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. We articulate the various causes of both forms of 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 and yet populations can be growing in abundance. Conversely, resident individuals can appear locally adapted (relative to non-resident individuals), and 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.
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 2000a; 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 (Hereford 2009; Leimu and Fischer 2008). 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 (Hansen 2006; Houle 1998; Mousseau and Roff 1987) 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 et al. 2008; Hendry and Kinnison 1999; Reznick and Ghalambor 2001).
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; Ceballos et al. 2017; Dirzo et al. 2014; Ripple et al. 2017; Urban et al. 2012; Wolf and Ripple 2017), all occurring at a pace far greater than the background rate (Ceballos et al. 2015; Pimm et al. 2014).

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; Haldane 1932; Wright 1931; 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 (Anderson and May 1978; Birch 1948; Elton and Nicholson 1942; Hutchinson 1959; Levins 1969; MacArthur 1972).
Recognition of these contrasting emphases on absolute versus relative fitness is not new. For instance, Dobzhansky (1968a,b) 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; Ellner et al. 2018; Lion 2018; Govaert et al. 2019). A related body of work integrates evolutionary and population dynamics through the lens of ‘evolutionary rescue’ (Carlson et al. 2014; Gonzalez and Bell 2013; Gonzalez et al. 2013). 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 paper 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 versus relative), phenomenon (process versus state), and
assessment (qualitative versus 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, and yet be declining in abundance (e.g., Appendix A1). We conclude by outlining the key processes that can give rise to – and maintain – maladaptation from these different perspectives.

**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 (see Appendix A2 for additional discussion). 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,b). Evolution and ecology are fundamentally linked through the concept of population mean absolute fitness ($W$) (Dobzhansky 1968a,b; Endler 1986). With discrete non-overlapping generations, this quantity can be the per-generation per-adult mean number of zygotes that survive 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 approximately

$$W = e^{(dN/N dt)}.$$  
Eq(1).

In this simple scenario, population mean absolute fitness is approximated as the population’s per capita growth rate (Crow and Kimura 1970; Kinnison and Hairston 2007; Orr 2009; Saccheri and Hanski 2006; 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, $W = 1$. This threshold thus serves as a qualitative absolute standard for (mal)adaptation: that is, a stable or growing population is adapted to present conditions ($r \geq 0; W \geq 1$), whereas a declining population is maladapted to present conditions ($r < 0; W < 1$). How far $W$ 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 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 time scale. 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). Time scale also can have a large effect on inferences for populations with cyclic changes in density (Sinervo et al. 2000). When studied over short time scales, maladaptation might be inferred when growth rates are negative and subsequent adaptation then might be inferred when growth rate is positive. When cyclic changes are studied over longer time scales, 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 time scale 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 (Gillespie 2010; Orr 2009; Hendry et al. 2018). Fisher’s Fundamental Theorem of Natural Selection (Burt 1995; Fisher 1930; Price 1972) 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 towards the local optimum but population size is stable (Lenormand 2002; Wade 1985; Wallace 1975; Whitlock 2002; see Appendix A3 for further discussion).

