady 2013, 2017
<i>Daphnia</i> in metal-polluted lakes	Resurrection experiments show that <i>Daphnia</i> evolved decreasing metal tolerance during the period of increasing metal pollution.	<i>Daphnia</i> persisted in the lakes through the period of heavy metal pollution.	Heavy metal exposure might have caused overall genetic damage that hampered adaptation. Alternatively, trade-offs exist between the evolution of contaminant tolerance and other traits mediating fitness.	Rogalski 2017
New populations of barnacle geese	Despite strong selection for increased body size, average body size actually decreased.	Population size increased dramatically during this period.	The environmental (plastic) effects of increasing competition for food, which reduces individual growth rates, more than offset any evolutionary tendency for increasing body size.	Larsson et al. 1988
Local maladaptation in a monkeyflower	Local populations had lower fitness than transplants.	Local populations are not in decline.	Rapid climate change experienced by the local population is similar to transplant climate, and the local population is in lag behind a new optimum.	Kooyers et al. 2019

Note: These examples highlight instances of an apparent disconnect between the relative and absolute perspectives of fitness.

Definitions and Frames of Reference

"I Do Not Think It Means What You Think It Means"
(Inigo Montoya, *The Princess Bride*)

Evolutionary biologists use the terms "adaptation" and "maladaptation" in diverse ways (Crespi 2000). For instance, adaptation can refer to the existence of a trait necessary for survival in a particular habitat (e.g., gills are an adaptation to water), the process of adaptive evolutionary change (e.g., adaptation in response to natural selection), or the state of having relatively high fitness (e.g., residents have higher fitness than immigrants). Maladaptation then reflects the flip side: the absence of a necessary trait, the process of declining fitness, or a state of having relatively low fitness. Importantly, the state of maladaptation can arise from several maladaptation processes (e.g., evolution, environmental change), and the process of adaptation does not necessarily imply a state of adaptation. So rather than promote

a single definition of maladaptation, we embrace the idea that the most appropriate definition in a given instance is context dependent and depends on the goals of the researcher (for additional discussion, see app. A, sec. A2). For this reason, researchers must clearly state their operational definition, what is being measured, what processes are in play, and the relevant temporal and spatial scales (fig. 1; box 1).

Frame of Reference: Absolute or Relative Fitness?

The following discussion is based closely on Endler (1986), who himself drew on writing by Dobzhansky (1968a, 1968b). Evolution and ecology are fundamentally linked through the concept of population mean absolute fitness (\bar{W} ; Dobzhansky 1968a, 1968b; Endler 1986). With discrete non-overlapping generations, this quantity can be the per-generation per-adult mean number of zygotes that survive

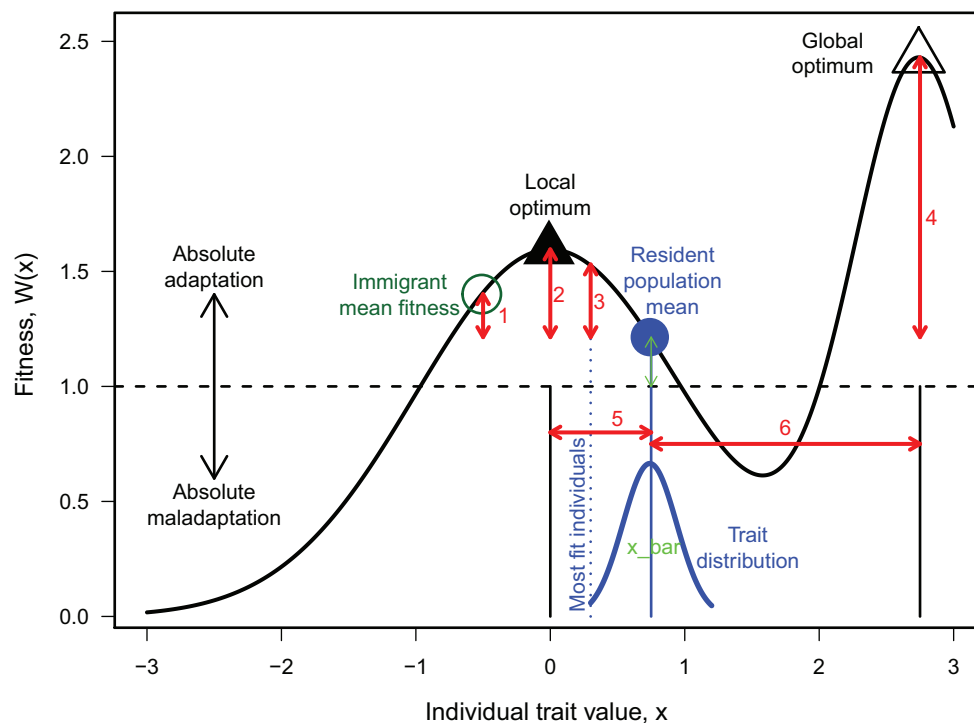


Figure 1: Fitness landscape (black curve) relating individual absolute fitness (W) to individual phenotypic trait value, x . The landscape has two optima: a local optimum (filled triangle) and a global optimum (open triangle). A focal resident population is shown, with its approximate mean fitness indicated as a filled blue circle and its trait distribution indicated by a blue curve below that circle. When judging the resident population's extent of (mal)adaptation, four fitness comparisons (vertical red arrows) and two trait comparisons (horizontal red arrows) are possible (see also Hendry and Gonzalez 2008). For absolute fitness (mal)adaptation, mean resident fitness is compared with a threshold mean fitness value of 1.0 that corresponds to replacement rate ($W \geq 1$: absolute adaptation; $W < 1$: absolute maladaptation). For relative fitness (mal)adaptation, mean resident fitness can be compared along the Y-axis to the mean fitness of (1) another population (open green circle), (2) the local optimum (filled black triangle), (3) the most fit resident phenotype in the resident population (vertical blue dotted line), or (4) the global optimum (open black triangle). For trait-based measures of (mal)adaptation, the same comparisons can be made but for mean trait values along the X-axis. This landscape is conceived as a single environment; different environments would yield different landscapes.

