Whither adaptation?

Andrew P. Hendry · Andrew Gonzalez

Abstract The two authors of this paper have diametrically opposed views of the prevalence and strength of adaptation in nature. Hendry believes that adaptation can be seen almost everywhere and that evidence for it is overwhelming and ubiquitous. Gonzalez believes that adaptation is uncommon and that evidence for it is ambiguous at best. Neither author is certifiable to the knowledge of the other, leaving each to wonder where the other has his head buried. Extensive argument has revealed that each author thinks his own view is amply supported by both theory and empirical evidence. Further reflection has revealed that the differences in opinion may start with the different disciplines in which we work: evolutionary ecology for Hendry and community ecology for Gonzalez. In the present paper, we each present devastating evidence supporting our own position and thus refuting that of the other. We then identify the critical differences that led to such opposing views. We close by combining our two perspectives into a common framework based on the adaptive landscape, and thereby suggest means by which to assess the prevalence and strength of adaptation.

Keywords Adaptive divergence · Adaptive radiation · Adaptive landscape · Contemporary evolution · Ecological speciation · Source–sink dynamics · Metapopulation · Metacommunities · Coevolution · Gene flow · Constraint

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Introduction

A shared goal of evolution and ecology is to understand the origins and maintenance of biological diversity. One might think that adaptation would have emerged by now as a general explanation, but both fields continue to debate its importance (see also Leigh 2007). In evolutionary biology, one camp argues that adaptation is an overwhelmingly powerful force (e.g., Simpson 1944, 1953; Williams 1966; Endler 1986; Charlesworth et al. 1982; Rose and Lauder 1996; Schluter 2000; Bell 2008), whereas other camps argue that random genetic effects and constraints can be just as important (Kimura 1983; Gould and Lewontin 1979; Gould 2002). In ecology, one camp argues that the (co)distribution of organisms is driven by adaptation to abiotic environments and interspecific interactions (Lack 1947; Chesson 2000; Chase and Leibold 2003), whereas another camp argues that random processes of birth, death, and dispersal are sufficiently explanatory (Caswell 1976; Bell 2001; Hubbell 2001). Individual researchers often feel strongly one way or the other, and a general consensus is lacking.

The two authors of the present paper have recently had to confront our own adaptation divide. During the course of extended arguments about the prevalence of adaptation, we eventually realized that our disagreement partly reflected different perceptions of what constitutes adaptation and maladaptation. Our ability to talk past each other, without initially realizing it, made us aware that our respective fields (evolutionary ecology and community ecology) were not often in conversation. The present paper is an attempt to initiate one such conversation.

The key to a profitable conversation, or argument, is for both parties to fully understand each other's perspective. We therefore start this paper by each presenting our own view of adaptation without excessive corruption from the other. This is why you won't see us adopt a common definition of (mal)adaptation at the outset. After these independent perspectives, we show how they can be profitably united through the framework of phenotypic adaptive landscapes. The resulting reconciliation suggests a path forward to quantifying the prevalence and importance of adaptation and maladaptation in nature. When enough empirical studies have progressed down this path, it will be time to revisit our argument and perhaps provide more definitive conclusions.

Hendry's Panglossian paradise

The various definitions of adaptation and maladaptation can be wearisome in their diversity, contradiction, and controversy (Williams 1966; Gould and Lewontin 1979; Rose and Lauder 1996; Crespi 2000; Nesse 2005; Hansen et al. 2006). I therefore simply outline my own view, which experience suggests is shared by at least some other evolutionary ecologists. At the outset, it is important to recognize that I am focusing on "local" adaptation—the relative fitness of local versus foreign individuals—rather than "adaptation" in the broad sense (e.g., the ability to use oxygen, or eat, or fly, or swim). After outlining my view of adaptation in the context of adaptive landscapes, I provide a summary of the empirical evidence.