**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 3000 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 to non-native (immigrant) fitness in the same environment (\( \bar{w}_R = \bar{W}_{Resident} / \max(\bar{W}_{Resident}, \bar{W}_{Immigrant}) \)). Second, a focal population’s fitness in its native (home) environment can be compared to its fitness in a foreign (away) environment (\( \bar{w}_H = \bar{W}_{Home} / \max(\bar{W}_{Home}, \bar{W}_{Away}) \); Blanquart et al. 2013; Kawecki and Ebert 2004). Another standardization uses mean rather than maximum fitness in the denominator (e.g., \( \bar{w}_R = \bar{W}_{Resident} / \text{mean}(\bar{W}_{Resident}, \bar{W}_{Immigrant}) \); 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 A4, noting that caution in 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 Appendix 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 is both inferior to immigrants (relative maladaptation) and its mean fitness is below 1 (absolute maladaptation) (Howells et al. 2012; Pergams and Lacy 2007; Saltonstall 2002; Yampolsky et al. 2014). At other times, however, relative and absolute inferences won’t correspond to each other (Table 2), such as when residents in polluted environments have lower fitness than immigrants (relative maladaptation) and yet the residents remain very abundant and successful (absolute adaptation) (Brady 2013; Brady 2017; Rogalski 2017; Rolshausen et al. 2015). 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 dynamics (Lane et al. 2019;
McAdam et al. 2019), or whether maladaptation is persistent or context dependent (Simons 2009; Farkas et al. unpublished manuscript). 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 yet absolute adaptation (the resident population is stable or growing). As a putative real example of this situation, Japanese knotweed (an invasive plant in the 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 (VanWallendael 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 yet absolute maladaptation. This situation can arise when – for example – severe environmental change threatens an entire array of populations without changing their relative degree of local adaptation. As an example, the butterfly *Boloria aquilonaris* is declining and predicted to go extinct in the Netherlands due to decreasing host plant quality. Yet this seemingly moribund population remains better adapted to its local environment than are 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 above discussion, 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 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 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 (Bolnick and Nosil 2007; Tallmon et al. 2004). 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 (Cain 1989; Darwin 1859; Endler 1986). Indeed, natural selection is the *sine qua non* of adaptation, causing traits to differ adaptively between environments (Schluter 2000b), local individuals to have higher fitness than foreign individuals (Hereford 2009; Leimu and Fischer 2008; Nosil et al. 2005), populations to persist through environmental change (Burger and Lynch 1995; Carlson et al. 2014; Gomulkiewicz and Holt 1995), and introduced species to successfully colonize and spread in new environments (Phillips et al. 2006). This adaptation by natural selection can occur rapidly (Hendry et al. 2008; Hendry and Kinnison 1999; Reznick and Ghalambor 2001) and over small spatial scales (Richardson et al. 2014). Moreover, adaptation generates strong convergence of traits in independent lineages colonizing similar environments (Dobler et al. 2012; Wake et al. 2011), 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%) (Hereford 2009; Leimu and Fischer 2008; Palacio-López et al. 2015). Even this 70% value is likely to be an over-estimate if research emphasis is placed on cases where local adaptation was anticipated a priori (Schluter 2000b). Further, 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 (Barton and Partridge 2000; Haldane 1957; 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 one standard deviation away from the optimum (35% of cases exceed two s.d.; 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 Appendix 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 above arguments 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 (Channell and Lomolino 2000; Harrison 1991; 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 gone extinct, revealing the 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 (Ceballos et al. 2017; Dirzo et al. 2014). 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 others examples, habitat change has driven on average 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 or 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 (Débarre and Gandon 2011; Gallet et al. 2018; Hendry 2016; Kinnison and Hairston 2007; Whitlock 2002; 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 (Hereford 2009; Kawecki and Ebert 2004; Leimu and Fischer 2008; Schluter 2000a). These transplants 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 which neglects 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 such as: Do immigrant genotypes increase in relative and absolute abundance?, and Does their range expand, or do they go 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 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 is 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 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; 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 (Farkas et al. unpublished manuscript). 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 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 paper) but also increasing attentiveness to optimal methodologies.

A particularly important complication arises owing to density-dependent fitness (Saccheri and Hanski 2006; Kinnison and Hairston Jr. 2007; Hendry 2017; Box 2). All populations at a stable demographic equilibrium will have a population mean fitness near one, 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 or 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 Appendix 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 Jr. 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 over-exploitation 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 papers in this Special Feature elaborate on some of these ideas.

Relative maladaptation is unsurprising because many factors are known to prevent populations from precise adaptation to their immediate local conditions (Crespi 2000; Hendry and Gonzalez 2008; Lenormand 2002). 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 (Lande 1998; Charlesworth and Charlesworth 1987; Lynch 1991). 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; Gigord et al. 2001; Lande 1976): 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) or 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 flipside: 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 also lower absolute fitness (Bonduriansky and Chenoweth 2009; Parker 1979; Pischedda and Chippindale 2006; Rankin et al. 2011; Smith and Maynard-Smith 1978; Williams 1975). 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 or sudden, and 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; MacAdam et
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 (Carlson et al. 2014; Gonzalez et al. 2013; 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 Galápagos, 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, pers. comm.). In such cases of “extinction debt” (Kuussaari et al. 2009; Tilman et al. 1994), 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 Gomulkiewicz 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 non-local 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 (see Appendix A8 for practical applications). 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 towards 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?