Box 1: Terms associated with maladaptation

Term	Definition
Maladaptation	1. State. Can refer to an individual or population with fitness less than replacement ($W < 1$; see absolute maladaptation) or less than some comparative fitness value ($w < 1$; see relative maladaptation). 2. State. Can refer to a particular trait known to cause maladaptation as defined above. 3. Process. The process of declining fitness of a population through time. Can be measured in absolute or relative terms.
Absolute maladaptation	Absolute fitness (W) of a population or individual with fitness less than replacement; thus, $W < 1$.
Relative maladaptation	Relative fitness (w) disadvantage of a population or individual. Relative fitness is measured as the absolute fitness of some focal entity divided by the absolute fitness of a comparative entity (e.g., $w_{\text{Resident}} = W_{\text{Resident}}/W_{\text{Immigrant}}$). Thus, $w < 1$.
Maladaptive	A term that can be used to describe a particular genotype or trait causing absolute or relative maladaptation (e.g., maladaptive performance, maladaptive genes, maladaptive traits).
Maladapting	A population in the process of declining fitness. For example, a population encountering environmental change and experiencing both relative and absolute fitness declines can be said to be “maladapting.”
Apparent maladaptation	Evidence for maladaptation when a population is in reality adapted (thus, a population appears to be maladapted when in fact it is adapted). This can occur through misdiagnosis (e.g., if inaccurate fitness proxies are used) or if temporal scale is insufficient. In the latter, transient dynamics of true maladaptation could be considered apparent if on average the population is, over time, adapted (see fig. B1).
Putative maladaptation	Can be used to describe plausible but inconclusive evidence for maladaptation (Crespi 2000), for instance, in nonmodel systems where fitness is measured incompletely. Thus, a reciprocal transplant showing revealing low resident compared with immigrant reproductive success but lacking data on survival to adulthood could be described as putative relative maladaptation.

to reproduce (Arnold and Wade 1984; Hendry et al. 2018). With continuous time dynamics, a closed population growing steadily at per capita rate $r = dN/N dt$ will have a mean fitness that is approximated by equation (1).

$$\bar{W} = e^{\left(\frac{1}{N} \frac{dN}{dt}\right)} \quad (1)$$

In this simple scenario, population mean absolute fitness is approximated as the population's per capita growth rate (Crow and Kimura 1970; Saccheri and Hanski 2006; Kinnison and Hairston 2007; Orr 2009; Wagner 2010), which has been equated with the level of adaptation (Sober 1984; Endler 1986). For a population at equilibrium ($r = 0$), each individual on average replaces itself with one zygote that survives to reproduce and, hence, $\bar{W} = 1$. This threshold thus serves as a qualitative absolute standard for (mal)adaptation: that is, a stable or growing population is adapted to present conditions ($r \geq 0$; $\bar{W} \geq 1$), whereas a declining population is maladapted to present conditions ($r < 0$; $\bar{W} < 1$). How far \bar{W} is above or below 1.0 then serves as a quantitative measure of (mal)adaptation. This sense of absolute maladaptation is the one typically invoked by ecologists (whether explicitly or implicitly) when they report negative rates of population growth (Ceballos et al. 2017;

Nowakowski et al. 2018). Of course, in empirical practice, population growth can have a more complex relationship with mean fitness than what we have just presented.

As one example of the complexity, empiricists rarely measure the above-described quantities but instead collect data on reproductive rates or changing population sizes over some period of time that can be shorter than a generation or can span multiple generations, which necessitates approaches tailored to the relevant timescale. For instance, when population growth is compounded over continuous time with variation in population mean fitness, the geometric mean (of the discrete time population means) rather than the arithmetic mean is the better measure of mean fitness (Charlesworth 1994), as often applied in analyses of bet hedging (e.g., Simons 2009). Timescale also can have a large effect on inferences for populations with cyclic changes in density (Sinervo et al. 2000). When studied over short timescales, maladaptation might be inferred when growth rates are negative, and subsequent adaptation then might be inferred when growth rates are positive. When cyclic changes are studied over longer timescales, however, adaptation might be inferred because the population persists in a stable limit cycle (Hassell et al. 1976; Kendall et al. 1999). Each inference is correct within the scope of the timescale

examined, or—more to the point—they mainly reflect different perspectives on population dynamics.

Evolutionary biologists frequently aspire to measure absolute individual fitness, ideally the number of zygotes an individual produces that themselves survive to reproduce (Arnold and Wade 1984; Endler 1986; Hendry et al. 2018). Such data are then typically used to calculate the relative fitness of a focal phenotype or genotype (Orr 2009) to thereby predict evolutionary change in allele frequency or mean trait values. Additionally, data on absolute individual fitness can be used to calculate the population's mean and variance of absolute fitness (Orr 2009; Gillespie 2010; Hendry et al. 2018). Fisher's fundamental theorem of natural selection (Fisher 1930; Price 1972; Burt 1995) states that the mean fitness should increase through time at a rate proportional to the variance in fitness, which sets an upper boundary on the opportunity for selection. Thus, absolute fitness can be estimated for individuals or for groups of individuals (e.g., genotypes), and each metric has a role to play in evolutionary or ecological theory and inference.

Typically, evolutionary biology quickly moves away from absolute fitness toward relative fitness (Endler 1986)—that is, absolute fitness divided by some standard reference (details below). Conceptually, relative fitness is more closely tied with changes in phenotype or allele frequency because the spread of an allele in a population depends on the absolute fitness of that allele *in relation to the absolute fitness of alternative alleles in the population*.

Practically, empirical fitness measures, whether absolute or relative, often are incomplete proxies of lifetime fitness that do not necessarily equate with population growth rate. A further complication is that absolute and relative fitness of a population can respond independently to selection, for instance, when the mean phenotype moves toward the local optimum but population size is stable (Wallace 1975; Wade 1985; Lenormand 2002; Whitlock 2002; for further discussion, see app. A, sec. A3).

Frame of Reference: Relative to What?