Phenotypic adaptive landscapes relate the mean fitness of real and hypothetical populations to their mean phenotypes, while assuming a particular phenotypic variance (Simpson 1944, 1953; Schluter 2000; Arnold et al. 2001). In the absence of constraints, mean phenotypes should evolve up-slope on these landscapes until they reach a local fitness peak (i.e., an "optimum"). This simple framework has proven useful for understanding evolutionary diversification but many complexities and complications arise. For example, adaptive landscapes can be altered by density- and frequency-dependence (Svensson and Sinervo 2000; Dieckmann et al. 2004). Additional complications include temporal variation in the landscape and genetic constraints on movement across a given landscape (Schluter 2000; Arnold et al. 2001).

Although real adaptive landscapes can be very complicated, I here assume the simplest possible situation—so as to best illustrate my points. First, I assume a single phenotypic trait with a constant variance. Second, I assume two populations residing in different environments, or using different resources, that are stable through time. Third, I assume that populations in the two environments have different optimal phenotypes, with fitness declining monotonically to either side (Fig. 1a). If individuals can switch their occupation/use of the environments/ resources so as to maximize fitness for a given phenotype, the outcome might be a single-function adaptive landscape with two high-fitness peaks separated by a low-fitness valley (Fig. 1b). Here, however, I assume that individuals cannot switch between the environments/resources, and I therefore retain the two-function adaptive landscape of Fig. 1a.

This landscape can be used to illustrate several important types of adaptation (Fig. 2). One is "adaptive divergence," whereby two populations differ phenotypically in the direction of their respective local optima. This adaptive divergence can range from complete (mean phenotypes under their respective optima) to absent (mean phenotypes do not differ in the appropriate direction). Another type of adaptation is proximity of the mean phenotype in a given population to a local optimum, with the magnitude of any such deviation defining the *degree* of maladaptation. When quantifying either type of adaptation, we can consider two different response variables: deviations of mean phenotypes from local optima (variation along the x-axis in Fig. 2) and corresponding differences in mean population fitness (variation along the y-axis in Fig. 2). I will variously invoke both response variables in the following sections. Of additional interest, although not considered here, is the spread of individual phenotypes around an optimum (Hansen et al. 2006), and the extent to which that variation might or might not be adaptive.

In the sections that follow, I draw on several lines of evidence to illustrate the prevalence and importance of adaptation. I focus particularly on natural populations, because their adaptation is the phenomenon we wish to explain, and on the results of meta-analyses, because this reduces the temptation to cherry pick the most supportive examples. I do not devote space to mathematical models, because these unquestionably show the power of natural selection in driving adaptation (Fisher 1930; Williams 1966; Endler 1986; Schluter 2000; Arnold et al. 2001; Dieckmann et al. 2004; Bell 2008). I also do not discuss evidence for adaptation at the genomic
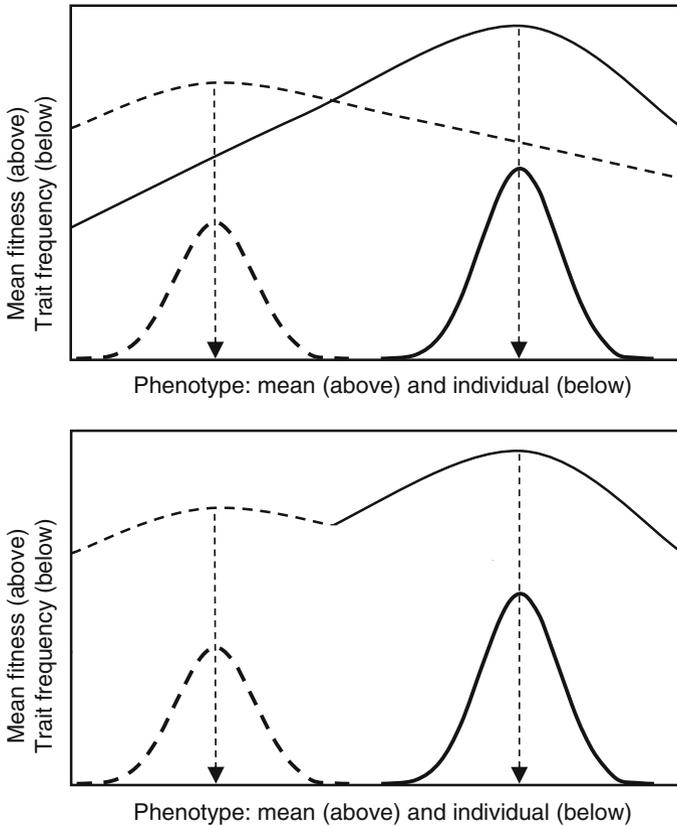
Fig. 1 A graphical representation of hypothetical adaptive landscapes and phenotypic distributions for two well-adapted populations (one shown with solid lines, one shown with dashed lines) that occupy two different environments (or use two different resources). The upper lines in each panel show the topography of the adaptive landscape; i.e., mean population fitness (*y*-axis) with respect to mean population phenotype (*x*-axis) and assuming a particular (unspecified) trait variance and the absence of strong density dependence. The lower lines show hypothetically distributions of phenotypes within each well-adapted population. The vertical dashed lines show locations of optimal phenotypes; corresponding to peaks on the adaptive landscape. The top panel approximates the situation where each population continues to use its original environment/resource regardless of phenotype, and so the two populations see different adaptive landscapes even at a common phenotype. The bottom panel approximates the situation where individuals could switch their use of environments/resources to optimally match their phenotype. Note that the functions and curves are simply for illustration and are not based on explicit equations