**Acknowledgements**

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Appendix A: Further considerations of maladaptation

A1: An example of the joint state of maladaptation and local adaptation

To illustrate the conundrum with a specific example, consider the massive recent climate-driven decline in global living coral coverage, exemplified by 75% of surveyed sites experiencing bleaching in 2015 - 2016 alone and a fivefold decrease in the period of time between severe bleaching events over the past four decades (Hughes et al 2018). From these declines, we can deduce that many coral species are maladapted to increasing Anthropocene temperatures (van Oppen and Lough 2018). Yet, many studies document corals’ local adaptation to temperature (Hughes et al. 2003; Howells et al. 2012; Palumbi et al. 2014). In short, coral populations can be simultaneously maladapted in the absolute demographic sense emphasized by ecologists, yet also locally adapted in the relative sense emphasized by evolutionary biologists. The reconciliation and integration of these different perspectives starts with a consideration of how different groups of biologists define and measure adaptation and maladaptation (Hendry and Gonzalez 2008). This reconciliation is a goal of this Synthesis, and of the Special Feature articles that follow (see “In this Feature”).

A2: Different uses of adaptation and maladaptation

Here, we consider the diversity of ways in which evolutionary biologists use the terms ‘adaptation’ and ‘maladaptation’ (Crespi 2000). Rather than promote a single definition of maladaptation, we suggest that different definitions are most helpful in different contexts,
but consequently researchers must clearly state their operational definition, what is being measured, and the relevant temporal and spatial scales (Fig. 1).

‘Adaptation’ is sometimes used to identify the existence of a trait or genotype that is responsible for high fitness (Gould and Lewontin 1979). For example, Jablonski and Chaplin (2011) stated that “Tanning is an adaptation to seasonally high UVR”. In this sense, ‘maladaptation’ would be a trait or genotype responsible for low fitness (e.g., Hale et al. 2016; Robertson et al. 2013; Singer and Parmesan 2018). (Mal)adaptation in this sense is qualitative (“the trait is an adaptation”) rather than quantitative (“the degree of adaptation is”) and, hence, this definition is not developed further in the present paper.

Another approach is to focus on ‘adaptation’ as a state of having high fitness relative to some benchmark: as in, “Reciprocal transplant experiments carried out over 5 years demonstrated that these populations are locally adapted” (Oakley et al. 2018). In this sense, maladaptation would be a state of having low fitness, such as lower mean fitness in *Timema* walking stick insects due to immigration of less-cryptic morphs (Bolnick and Nosil 2007). In a later section of this paper we discuss what benchmarks may be used for judging whether fitness is high or low. Note that researchers frequently use genotypes or phenotypes (e.g., the frequency of locally cryptic *Timema* morphs) as proxies for fitness when evaluating the state of (mal)adaptation.

Alternatively, ‘adaptation’ is used to invoke a process of evolving more appropriate genotypes or phenotypes or increased fitness through time: as in “we measured the rate of adaptation” (Gerstein et al 2011). In continuous time, for example, the process of adaptation can be specified as the derivative of mean fitness with respect to time (Crow and Kimura 1970; Orr 2009; Wagner 2010) or as the proportional change in mean fitness.
per generation (Hendry et al. 2018); or it can be specified as the corresponding rate of change in mean phenotype (Hendry and Kinnison 1999) or allele frequency (Crow and Kimura 1970). This process-based invocation of adaptation requires the presence of some initial non-optimality. In this sense of process, ‘maladaptation’ entails decreasing fitness through time.

Traditionally, biologists like to restrict use of the word ‘adaptation’ to situations arising from evolution by natural selection. Yet, evolution and selection are not the only processes leading to the state of having high or low fitness, or the process of increasing or decreasing fitness. This is because both uses of the term depend both on the population’s trait distribution, and on the environment, so changes in either can alter fitness. Thus, studies of (mal)adaptation should always specify the inferred role of evolution.

**A3: Selection with and without population decline**

Consider a population at carrying capacity vs. a population short of carrying capacity. If an allele arises that increases survival to maturity without reducing some other component of fitness, it will have higher relative fitness compared to other alleles and will increase in frequency. In a population at carrying capacity (e.g., number of tree cavities available for cavity-nesting birds), however, the number of offspring produced per adult will not increase across generations. In a population below carrying capacity, the same allele will increase in frequency and increase population size – because (in this example) the reproduction of surviving adults is not yet constrained by the number of nest sites. Hence, maladaptation will not strongly influence population dynamics unless selection (1) drops the population below carrying capacity (surviving adults are fewer than the number of nest
sites), (2) acts at the density-limiting stage (e.g., acting on variation in the ability of adults to evict a competing species from the nest cavities), or (3) influences the evolution of carrying capacity itself (e.g., adults evolve the ability to excavate their own nest holes). Another way of highlighting this distinction is that selection without population decline is simply producing an equivalent amount of mortality that otherwise would have been random.