When calculating relative fitness (w_i) for a genotype or phenotype i , many possible references could be chosen for the denominator (fig. 1). A common reference in population genetics is to compare individual fitness to population mean fitness (e.g., $w_i = W_i/\bar{W}$; Lande and Arnold 1983). Hundreds of studies use this standardization to measure selection on traits in natural populations (Kingsolver et al. 2001; Siepielski et al. 2017). This reference point is also particularly useful for calculating expected changes in allele frequencies over time when i denotes an allele. Alternatively, the reference point is sometimes the most fit observed phenotype or genotype in the population: $w_i = W_i/\max(W_i)$, which ranges from 0 to 1. For instance, this standardization

was used by Thurman and Barrett (2016) to compare 3,000 estimates of genotypic selection from 79 studies.

In studies of local adaptation (e.g., reciprocal transplant experiments), two references are commonly used. First, native (resident) fitness can be compared with nonnative (immigrant) fitness in the same environment ($\bar{w}_R = \bar{W}_{\text{Resident}}/\max(\bar{W}_{\text{Resident}}, \bar{W}_{\text{Immigrant}})$). Second, a focal population's fitness in its native (home) environment can be compared with its fitness in a foreign (away) environment ($\bar{w}_H = \bar{W}_{\text{Home}}/\max(\bar{W}_{\text{Home}}, \bar{W}_{\text{Away}})$; Blanquart et al. 2013; Kawecki and Ebert 2004). Another standardization uses mean rather than maximum fitness in the denominator (e.g., $\bar{w}_R = \bar{W}_{\text{Resident}}/\text{mean}(\bar{W}_{\text{Resident}}, \bar{W}_{\text{Immigrant}})$; Hereford 2009).

Various frames of reference are also applied when inferring the fitness and adaptation of traits—as opposed to fitness itself. We discuss these trait-based approaches in appendix A, section A4, noting that caution is needed whenever fitness is inferred from trait values rather than measured directly. In principle, fitness also can be specified relative to some plausible but hypothetical traits or scenarios, which can be evaluated through modeling and/or breeding experiments (see app. A, sec. A5).

Tying It Together

Inferences about relative and absolute maladaptation will sometimes correspond to each other, such as when climate warming causes a phenotype-environment mismatch (relative maladaptation) that generates population declines (absolute maladaptation; e.g., Both et al. 2006; Pörtner and Knust 2007; Willis et al. 2008) or when a resident population both is inferior to immigrants (relative maladaptation) and has a mean fitness below 1 (absolute maladaptation; Saltonstall 2002; Pergams and Lacy 2007; Howells et al. 2012; Yampolsky et al. 2014). At other times, however, relative and absolute inferences will not correspond to each other (table 2), such as when residents in polluted environments have lower fitness than immigrants (relative maladaptation) yet the residents remain very abundant and successful (absolute adaptation; Brady 2013, 2017; Rolshausen et al. 2015; Rogalski 2017). Conversely, a declining local population (absolute maladaptation) might nevertheless maintain a relative fitness advantage in its home environment over individuals from other populations in the same environment (relative adaptation; Brady 2012; Lane et al. 2019).

Because of the complementary information gained from studying both relative and absolute fitness, we advocate reporting and interpreting results in the light of both perspectives, as contemporary studies are increasingly doing (table 3). Combining these perspectives can yield important insights, such as whether relative adaptation that lags environmental change impacts population size or community

Table 3: Recent studies of maladaptation that incorporate both relative and absolute perspectives

System	Primary cause of maladaptation	Inference regarding trait maladaptation	Inference regarding relative fitness	Inference regarding absolute fitness	Key reference(s)
Misty outlet stream stickleback	High gene flow from an adjacent lake population.	Substantial deviation of observed from expected phenotypes in the outlet.	Transplant experiments in the outlet show weak (if any) local adaptation.	Population densities in the outlet are very low.	Moore and Hendry 2009; Moore et al. 2007
<i>Timema</i> walking-sticks	High gene flow between adjacent populations on different host plants.	High frequency of maladaptive (i.e., noncryptic) morphs on each host plant.	Reciprocal transplants show strong selection against maladaptive morphs.	Higher frequencies of maladaptive morphs lead to lower population sizes.	Bolnick and Nosil 2007; Nosil 2009; Farkas et al. 2016
Dutch fly-catchers	Climate change that is advancing the dates of spring warming.	Departure dates from overwintering sites are too late to enable early egg-laying date on arrival at breeding sites.	Selection typically favors earlier spring breeding.	Where the migration versus laying date mismatch is greatest, populations are declining at the highest rate.	Both et al. 2006
Flowering plants in “Thoreau’s woods”	Climate change that is advancing the dates of spring warming.	Some species do not advance their spring flowering dates despite advancing spring temperatures.	Selection typically favors earlier spring flowering.	Species least able to advance their spring flowering dates have become extirpated.	Willis et al. 2008
Dutch great tits	Climate change that is advancing the dates of spring warming.	Climate change is increasing the mismatch between dates of egg laying and dates of peak food abundance.	Nesting survival decreases as the mismatch increases.	Populations are not declining because reduced nestling survival decreases competition among fledglings.	Reed et al. 2013
Hawaiian crickets	An invasive parasitoid is attracted to the mating signals of an (also invasive) cricket.	Loud mating calls by male crickets attract the invasive flies.	In fewer than 20 generations, 90% of population shifted to a silent “flatwing” mutation.	A massive decline in cricket abundance following invasion of the fly.	Zuk et al. 2006
Columbian ground squirrels	Increased snowfall delays snowmelt and the timing of emergence from hibernation.	Phenological trait (i.e., emergence) is delayed.	Relative fitness was indistinguishable between local and transplants squirrels. Emergence appears to be plastic.	Delayed timing of emergence causes population declines.	Lane et al. 2019

Note: The goal of this table is to highlight cases where studies from nature have considered both perspectives, regardless of the specific cause of maladaptation (e.g., gene flow vs. environmental change), regardless of whether the two perspectives yield similar interpretations, and even if the precise inferences are not yet entirely certain.