level, because this topic falls outside the purview of phenotypic adaptive landscapes.

Reciprocal transplants

Insights into *adaptive divergence* can be gained by using reciprocal transplants to test the prediction that fitness in a given environment is higher for local individuals (from that environment) than for foreign individuals (from other environments)
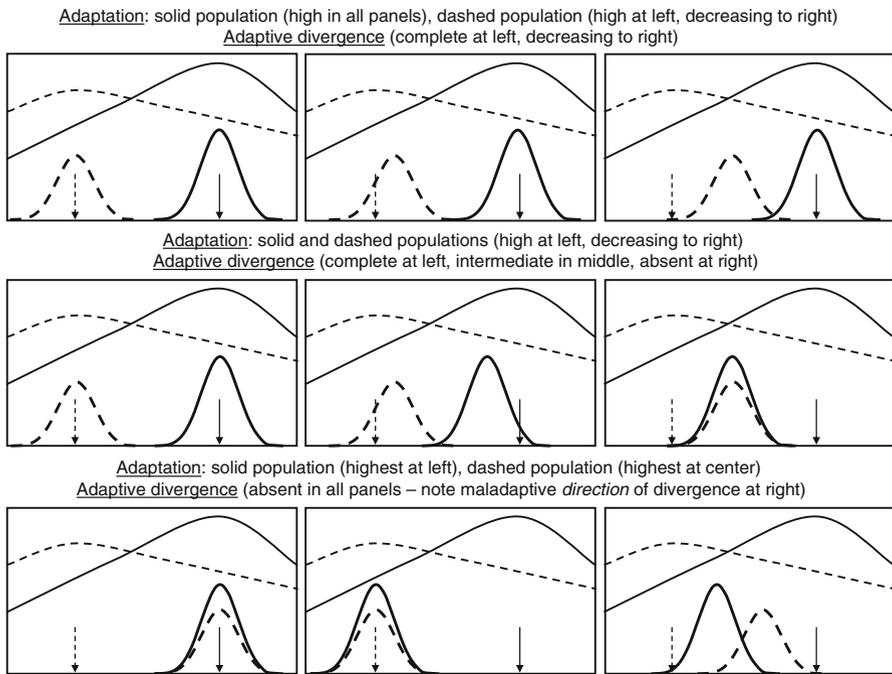
Fig. 2 Various degrees and types of local adaptation as discussed by Hendry. All panels show the same hypothetical adaptive landscapes (from Fig. 1a) but consider populations with different mean phenotypes. The text above each row of panels provides interpretations of (1) adaptation within the populations and (2) adaptive divergence between the populations