**A4: On the use of traits to assess (mal)adaptation**

Trait (mal)adaptation can be evaluated by comparing extant trait values to an inferred optimum based on other populations adapted to similar habitats (e.g., Moore et al. 2007); biomechanical principles (e.g., Hajela and Lin 1992); or phenotypic/genetic manipulations (Sinervo and Basolo 1996). A critically important caveat, however, is that fitness alone – not merely trait value – is diagnostic of (mal)adaptation. A trait that is *maladapted* in a reference population might turn out to be *adapted* in the focal population, a difference in outcome that could be mediated for instance by unidentified differences in selection between the two habitats. Thus, trait values that deviate from presumed optima should be interpreted cautiously in the absence of corresponding fitness values. Ideally, one would track changing abundance of populations that differ for traits that make them more or less well adapted, to contrast absolute versus relative maladaptation associated with those traits. For instance, Both et al. (2006) showed that populations of flycatchers whose migration timing was least well suited for changing environments were the same populations showing the greatest numerical declines. As another example, Willis et al. (2008) shows that the plant species least capable of adjusting their flowering date in...
response to climate warming were the most likely to become locally extirpated. In both cases, relative maladaptation coincided with absolute maladaptation to contribute to population decline or extinction.

**A5: Hypothetical and manipulated reference points for optimal traits**

Biomechanical or biophysical models can define optimal traits from first principles of physics or engineering. For example, fluid dynamic models suggest that an undulating fin can maximize force production when the ratio of undulation length to amplitude is about 20; presumably not coincidentally, this ratio has evolved in at least eight independent instances of aquatic animals evolving undulating swimming (Bale et al. 2015). Or, optimal foraging theory generates predictions about an organisms’ expected diet, which can be compared with its actual strategy (Pyke et al. 1977). Knowledge or expectation of constraints can help guide these approaches (Hansen and Houle 2008). Sometimes, hypothetical phenotypes can be made real through genetic manipulations via selective breeding (Arnold et al. 2012), gene editing (Hart et al. 2015), ‘resurrection’ ecology from resting eggs or seeds (Orsini et al. 2013; Franks et al. 2018), or phenotypic manipulations (Griffith and Watson 2005; Preziosi et al. 1999). In particular, estimates of fitness surfaces are often aided by hybridization that inflates the available phenotypic variance and (perhaps) breaks down covariances among traits (Lexer et al. 2003). Such approaches can also reveal heterosis, in which hybrid phenotypes outperform either source population (Crow 1948; Moll et al. 1965; Thornhill 1993; Whitlock et al. 2000), which might be considered a new standard for ‘high’ fitness. Similarly, hypothetical environments can be made real through environmental manipulations, such as warming or CO₂ treatments.
Such experimental approaches permit inferences about relative fitness for traits (or in environments) that do not naturally occur.

**A6: The influence of migration on absolute and relative fitness**

In reference to Figure 2, if we assume a migration rate \( m \) and ignore density dependence, the post-migration fitness in a simple Lande (1976, 1979) framework is

\[
\bar{W}_m = m\bar{W}_I + (1 - m)\bar{W}_R
\]

(Hendry et al. 2001; Lande 1976; Lande 1979). Solving for the isocline at which \( \bar{W}_m = 1 \) (absolute fitness is at replacement for the residents), we have \( \bar{W}_I = (1 - (1 - m)\bar{W}_R)/m \). The resulting red dashed line in the figure separates absolute adaptation from absolute maladaptation after adjusting for immigration, revealing two interesting regions of state space. The upper wedge labelled “migratory rescue” corresponds to situations where the resident population would be moribund in the absence of immigration, but is rescued and able to increase owing to the arrival of more fit immigrant genotypes. Such maladapted populations are often called demographic ‘sink populations’ (Pulliam 1988), and their persistence in such states of local maladaptation has long been described in the context of source-sink dynamics (Dias 1996). Conversely, the lower wedge, which we call the “Barton zone” after Barton (Barton 1992), is where maladapted immigrants reduce mean fitness to the point where an otherwise adapted population declines.