dynamics (Lane et al. 2019; McAdam et al. 2019) or whether maladaptation is persistent or context dependent (Simons 2009; T. E. Farkas, G. Montejó-Kovacevich, A. P. Beckerman, and P. Nosil, unpublished data). To generalize further, figure 2 represents the relationship between relative and absolute fitness for a resident population subject to immigration from a different environment. We plot the mean absolute fitness (\bar{W}) of residents in their native environment (\bar{W}_R) against the mean absolute fitness of immigrants from some other environment (\bar{W}_I). The diagonal blue line represents identical fitness for immigrants and residents ($\bar{W}_I = \bar{W}_R$). Below this line, residents have higher fitness than immigrants ($\bar{W}_R/\bar{W}_I > 1.0$), indicating relative adaptation of residents. Above this line, immigrants have higher fitness than residents ($\bar{W}_R/\bar{W}_I < 1.0$), indicating relative maladaptation of residents (e.g., Kooyers et al. 2019). On the same graph, absolute adaptation versus maladaptation of the focal population is indicated by the vertical black line at $\bar{W} = 1$, with maladaptation to the left ($\bar{W} < 1$). In much of the figure space, the absolute and relative perspectives correspond. That is, stable or increasing populations are

relatively well adapted, whereas declining populations are relatively maladapted. However, the two perspectives do not correspond in some areas of the figure—and we now focus on those interesting situations.

The bluish triangle in the top right quadrant corresponds to a population that is simultaneously in a state of relative maladaptation (residents have lower fitness than immigrants) and absolute adaptation (the resident population is stable or growing). As a putative real example of this situation, Japanese knotweed (an invasive plant in northeastern North America) exhibits high population growth, but within the species' invasive range resident genotypes tend to perform more poorly relative to immigrant genotypes transplanted from elsewhere in the invasive range (Van Wallendael et al. 2018). Other examples are suggested in table 2.

Conversely, the white triangle in the lower left quadrant of figure 2 corresponds to a state of simultaneous relative adaptation and absolute maladaptation. This situation can arise when, for example, severe environmental change threatens an entire array of populations without changing their

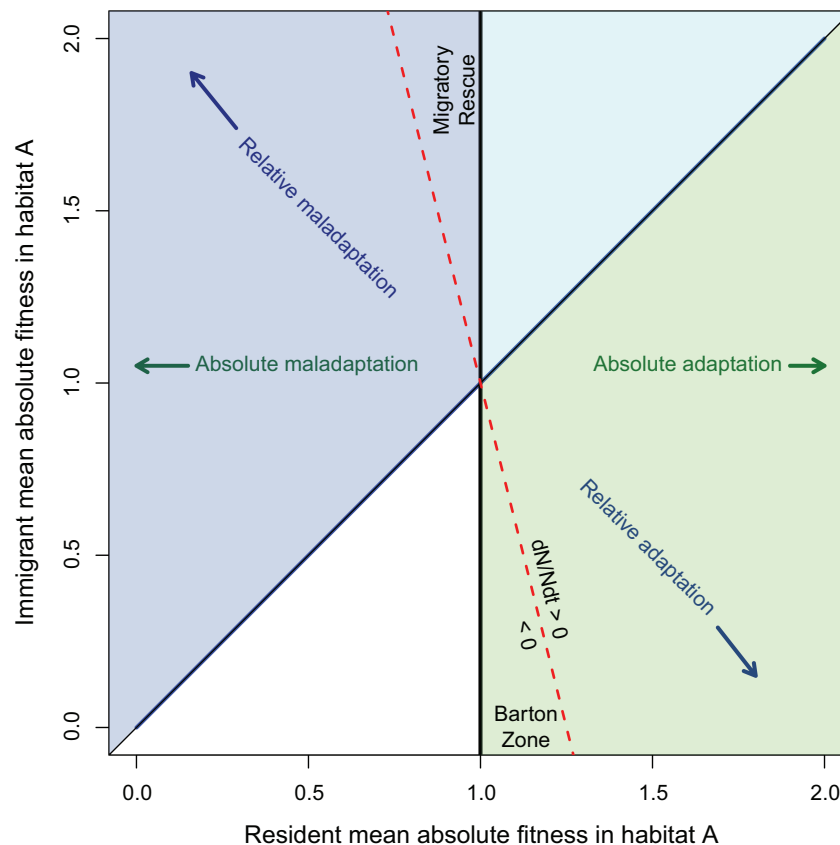


Figure 2: Depiction of the relationship between relative and absolute measures of fitness, where the reference point for relative fitness involves a comparison of native versus immigrant genotypes. Focusing on a single resident population, we can measure the mean fitness of both the residents (X-axis) and immigrants (Y-axis) and contrast the fitness of residents versus immigrants. See the text for a description.

relative degree of local adaptation. As an example, the butterfly *Boloria aquilonaris* is declining and predicted to become extinct in the Netherlands due to decreasing host plant quality. Yet this seemingly moribund population remains better adapted to its local environment than immigrants from the stable Belgian population (Turlure et al. 2013). As another example, Lane et al. (2019) report on environmental change causing declines in populations of a ground squirrel, yet the authors find equivalent responses for imported populations. Other putative examples are provided in table 3.

Figure 2 also makes clear the relationship between (mal)adaptation as a state versus a process. In the discussion above, we have focused on state (a point on the figure). The process of maladaptation entails a resident population's fitness moving horizontally from right to left, with the process of adaptation being the opposite. Thus, the process of (mal)-adaptation can occur whether the population is presently adapted or maladapted in either a relative or an absolute sense. As one example, evolutionary rescue is a process of adaptation moving a population from a state of absolute maladaptation to a state of absolute adaptation (Marshall et al. 2016)—that is, from left to right across the black line in figure 2. Conversely, evolutionary suicide (Gyllenberg et al. 2002) or evolutionary traps (Schlaepfer et al. 2002) entail change in the opposite direction. Finally, as described in appendix A, section A6, the lines in figure 2 can be modified (red dashed line) to account for the negative or positive effects of immigrants on the mean fitness of a resident population (Tallmon et al. 2004; Bolnick and Nosil 2007). Populations can, of course, move across the space depicted in the figure due to environment change, evolutionary and demographic responses, and eco-evolutionary feedbacks. For instance, Urban et al. (2019) demonstrate how maladaptation can facilitate eco-evolutionary interactions in a community framework and thereby mediate range and invasion dynamics.