(Kawecki and Ebert 2004; Nuismer and Gandon 2008). Reviewing such studies, Schluter (2000) reported that local individuals outperformed foreign individuals in 32 of 42 cases, and that the difference was often very strong within a given study. Updating and modifying this analysis, Joe Hereford (unpublished data) found that local individuals outperformed foreign individuals in 71% of 777 estimates, and that the average magnitude of local adaptation (proportional increase in fitness for local individuals) was 0.45. In addition to such inferences about adaptive divergence in fitness (y-axis), inferences about adaptive divergence in traits (x-axis) can be made in transplant experiments by measuring selection on phenotypes (e.g., Byars et al. 2007). Profitable use can also be made of hybrids, which should often show low fitness in both parental environments, and should experience selection in the direction of local phenotypes (e.g., Nagy 1997; Schluter 2000). No suitable meta-analyses are available to test these ideas.

Reciprocal transplant experiments thus provide frequent evidence for adaptive divergence in fitness—although several biases may act in favor of this conclusion. First, many studies focus on populations in environments where phenotypes were already known to differ (Schluter 2000; J. Hereford, unpublished data). Second, studies failing to find local adaptation may be published less often. Third, reciprocal transplant experiments often do not control for prior experience, maternal effects, or phenotypic plasticity. Even if such biases are not important, a skeptic (see Gonzalez)

might emphasize that 29% of the estimates actually fail to support local adaptation. The problem here, however, is that the evidence for local adaptation is probably compromised by the frequent use of incomplete fitness surrogates (e.g., survival only) and short lengths of time over which fitness is assessed (e.g., a few weeks). Indeed, J. Hereford (unpublished data) found that evidence for local adaptation increased with more inclusive fitness surrogates (e.g., survival plus fecundity). A final point to consider is the lack of strong evidence for local adaptation in a recent meta-analysis of experiments on interacting species, particularly hosts and parasites (Hoeksema and Forde 2008). These results are difficult to interpret, however, because an apparent lack of local adaptation by parasites may simply reflect the presence of some local adaptation by hosts (or vice versa).

Selection in nature

If the mean phenotype in a population is *not* in the immediate vicinity of an adaptive peak, then that trait should be subject to directional selection (Endler 1986; Schluter 2000; Arnold et al. 2001). Perhaps insight into adaptation can therefore be gained from Kingsolver et al.'s (2001) review of more than 2,500 selection estimates in natural populations (i.e., regression coefficients of fitness estimates on individual phenotypes). Contrary to the above prediction, selection was generally very weak (standardized selection gradient = 0.16), and 95% of the estimates were non-significant. Moreover, some authors have argued that this dataset is inherently biased toward stronger selection (Hereford et al. 2004; Hersch and Philips 2004; but see Knapcyzk and Conner 2007). Regardless of any such bias, a remaining problem is the lack of an objective criterion by which to discriminate "weak" versus "strong" selection. Hereford et al. (2004) developed such a criterion: comparing selection on a given trait to selection on fitness itself, inferring that directional selection was often very strong. The problem is that the estimates were unrealistically high, and so the suggested criterion needs further consideration (Hendry 2005; Kingsolver and Pfennig 2007). A more objective approach might be to ask whether selection is stronger in populations that are farther from their local optima, such as those constrained by gene flow. In one of the few such studies, Bolnick and Nosil (2007) showed that reduced adaptation in *Timema* walking sticks leads to stronger selection. This finding suggests that the seemingly weak estimates in the Kingsolver et al. (2001) database really do reflect the absence of major constraints on local adaptation.