**A7: Maladaptation of variance**

Variance that is too high could come from various forms of genetic load, such as from mutation, migration, or recombination (Table 2; Hendry et al. 2018). Additionally, Hansen
et al. (2006) used estimates of developmental instability to calculate that 14% of the phenotypic variance within populations might be maladaptive noise. Such maladaptation might be inferred from estimates of stabilizing selection acting to reduce variance – because such selection should not be strong when populations are adapted to stable optima (Haller and Hendry 2014). Variance that is too low could come from inter-breeding that prevents disruptive selection, such as from competition, from maintaining phenotypic diversity. Such maladaptation might be inferred from estimates of disruptive selection acting to increase variance (Bolnick and Lau 2008). Meta-analyses of quadratic selection coefficients suggest that stabilizing and disruptive selection are statistically detectable in at least 16% of cases – but that such inferences are severely hampered by low sample sizes (Kingsolver et al. 2001).

**A8: Practical applications of maladaptation**

In applied settings, maladaptation can be seen as either an obstacle or a tool depending on the context (Carroll et al. 2014; Chan et al. 2016; Hendry et al. 2011). The obstacle side of maladaptation arises in the context of conservation efforts aimed at sustaining, recovering, or restoring populations. In such cases, the goal is to reduce maladaptation. The tool side of maladaptation arises in attempts to limit undesirable populations (e.g. weeds, pests, parasites, pathogens, or invasive species) from negatively impacting biodiversity or human well-being. In such cases, the goal is to increase maladaptation. Of course, the obstacle and tool aspects converge in a number of contexts, such as harvested fish populations that are evolving smaller size and for which harvesting strategies can be modified to reduce that evolution (Heino et al. 2015; Hutchings 2009).
Each of the definitions and interpretations of maladaptation presented above tells us something different about its role as an obstacle and a tool. For instance, because conservation biologists are most concerned with population persistence, absolute (mal)adaptation is perhaps most informative. Even so, an understanding of relative (mal)adaptation holds value; for instance, in guiding restoration efforts such as assisted migration and supplementation programs. Also, evolutionary biologists are typically most interested in trait change, which depends on relative fitness. Moreover, traits themselves can have per-capita effects on communities and ecosystems, independent of their influence on organismal fitness (Hendry 2017).

Optimal inference becomes most complex for researchers interested in eco-evolutionary feedbacks, which depend on both relative and absolute (mal)adaptation. Eco-evolutionary models require simultaneous equations, one expressing population dynamics that are, by definition dependent, on mean absolute fitness \( \frac{dN}{dt} = \ln(W) \times N \), and the other expressing evolutionary change in a focal trait \( x \left( \frac{dx}{dt} = \hbar^2 s, \text{the Breeder's Equation} \right) \). Here, the selection gradient \( s \) is dependent on variation in relative fitness, measured as the partial derivative of mean absolute fitness with respect to the trait mean \( (s = \frac{d \bar{W}}{d \bar{x}}) \). Hence, a researcher will, at times, need to consider both aspects of fitness simultaneously.