How (Mal)adapted Is Life?

Throughout the history of evolutionary biology, scientists have tended to emphasize the prevalence and power of natural selection (Darwin 1859; Endler 1986; Cain 1989). Indeed, natural selection is the sine qua non of adaptation, causing traits to differ adaptively between environments (Schluter 2000a), local individuals to have higher fitness than foreign individuals (Nosil et al. 2005; Leimu and Fischer 2008; Hereford 2009), populations to persist through environmental change (Burger and Lynch 1995; Gomulkiewicz and Holt 1995; Carlson et al. 2014), and introduced species to successfully colonize and spread in new environments (Phillips et al. 2006). This adaptation by natural selection can occur rapidly (Hendry and Kinnison 1999; Reznick

and Ghalambor 2001; Hendry et al. 2008) and over small spatial scales (Richardson et al. 2014). Moreover, adaptation generates strong convergence of traits in independent lineages colonizing similar environments (Wake et al. 2011; Dobler et al. 2012), strongly shapes ecological dynamics (Hendry 2017; Des Roches et al. 2018), and can make critical contributions to speciation (Nosil 2012). Adaptation by natural selection is clearly an effective process and a widespread state. Or is it?

Closer examination suggests that adaptation might not be as ubiquitous and strong as the foregoing testimonials are often taken to imply. For instance, meta-analyses of reciprocal transplant experiments find that the classic resident-advantage signature of local adaptation in fact occurred in only about 70% of tests (the null being 50%; Leimu and Fischer 2008; Hereford 2009; Palacio-López et al. 2015). Even this 70% value is likely to be an overestimate if research emphasis is placed on cases where local adaptation was anticipated a priori (Schluter 2000a). Furthermore, recent reciprocal transplant studies are increasingly revealing clear evidence of relative maladaptation in nature (Brady 2013, 2017; Rolshausen et al. 2015; Samis et al. 2016; Rogalski 2017; Kooyers et al. 2019).

As another line of argument, well-adapted populations should experience negligible selection (Haller and Hendry 2014; Hendry 2017). Therefore, every instance of directional selection could be considered evidence of relative maladaptation (Haldane 1957; Barton and Partridge 2000; Austen et al. 2017). Taken a step further, estimates of selection for natural populations can be used to estimate the distance between a population's mean trait value and the optimum trait value (Estes and Arnold 2007). Applying this approach to meta-analyses of selection coefficients suggests that in 64% of studied cases, the population trait mean could be more than 1 standard deviation away from the optimum (35% of cases exceed 2 standard deviations; Estes and Arnold 2007). (Beyond the adaptive fit of trait means, analogous logic can be used to assess the extent to which trait variances are adaptive or not—as explained in app. A, sec. A7.) As a caveat, many selection studies do not account for important components of fitness (Austen et al. 2017), in which case evidence of directional selection could be erroneous (see Cotto et al. 2019).

The arguments described above for prevalent maladaptation draw on evidence from an evolutionary emphasis on relative fitness (table 4). Yet maladaptation also appears pervasive from an ecological emphasis on absolute fitness—with key signatures coming from persistent population declines, range contractions, and local and global extinctions (Harrison 1991; Channell and Lomolino 2000; Stuart et al. 2004; Muscente et al. 2018). As one historical indicator, most of the populations and species that have existed through Earth's history have become extinct, revealing the

Table 4: Classic studies emphasizing maladaptation, the important inferences they generated about traits and relative maladaptation, and the missing inferences about absolute maladaptation

System	Hypothesis	Inference regarding trait maladaptation	Inference regarding relative fitness	Missing inference about absolute fitness	Key reference(s)
Lake Erie water snakes	High gene flow from mainland populations prevents precise adaptation in island populations.	Island populations contain numerous noncryptic color morphs that are more typical of mainland populations.	Selection was found to disfavor the noncryptic morph on the islands.	Do island water snake populations suffer reduced densities as a result of maladaptive gene flow?	Camin and Ehrlich 1958; King and Lawson 1995
Texas mosquito-fish	Fish in a freshwater pond were maladapted to freshwater, due either to high gene flow from brackish populations or to recent colonization.	Low reproductive effort in the pond fish relative to brackish fish.	Survival in freshwater tanks was lower for the pond fish than for other freshwater populations and was not higher than fish from nearby brackish populations.	Does maladaptation in the pond fish cause low population density?	Stearns and Sage 1980
Riparian spiders	High gene flow from aridland spider populations causes maladaptation in a riparian spider population.	The riparian spider population showed phenotypes more typical of adjacent aridland spiders, but not after gene flow was experimentally reduced.	Experimental enclosures showed that selection acts against the aridland phenotype in riparian habitats.	Does maladaptation in the riparian population cause low population density?	Riechert 1993

ultimate predominance of maladaptation over macroevolutionary time (Novacek and Wheeler 1992). On much shorter time spans, human activities have dramatically and rapidly accelerated population extirpations and species extinctions (Dirzo et al. 2014; Ceballos et al. 2017). For instance, in a detailed assessment of 177 mammal species, Ceballos et al. (2017) found that each species lost at least 30% of its range, while 40% of these species lost more than 80%. As other examples, habitat change has driven on average a 60% decline in abundances of sampled wildlife populations (WWF 2018), while an estimated 40% of the globe's bird species are in decline (BirdLife International 2018), as are 81% of sampled amphibian species (Nowakowski et al. 2018; WWF 2018).

To conclude, many populations appear to be maladapted to their current environment, from a relative perspective, an absolute perspective, or both.

Detecting Relative and Absolute Maladaptation

Our core message is that biologists of all stripes will benefit from estimating both relative and absolute measures of

(mal)adaptation over multiple generations because these complementary perspectives contribute complementary insights—as others also have argued (Whitlock 2002; Kinison and Hairston 2007; Débarre and Gandon 2011; Hendry 2016; Gallet et al. 2018; fig. 2). Unfortunately, studies measuring, reporting, and interpreting reliable estimates of both relative and absolute fitness are rare, partly owing to incomplete or imperfect fitness metrics resulting from unobservable mortality (the “invisible fraction”: Weis 2018) or reproductive success (e.g., pollen), unrealistic starting conditions (e.g., equal spacing of seedlings or unrealistic densities), or limited study durations (less than a generation). Keeping these practical limitations in mind, we now consider some compromise approaches to assessing (mal)adaptation.