Selection estimates can also, with a number of assumptions, be used to infer the shape of adaptive landscapes in the vicinity of a population (Phillips and Arnold 1989). This shape can then be used to infer distances between mean phenotypes and the local optimum. Estes and Arnold (2007) estimated these distances to be less than one standard deviation for 46% of the Kingsolver et al. (2001) data, and less than two standard deviations for 65%. Estes and Arnold (2007) concluded that "such proximity confirms the intuition of many naturalists that populations are highly adapted to local conditions." Although I agree, it might be debatable whether two (or even one) standard deviation from the optimum represents "high" adaptation. And, of course, 35% of the data were estimated to come from populations with

mean phenotypes more than two standard deviations away from the local optimum. Although these ambiguities might be used to argue for only weak adaptation (see Gonzalez), the data may be biased in this direction. The reason is that measurement error and imperfect fitness surrogates will artificially inflate selection estimates for populations that are near local optima (Hereford et al. 2004; Hersch and Phillips 2004). Thus, a major difficulty in applying the Estes and Arnold (2007) approach is the accurate estimation of directional and stabilizing selection, which generally requires much larger sample sizes than are typically employed (Kingsolver et al. 2001; Hersch and Phillips 2004). Finally, it is important to recognize that large phenotypic deviations from optima may have little fitness consequence if the adaptive landscape is relatively flat. That is, a given deviation of mean phenotype from the optimum (x-axis) will have less effect on overall fitness (y-axis) when the shoulder of a fitness peak is soft than when it is sharp.

Contemporary evolution

When populations experience environmental change, fitness should initially decline but then recover through adaptation (Burt 1995). More specifically, environmental changes that shift the phenotypic optimum should induce strong selection and cause evolutionary change. The realization that this could occur quickly began to propagate in the 1960s with the advent of several studies arguing for adaptive change on sometimes very short temporal (decades) or spatial (meters) scales (e.g., Berry 1964; Johnston and Selander 1964; Jain and Bradshaw 1966). Many additional studies have since provided further examples of such contemporary adaptation (reviews: Hendry and Kinnison 1999; Kinnison and Hendry 2001; Reznick and Ghalambor 2001; Hendry et al. 2008). Moreover, a few of these studies have documented *trajectories* of phenotypic change, and found that these broadly match theoretical expectations for evolution on adaptive landscapes (Fig. 3). That is, phenotypic change is most rapid immediately after a disturbance and then gradually tapers off as the new optimum is approached (Reznick et al. 1997; Kinnison and Hendry 2001).