Appendix B: Temporal dynamics and maladaptation

[Figure B1 goes here]
Literature Cited


### Tables

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

<table>
<thead>
<tr>
<th>Type of genetic load</th>
<th>Key references</th>
<th>Description</th>
<th>Relationship to maladaptation framework</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genetic load (encompasses all types of load specified below)</td>
<td>Crow 1970; Haldane 1937; Muller 1950; Wallace 1970</td>
<td>Typically formulated as ( \frac{W_{\text{max}} - \bar{W}}{W_{\text{max}}} ) and often thought of as ‘substitutional’ load, which indicates that ( W_{\text{max}} ) occurs due to segregating genotypes already present in population. (Contrasts with ‘lag load’ below.)</td>
<td>All forms of genetic load indicate relative maladaptation and are ambiguous with regard to absolute maladaptation. In Fig. 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.</td>
</tr>
<tr>
<td>Lag load</td>
<td>Burger and Lynch 1995; Chevin et al. 2017; Smith 1976</td>
<td>Typically ( \frac{\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.</td>
<td>In Fig. 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).</td>
</tr>
<tr>
<td>Segregation load (or balanced load)</td>
<td>Crow 1970; Haag and Roze 2007; Kimura and Crow 1964</td>
<td>Segregation of deleterious recessive alleles into homozygotes, occurring in some but not all individuals in the population.</td>
<td>Likely a common source of relative and absolute maladaptation in wild populations, especially in the case of heterozygote advantages.</td>
</tr>
<tr>
<td>Drift load</td>
<td>(Lynch et al. 1995; Whitlock et al. 2000; Willi et al. 2013)</td>
<td>Segregating load that has become fixed in the population due to drift.</td>
<td>A potential source of relative and absolute maladaptation in small populations.</td>
</tr>
<tr>
<td>Migration load</td>
<td>(Bolnick and Nosil 2007; Garcia-Ramos and Kirkpatrick 1997)</td>
<td>Inflow of maladapted alleles from populations not adapted to the local environment.</td>
<td>A likely cause of maladaptation in many classic and contemporary (Table 3) instances of relative maladaptation.</td>
</tr>
<tr>
<td>Mutation load</td>
<td>(Kimura et al. 1963; Muller 1950; Agrawal and Whitlock 2012; Lynch and Gabriel 1990)</td>
<td>Due to ongoing inputs of deleterious mutations.</td>
<td>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).</td>
</tr>
<tr>
<td>Load Type</td>
<td>Description</td>
<td>Characteristics</td>
<td></td>
</tr>
<tr>
<td>----------------------------------</td>
<td>------------------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Recombination load</td>
<td>Genetic recombination resulting in the disassociation of favorable combinations of loci. Loss of linkage disequilibrium (across loci) favored by selection.</td>
<td>Presumably a common source of relative and absolute maladaptation, but also (like mutation or migration) a likely contributor to future adaptation.</td>
<td></td>
</tr>
<tr>
<td>Meiotic drive load (or selfish chromosomal transmission)</td>
<td>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.</td>
<td>Not well described in wild populations, but theoretically capable of causing both relative and absolute maladaptation.</td>
<td></td>
</tr>
<tr>
<td>Non-local load</td>
<td>Neutral mutations are deleterious in non-local environments, causing ‘non-local maladaptation’.</td>
<td>Non-local maladaptation (i.e. of imported genotypes) can falsely indicate local adaptation via selection rather than via conditionally maladaptive drift of the imported reference population.</td>
<td></td>
</tr>
</tbody>
</table>

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. Some examples of relative maladaptation without apparent negative population dynamic consequences. These examples highlight instances of an apparent disconnect between the relative and absolute perspectives of fitness.

<table>
<thead>
<tr>
<th>System</th>
<th>The relative perspective</th>
<th>The absolute observation</th>
<th>Hypothesized explanation</th>
<th>Key references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trinidadian guppies</td>
<td>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.</td>
<td>Guppies are extremely abundant in oil-polluted environments, perhaps more so than in many pristine environments.</td>
<td>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 &quot;enemy release&quot; compensates for lack of abiotic adaptation.</td>
<td>Rolshausen et al. 2015</td>
</tr>
<tr>
<td>Trinidadian guppies</td>
<td>When guppies from highly-parasitized populations are introduced into parasite-free environments they rapidly evolve increased parasite resistance.</td>
<td>The introduced guppies showed rapid increases in population size following the experimental introduction.</td>
<td>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.</td>
<td>Dargent et al. 2013; 2016</td>
</tr>
<tr>
<td>Roadside frogs</td>
<td>Wood frogs exposed to high-salt environments beside roads perform poorly in all environments, whether salty or not.</td>
<td>Wood frogs are very abundant in roadside ponds, perhaps more so than in many woodland ponds away from roads.</td>
<td>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.</td>
<td>Brady 2013; 2017</td>
</tr>
<tr>
<td>Daphnia in metal-polluted lakes</td>
<td>Resurrection experiments show that Daphnia evolved decreasing metal tolerance during the period of heavy metal pollution.</td>
<td>Daphnia persisted in the lakes through the period of heavy metal pollution.</td>
<td>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.</td>
<td>Rogalski 2017</td>
</tr>
</tbody>
</table>
increasing metal pollution.

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
Table 3. Some recent studies of maladaptation that incorporate both relative and absolute perspectives.