A gold standard for assessing (mal)adaptation remains the reciprocal transplant experiment, measuring the fitness of resident and immigrant types in a given environment (Schluter 2000b; Kawecki and Ebert 2004; Leimu and Fischer 2008; Hereford 2009). These transplant experiments typically focus on relative fitness differences, which make them sensitive to one's choice of which populations to

compare (e.g., Hargreaves and Eckert 2018), and they neglect to consider absolute maladaptation. However, some transplant studies can be extended to track changes in absolute abundance across generations (Angert and Schemske 2005; Hargreaves and Eckert 2018), thus yielding insight into absolute maladaptation as well. These data can be used to answer important questions. For example, do immigrant genotypes increase in relative and absolute abundance? And does their range expand, or do they become extinct? Such experiments are difficult, yet they represent an important improvement for future work.

Lacking data on fitness itself, estimates of trait maladaptation can yield provisional insights, as discussed in appendix A, section A4. Similarly, genomic data can be very useful in detecting the molecular fingerprints of past natural selection (the process of adaptation). Yet such inferences remain one-sided, as we have no assays at present for the fingerprints of past maladaptation (as a process). That is, while metrics such as dN/dS or Tajima's D are used to infer adaptation in genomic data, no equivalent metrics exist to detect maladaptation, except insofar as past natural selection suggests that the population was not initially well adapted enough. And, of course, genomic data are not very informative about maladaptation as a present-day state because genomes provide a historical record rather than a measure of present-day performance (Shaw 2019). However, genomic data can yield inferences of recently changing population sizes (absolute fitness), such as through coalescent model estimates of changing population size through time (Drummond et al. 2005).

We must also remember that current approaches can yield spurious results, which we might call only "apparent maladaptation." First, the familiar effects of sampling error (Hersch and Phillips 2004) can lead to inaccurate parameter estimates. Second, estimating only one component or correlate of fitness can be misleading with respect to lifetime fitness, such as through trade-offs between fitness components (Reznick 1985; Roff 1993; Rollinson and Rowe 2018; Cotto et al. 2019). Third, short-term studies, both within and across generations, can miss key episodes in temporally varying selection (fig. B1, available online; Simons 2002, 2009; Carlson and Quinn 2007; Siepielski et al. 2017). Fourth, context dependence can be critical, such as when a camouflage-environment mismatch is maladaptive in some contexts but not in others (results mediated by, for instance, behavioral change or the temporary absence of a predator; T. E. Farkas, G. Montejó-Kovacevich, A. P. Beckerman, and P. Nosil, unpublished data). Fifth, inappropriate categorization of habitats can give the appearance of maladaptation (Stuart et al. 2017). Sixth, neutral alleles in a local environment can act deleteriously in another environment (i.e. "conditionally deleterious"). The result looks like local adaptation (transplanted genotypes perform poorly

away from home) but is due to relaxed rather than positive selection (Mee and Yeaman 2019). The key point here is simply that robust inferences of (mal)adaptation require not only an expansion of perspective (the point of our article) but also increasing attentiveness to optimal methodologies.

A particularly important complication arises owing to density-dependent fitness (Saccheri and Hanski 2006; Kinnison and Hairston 2007; Hendry 2017; box 2). All populations at a stable demographic equilibrium will have a population mean fitness near 1, at least in the long term, despite potentially very different population sizes owing to different carrying capacities. One might reasonably argue that in many cases a more abundant (e.g., more dense) population has higher fitness than a less abundant population, despite their identical mean population fitnesses at carrying capacity. In such cases, population size or density could be a better proxy for (mal)adaptation than would be population growth rate (box 2). However, population sizes can change for reasons unrelated to adaptation, such as loss of habitat or increased trait-independent mortality due to harvesting, predation, or parasitism (Rothschild et al. 1994; Stenseth et al. 1997; Bender et al. 1998; Hochachka and Dhondt 2000; Keane and Crawley 2002). Hence, the ideal inferential approach is likely a joint consideration of population size and population growth rate or population mean fitness (box 2). It is also important to remember that plenty of adaptive evolution can take place while population size remains stable as long as the degree of (mal)adaptation is sufficient to fill the carry capacity—including situations of selection without changes in population size (see app. A, sec. A3). Finally, it is possible that carrying capacity itself could change through evolution, such as when selection leads to the use of new resources or evolution of resource-related traits (Kinnison and Hairston 2007; Hendry 2017; Abrams 2019).

Finally, environmental and evolutionary change can generate strong feedback loops, with sometimes complex effects (Kinnison et al. 2015; Hendry 2017; Govaert et al. 2019; Urban et al. 2019). For instance, some models suggest that adaptation in a herbivore's resource conversion rate can lead to resource overexploitation and increased predator abundance, both of which suppress herbivore abundance (so-called adaptive decline; Abrams 2019). In such cases, the evolutionary process of adaptation changes the environment in ways that lead to absolute maladaptation.

How Does Maladaptation Persist?