The above conclusions are, however, not immune to criticism. First, some of the documented phenotypic changes are likely plastic rather than genetic (Hendry et al. 2008; Gienapp et al. 2008). Even excluding the ambiguous cases, however, we still have many clear examples of genetically-based adaptive phenotypic change on short time scales (Hendry and Kinnison 1999; Kinnison and Hendry 2001; Hendry et al. 2008). Second, although contemporary adaptation is well documented for particular traits, few studies examine the consequences for fitness (Kinnison and Hairston 2007). And yet those few do report noteworthy effects. First, Hairston et al. (2005) estimated that population growth in Darwin's finches was just as strongly influenced by evolutionary changes in beak size as it was by ecological changes in food availability. Second, Pelletier et al. (2007) showed that 18% of the variation in the population growth rate of Soay sheep could be explained by changes in body weight. Third, Kinnison et al. (2008) showed that adaptation in introduced salmon increased offspring production by 29% after 26 generations. These results are
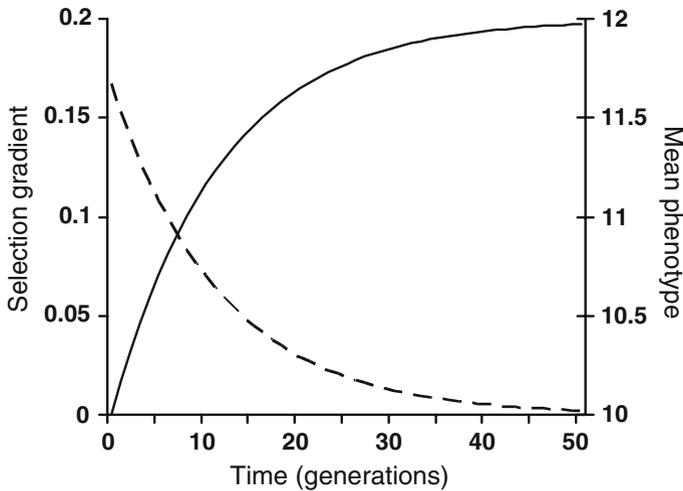
Fig. 3 Expected trajectories of selection (dashed line) and mean phenotype (solid line) for a population that experiences an abrupt shift in optimal phenotype. We model this shift as a change in the peak of the adaptive landscape from a value of 10 in generation zero to a value of 12 in generation one (units are arbitrary). The resulting trajectories are based on the equation $\Delta z = G\beta$, where Δz is the per-generation change in mean phenotype, G is the additive genetic variance (here 2.5), and β is the selection gradient (slope of the relationship between phenotype and fitness). The selection gradient is calculated as $\beta = [-z - \theta]/[\omega^2 + P]$, where z is the mean phenotype, θ is the optimum phenotype, P is the phenotypic variance (here 5), and ω^2 is the strength of stabilizing selection around the optimum (here 25). Changes in any of the parameter values does not change the asymptotic nature of the trajectories

certainly encouraging but more studies are needed before drawing broad general-izations about how selection improves fitness on short time scales.

Invasive species

If populations are adapted to their local environments, they might be expected to have low success in different environments. So what should we then make of invasive species, which sometimes become more dominant and widespread in their introduced range than in their native range? A first important point is that only a very small fraction of introduced organisms actually become invasive. Instead, very few introduced species are ever seen in the wild, very few of those establish viable populations, and very few of those become invasive (Williamson and Fitter 1996; Sax and Brown 2000). The general failure of introduced species to become invasive is thus quite consistent with a major role for local adaptation in nature. A second important point is that any demographic costs of initial maladaptation in introduced species can sometimes be offset by reduced competition and the availability of benign environments. Related to this, some introduced species appear to become invasive owing to the absence of their natural "enemies," such as parasites or predators (Liu and Stiling 2006).

For the relatively few species that do become invasive, adaptation might be very important (Facon et al. 2006). First, some invasive species appear "pre-adapted" to

human-disturbed environments, which is where they often prosper in their invasive range. Second, some species may be taxonomically pre-adapted to resist enemies in the introduced range (Parker et al. 2006; Ricciardi and Ward 2006). Third, the speed at which a wave of invasion propagates through space can be accelerated by evolutionary changes occurring after the initial introduction (García-Ramos and Rodríguez 2002; Phillips et al. 2006). Fourth, many of the best-documented examples of contemporary evolution come from introduced species (Reznick and Ghalambor 2001; Cox 2004). Although the above statements are not universally accepted, nor universally true, they are sufficiently supported to reveal that the success of invasive species does not contradict the importance of adaptation in nature.

The fossil record

If adaptation has contributed to the success and diversity of life, it should leave a signature in the fossil record. Some early paleontologists—most notably the conceptual originator of the phenotypic adaptive landscape—argued that such signatures were prevalent (Simpson 1944, 1953). Modern paleontologists, however, often reserve such judgments pending the outcome of formal statistical tests. The standard approach is now to invoke selection only if fossil data can conclusively reject a null hypothesis of random change—and this rarely happens (Hunt 2007). Although these results might be used to argue against the importance of adaptation, it is now clear that the existing methods have been inappropriately biased against detecting selection.