<table>
<thead>
<tr>
<th>System</th>
<th>Primary cause of maladaptation</th>
<th>Inference regarding trait maladaptation</th>
<th>Inference regarding relative fitness</th>
<th>Inference regarding absolute fitness</th>
<th>Key references</th>
</tr>
</thead>
<tbody>
<tr>
<td>Misty outlet stream stickleback</td>
<td>High gene flow from an adjacent lake population</td>
<td>Substantial deviation of observed from expected phenotypes in the outlet.</td>
<td>Transplant experiments in the outlet show weak (if any) local adaptation.</td>
<td>Population densities in the outlet are very low.</td>
<td>Moore and Hendry 2009; Moore et al. 2007</td>
</tr>
<tr>
<td>Timema walkingsticks</td>
<td>High gene flow between adjacent populations on different host plants.</td>
<td>High frequency of maladaptive (i.e., non-cryptic) morphs on each host plant.</td>
<td>Reciprocal transplants show strong selection against maladaptive morphs.</td>
<td>Higher frequencies of maladaptive morphs lead to lower population sizes.</td>
<td>Bolnick and Nosil 2007 (Farkas et al. 2016; Nosil 2009)</td>
</tr>
<tr>
<td>Dutch flycatchers</td>
<td>Climate change that is advancing the dates of spring warming.</td>
<td>Departure dates from over-wintering sites are too late to enable early egg laying date on arrival at breeding sites.</td>
<td>Selection typically favors earlier spring breeding.</td>
<td>Where the migration vs. laying date mismatch is greatest, populations are declining at the highest rate.</td>
<td>Both et al. 2006</td>
</tr>
<tr>
<td>Flowering plants in &quot;Thoreau's woods&quot;</td>
<td>Climate change that is advancing the dates of spring flowering.</td>
<td>Some species do not advance their spring flowering dates despite advancing spring temperatures.</td>
<td>Selection typically favors earlier spring flowering.</td>
<td>Species least able to advance their spring flowering dates have become extirpated.</td>
<td>Willis et al. 2008</td>
</tr>
<tr>
<td>Dutch great tits</td>
<td>Climate change that is advancing the dates of spring warming.</td>
<td>Climate change is increasing the mismatch between dates of egg laying and dates of peak food abundance.</td>
<td>Nestling survival decreases as the mismatch increases.</td>
<td>Populations are not declining because reduced nestling survival decreases competition among fledglings.</td>
<td>Reed et al. 2013</td>
</tr>
<tr>
<td>Hawaiian crickets</td>
<td>An invasive parasitoid is</td>
<td>Loud mating calls by male crickets</td>
<td>In fewer than 20 generations, 90% A massive decline in cricket</td>
<td></td>
<td>Zuk et al. 2006</td>
</tr>
</tbody>
</table>
attracted to the mating signals of an (also invasive) cricket.

attract the invasive flies.
of population abundance
shifted to a silent 'flatwing' mutation.

of population abundance
following invasion of the fly.

of population abundance

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.

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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 versus environmental change), regardless of whether the two perspectives yield similar interpretations, and even if the precise inferences are not yet entirely certain.
<table>
<thead>
<tr>
<th>System</th>
<th>Hypothesis</th>
<th>Inference regarding trait maladaptation</th>
<th>Inference regarding relative fitness</th>
<th>Missing inference about absolute fitness</th>
<th>Key references</th>
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</thead>
<tbody>
<tr>
<td>Lake Erie water snakes</td>
<td>High gene flow from mainland populations prevents precise adaptation in island populations.</td>
<td>Island populations contain numerous non-cryptic color morphs that are more typical of mainland populations.</td>
<td>Selection was found to disfavor the non-cryptic morph on the islands.</td>
<td>Do island water snake populations suffer reduced densities as a result of maladaptive gene flow?</td>
<td>Camin and Ehrlich 1958; King and Lawson 1995</td>
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<tr>
<td>Texas mosquitofish</td>
<td>Fish in a freshwater pond were maladapted to freshwaters, due either to high gene flow from brackish populations or to recent colonization.</td>
<td>Low reproductive effort in the pond fish relative to brackish fish.</td>
<td>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.</td>
<td>Does maladaptation in the pond fish cause low population density?</td>
<td>Stearns and Sage 1980</td>
</tr>
<tr>
<td>Riparian spiders</td>
<td>High gene flow from aridland spider populations causes maladaptation in a riparian spider population.</td>
<td>The riparian spider population showed phenotypes more typical of adjacent aridland spiders, but not after gene flow was experimentally reduced.</td>
<td>Experimental enclosures showed that selection acts against the aridland phenotype in riparian habitats.</td>
<td>Does maladaptation in the riparian population cause low population density?</td>
<td>Riechert 1993</td>
</tr>
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### Box 1. Terms associated with maladaptation