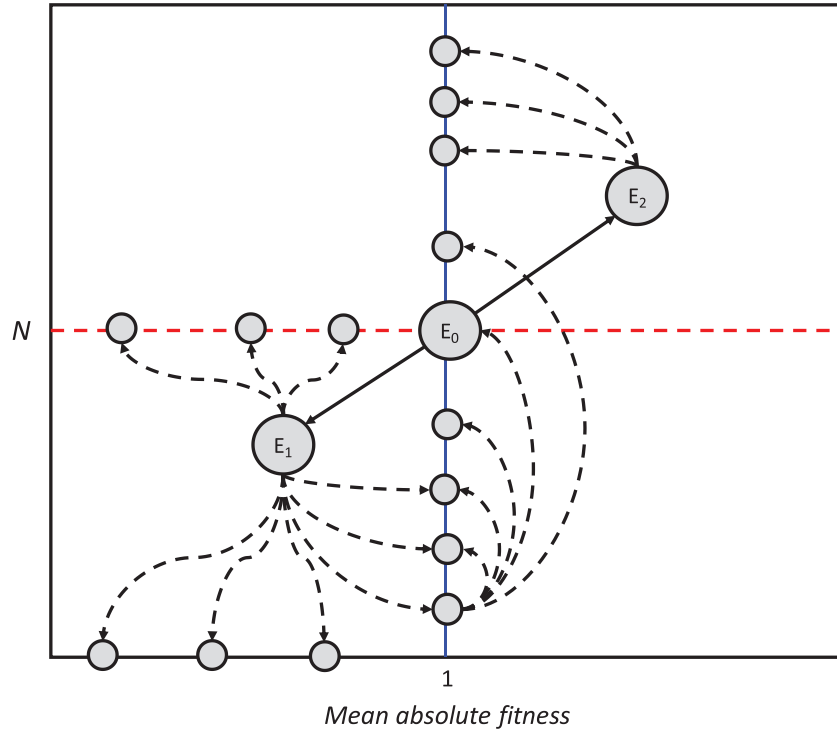
Given that maladaptation (relative and absolute) is apparently common, a major research goal should be to determine how it persists and where we should expect it to be stronger or weaker. Here, we summarize some of the leading hypotheses, and the articles in this special feature elaborate on some of these ideas.

Box 2: Maladaptation and population size

A major complicating factor in detecting absolute (mal)adaptation is density dependence. The reason is that all populations persisting in perpetuity will have a long-term average population mean fitness of unity (i.e., $W = 1$). In such cases, the joint examination of the dynamics of mean absolute fitness and mean population size can help to evaluate (mal)adaptation. Imagine a population (E_0) well adapted to a particular environment and having a population size (red horizontal line in box 2 figure) at the local carrying capacity, thus having a mean absolute fitness of unity (blue vertical line in box 2 figure).

Now imagine an environmental change (E_1) that causes maladaptation and thus depresses population mean fitness below unity and causes a population decline. The potential eco-evolutionary outcomes are several. First, subsequent adaptation might not be sufficient to achieve a mean fitness greater than unity before extinction occurs (dashed lines leading downward to X-axis). Second, population size might increase without mean fitness ever reaching unity (dashed lines leading upward), which can only occur through demographic rescue from immigration. Third, the population might follow a trajectory of increasing mean fitness and still decreasing (but at a slower rate) population size until a mean absolute fitness of unity is achieved (dashed arrows leading from E_1 to the blue line). The populations might equilibrate here at these lower than initial population sizes (Abrams 2019). In such cases, the population has the same absolute mean fitness as before the disturbance (E_0) but is now at a lower population size, which can be considered a form of maladaptation that is not reflected in mean fitness. Once having reached a mean absolute fitness of unity, absolute fitness and therefore mean population size might continue to increase (dashed curves in the lower right portion of the figure) before equilibrating back to a mean fitness of unity but at a larger population size—true “evolutionary rescue.”

Of course, it is also possible for environmental change to increase mean fitness above unity and therefore increase population size (E_2). In such cases, population size should continue to increase while mean fitness declines (unless additional favorable environmental change occurs) until the population equilibrates at a higher population size. Or mean fitness will drop below replacement rates transiently until the population returns to its original carrying capacity.



Box 2 Figure: Joint examination of the dynamics of mean absolute fitness and mean population size. See box text for definitions of symbols.

Relative maladaptation is unsurprising because many factors are known to prevent populations from precise adaptation to their immediate local conditions (Crespi 2000; Lenormand 2002; Hendry and Gonzalez 2008; Brady et al. 2019). These factors have been enumerated before in reviews of concepts such as “genetic load” (table 1). We briefly reiterate some key examples. First, genetic drift can increase the prevalence of mildly deleterious alleles or decrease the prevalence of weakly beneficial alleles (i.e., nearly neutral theory; Ohta 1992), thus causing maladaptation relative to optimality—and more so in populations experiencing greater drift. In the extreme, drift and inbreeding can cause absolute maladaptation leading to extinction of small populations (Charlesworth and Charlesworth 1987; Lynch 1991; Lande 1998). Ironically, strong selection can reduce effective population sizes enough to drive drift that reduces fitness (Falk et al. 2012). Second, high mutation rates (e.g., from pollution) can introduce considerable deleterious genetic variation (Yauk et al. 2008). Third, gene flow from surrounding populations can introduce maladapted alleles—although, of course, gene flow can also have positive consequences for local adaptation (Garant et al. 2007). Fourth, frequency-dependent selection within populations can lead to persistent maladaptation (Ayala and Campbell 1974; Lande 1976; Gigord et al. 2001); that is, alleles that are initially favored by selection when rare can become maladapted once common (Fisher 1930). Frequency-dependent selection can also constrain populations’ ability to adapt to environmental change (Svensson and Connallon 2018).

Perhaps most important of all, especially in the modern context, environmental fluctuations can generate substantial maladaptation—because evolution, even rapid, cannot keep pace (e.g., Kooyers et al. 2019; McAdam et al. 2019). Such environmental changes can be abiotic (temperature, precipitation, etc.) or biotic, such as invasive species (Vilà et al. 2011), emerging pathogens (Daszak et al. 2000), or antagonistic coevolution (Nuismer 2017). Indeed, host-parasite reciprocal transplants often reveal a complex mix of adaptation and maladaptation by one player or another (Hoeksema and Forde 2008). As an important aside, these environmental changes cause maladaptation without any evolution; that is, the process of maladaptation does not have to be a genetic process. Yet if so, we must grapple with the flip side: Does improved fitness that results from environmental change (e.g., loss of a predator) reflect the process of adaptation—despite the lack of genetic change?

Sexual selection is a particularly intriguing source of maladaptation because it can entail a conflict between relative and absolute fitness: traits that increase breeding success can reduce viability, potentially conferring both higher relative fitness and lower absolute fitness (Williams 1975; Smith and Maynard-Smith 1978; Parker 1979; Pischedda and Chipindale 2006; Bonduriansky and Chenoweth 2009; Rankin

et al. 2011). A particularly notable example is sexual selection for exceptionally elaborate traits (Fisher 1930; Lande 1980). In extreme cases, “runaway evolution” due to sexual selection might cause population extinction via reduced carrying capacities that make populations more vulnerable to extinction via demographic stochasticity (Matsuda and Abrams 1994). Self-fertilization in plants has been suggested as another instance of an adaptation with only short-term benefit, eventually leading to absolute maladaptation (e.g., the dead-end hypothesis; Stebbins 1957; Wright et al. 2013). Cases where natural selection leads to population declines and extinctions have been variously dubbed “Darwinian extinction” (Webb 2003), “evolutionary suicide” (Gyllenberg et al. 2002), or “self-extinction” (Matsuda and Abrams 1994). Theoretical and empirical findings suggest that such extinction might be common and can exhibit various temporal dynamics, ranging from gradual to sudden and from monotonic to oscillatory (Webb 2003).

Relative maladaptation has many likely causes, as described above, whereas the persistence of absolute maladaptation requires additional explanations. First, episodic maladaptation can simply reflect inherent delays in the process of adaptation to changing conditions—sometimes called lag load (Cotto et al. 2019; Kooyers et al. 2019; McAdam et al. 2019; table 1). A clear example is seen in evolutionary rescue, where a population declining in abundance as a result of environmental change begins to evolve toward the new optimum (Gonzalez et al. 2013; Carlson et al. 2014; Uecker et al. 2014). Such delays can also arise from cyclical dynamics driven by intraspecific competition (e.g., Sinervo et al. 2000), predator-prey cycles (e.g., Stenseth et al. 1997), or host-pathogen interactions (e.g., Hochachka and Dhondt 2000).

Second, cases of absolute maladaptation might not be truly persistent but instead simply a delay of the inevitable. A poignant example is the Pinta Island tortoise in the Galápagos, which is clearly maladapted to human predation and invasive animals. From a population size originally in the thousands, abundance declined over more than 100 years until only “Lonesome George” was left (J. Gibbs, personal communication). In such cases of “extinction debt” (Tilman et al. 1994; Kuussaari et al. 2009), population declines to extinction might be slow because absolute maladaptation is weak, because mortality occurs mainly at juvenile stages, because initial population sizes are large, or because of compensatory mechanisms such as relaxation from density dependence.

Third, populations suffering absolute maladaptation can be sustained by immigration. Such populations are considered demographic “sinks” (Holt 1985; Pulliam 1988), kept from extinction by “demographic rescue.” This rescue also imports new genotypes that may increase the recipient populations’ relative fitness as well (Holt 1997; Holt et al. 2004).

As a result, demographic rescue can sometimes help a population evolve its way out of the sink (Holt and Gomuliewicz 1997; Whiteley et al. 2015). Conversely, populations at species' geographic range edges may be sinks because of immigration that prevents their local adaptation to extreme range-edge environments (Kirkpatrick and Barton 1997). Relatedly, if sink habitats disproportionately attract individuals with relatively low fitness, sink dynamics could explain both absolute and relative maladaptation (Brady 2013).

Where Now?

The remainder of this special feature presents a series of articles that touch on important aspects of maladaptation. Lane et al. (2019) provide an example of the apparent disconnect between absolute and relative fitness perspectives, reporting on a case of absolute maladaptation occurring despite adaptive trait change. Mee and Yeaman (2019) highlight the importance of context for understanding maladaptation, with theory showing that neutral mutations can be deleterious in nonlocal environments. Kooyers et al. (2019) provide an example of local maladaptation, invoking lag load as the source of relative fitness disadvantage. Cotto et al. (2019) use theory to show that individual fitness components can increase despite maladaptation, underscoring the caution necessary when inferring incomplete fitness measures. McAdam et al. (2019) find that lag load in a seed predator enhances predation evasion in its prey: failure to evolve the optimal trait in one species facilitates success in another. Urban et al. (2019) also provide a community perspective on maladaptation, developing theory to show that maladaptation can shape range and invasion dynamics and their responses to environmental change.

Maladaptation in the various forms described here appears to be quite common in nature, and it will likely become more common in our rapidly changing world (for practical applications, see app. A, sec. A8). Yet on the whole, evolutionary biologists have tended to evaluate fitness and trait variation through a lens of adaptation, not (mal)adaptation. This lens likely skews our understanding of the distribution of maladaptation and the processes that cause it in the natural world. Whether because we tend to look for adaptation in places we expect to find it or because we have lacked a clear framework to describe maladaptation, our use of language focused on adaptation may bias us toward a glass-half-full perspective. We hope the framework presented here encourages others to study and discuss maladaptation on perhaps equal footing with adaptation. We see a need for more inquiry into the frequency, distribution, and causes of maladaptation, developing our understanding of why so many populations appear maladapted. What conditions promote adaptation versus maladaptation?

What are the relative effects (and speeds) of environmental and genetic changes in (mal)adaptation? And, critically for conservation, when is adaptive evolution fast enough to prevent extinction in the face of the many forces generating maladaptation?

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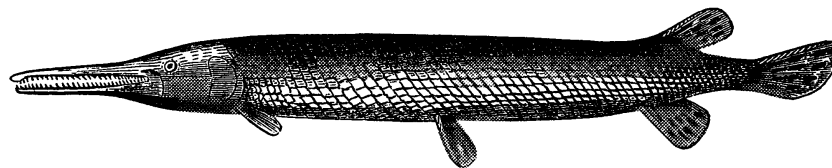
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Special Feature Editor: Joseph Travis



“The Gar (*Lepidosteus osseus*) . . . soon disappeared by sinking out of sight, but reappeared soon near the shore, giving us an opportunity of watching it. It remained as motionless as an *Esox* for several minutes, and on the approach of a minnow would come as near the shore as possible, moving steadily backwards. If the fish came to about where the gar previously had been, it was seized in an instant, and the *Lepidosteus* would remain motionless until the approach of another Minnow would cause it to again draw back.” From “Notes on Fresh-Water Fishes of New Jersey” by Charles C. Abbott (*The American Naturalist*, 1870, 4:99–117).