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
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</table>
| 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, over time, the population is adapted (see Fig B1). |
| Putative maladaptation| Can be used to describe plausible but inconclusive evidence for maladaptation (Crespi 2000), for instance in non-model systems where fitness is measured incompletely. Thus, a reciprocal transplant showing revealing low resident compared to immigrant reproductive success—but lacking data on survival to adulthood—could be described as putative relative maladaptation. |
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 the figure) at the local carrying capacity, thus having a mean absolute fitness of unity (blue vertical line in the 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 on the lower right portion of the panel) 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 goes here]
Figure legends

Figure 1. A 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 to 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 dash), 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.

Figure 2: Depicting 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 text for description.
Figure B1. Temporal dynamics and maladaptation. Temporal evolutionary dynamics may lead to maladaptation (A) and apparent maladaptation (B, C). (A) Adaptive dynamics passing through transient maladaptive states. (i) Displaced Gaussian fitness surfaces reflecting the difference in relative fitness ($\bar{w}$) of a given phenotype with mean trait ($\bar{x}$) in two different environments (blue, red). Relative fitness is measured in terms of the most fit trait value. (ii) The average phenotypes – and probability distributions $\Phi(\bar{x})$ – of populations $X$ (blue) and $Y$ (red) as they undergo adaptive evolution toward mean trait states that maximize their respective mean fitness. The black vertical marks the initial state; for each population three consecutive probability distributions $\Phi(\bar{x}(t))$ are shown, after 5, 50, and 500 generations of evolution. Population $Y$ (red) evolves more quickly and passes through trait states that have higher fitness (than Population $X$’s trait states) in both environments. (iii - v) Fitness plots that a hypothetical researcher would obtain when performing reciprocal transplant assays at $t_5$, $t_{50}$ and $t_{500}$. Fitness (y-axis) of the average phenotype is plotted for each population (blue and red lines) and for each environment (x-axis). (iii, iv) Reciprocal transplant assays performed during transient states ($t_5$, $t_{50}$) would suggest that population $X$ is maladapted to its environment although both populations undergo deterministic adaptive evolution. (v) Only assays performed close to equilibrium state ($t_{500}$) suggest local adaptation. (Fitness surfaces and distributions of the average phenotypes were calculated using realistic parameterizations of equations 13 and 18c in Lande (1976)). (B) Conceptual demonstration of how temporal variance in fitness leads to temporary states of maladaptation even in locally adapted populations. Solid thick lines illustrate mean fitness in populations $P_1$ and $P_2$ that are locally adapted to environments $E_1$ and $E_2$ respectively in a reciprocal transplant. However, temporal environmental
variation causes natural selection to fluctuate, leading to nonzero variance in local mean fitness over time, indicated by confidence limits. The expectation of observing maladaptation when, in fact, populations are locally adapted, depends on the ratio of temporal variance in fitness within environments to variance in fitness across environments due to local adaptation. If temporal variance in fitness within environments is low (i), the probability of observing maladaptation in the locally adapted populations is low. With higher temporal variance in fitness within environments relative to variance in fitness due to local adaptation across environments (ii), point observations of local maladaptation (thin solid lines) relative to local adaptation (dashed lines) become more likely. (C) A second cause of apparent maladaptation is the evolution of risk-averse or “bet-hedging” traits. Bet hedging maximizes long-term fitness by reducing temporal variance in fitness at the cost of expressing low fitness under average or expected conditions, causing incongruities in trait optimality over different temporal scales (Simons 2002). Here, a population that maximizes geometric-mean fitness \( W_{G_{\text{max}}} \) (dashed line) may be seen as truly locally adapted. The trait that maximizes expected, or arithmetic-mean fitness \( W_{A_{\text{max}}} \) (solid line) is suboptimal (yellow marker) over the longer term; thus, the trait that maximizes geometric-mean fitness over the longer term will appear to be suboptimal (red marker) under expected, or “average” conditions.
Figure 1