One bias is that null models are extremely difficult to reject simply on statistical grounds, particularly in deference to directional trends (Sheets and Mitchell 2001). If one instead uses formal model selection to weigh, on an equal footing, the support for alternative models (e.g., random, direction, stabilizing), stronger evidence for selection often emerges (Hunt 2007). Another bias is that previous tests have typically not included the most appropriate models of selection, such as a shifting peak on an adaptive landscape (Fig. 3). In the few cases where this type of model has been applied to fossil data, it has received strong support (Hansen 1997; Estes and Arnold 2007; Hunt et al. 2008). Additional applications of these newer methods will undoubtedly provide additional evidence for selection and adaptation in fossil sequences. Moreover, it is important to remember that even apparently random phenotypic changes may simply reflect random changes in selection, and therefore still reflect strong adaptive evolution (e.g., Grant and Grant 2002).

Ecological speciation

The evidence reviewed above points to selection and adaptation as the main drivers of phenotypic evolution within species. The same may be true for the origin of new species. This is the theory of "ecological speciation," wherein adaptation to different environments generates reproductive isolation. This transition from adaptive divergence to speciation can occur through the evolution several different reproductive barriers (Schluter 2000; Coyne and Orr 2004; Rundle and Nosil 2005). As one example, assortative mating can arise if the traits under divergent selection

also influence mate choice. As another example, hybrids between divergent forms can be maladapted for both parental environments and might therefore suffer low fitness in nature—even in the absence of genetic incompatibilities. Many recent studies have found evidence for ecological speciation (Schluter 2000; Rundle and Nosil 2005) but I know of only one relevant meta-analysis. Funk et al. (2006) used more than 500 species pairs to show that increasing ecological divergence (indexed by body size) is at least partly tied to increasing reproductive isolation. Moreover, Hendry et al. (2007) reviewed compelling evidence that adaptation can initiate reproductive isolation very quickly—thus linking contemporary adaptation to ecological speciation.

Hendry's withering summary

The evidence reviewed above confirms the prevalence and strength of adaptation in nature. First, reciprocal transplants usually find that local individuals have higher fitness than do foreign individuals. Second, selection in natural populations is often very weak, suggesting populations are well adapted to their local environments. Third, populations experiencing environmental change often show contemporary evolution in an adaptive direction. Fourth, introduced species rarely become invasive, and those that do become invasive often show signs of adaptive evolution. Fifth, new methods for analyzing fossil sequences have provided increasing evidence for selection and adaptation. Finally, adaptive divergence plays an important role in the formation of new species. Although the above evidence is sometimes equivocal, it clearly places the burden of proof on those who would argue that adaptation is rare and weak. Exit Hendry. Enter Gonzalez.

Gonzalez's maladaptationist leanings

The argument I will make is not for a return to Spandrelism (Gould and Lewontin 1979), which argues against the "just so stories" of early adaptationism and optimization, but rather a call for the study of maladaptation per se (see also Crespi 2000; Nesse 2005). An appropriate architectural metaphor would perhaps be the leaning tower of Pisa. This bell tower would ideally stand vertical—the top 3.9 m closer to upright—and thus assume a more "optimal" stance. However, the dynamic nature of the substrate on which the tower stands and the design constraints of its foundation prevent it from doing so. Without intervention (in 2008 70 tons of soil were removed from the foundations causing the tower to stop moving for the first time in its history), the tower would have fallen sooner rather than later, but whilst it is standing it functions as a bell-tower. Indeed, no recent attempt has been made to *fully* redress the angle of tilt. Quite the opposite, as an interesting architectural oddity, the desire has been to solidify the foundations and maintain the tower in its pendent state. In evolutionary terms the tower is maladapted to its environment, both because of design constraints (the foundations) and the dynamic nature of the substrate. Better-adapted bell towers that stand alone without the need for straightening can be envisaged (the functional adaptive landscape is quite

straightforward in this case!) but because of tourism this particular maladaptation has a surprisingly high fitness; likely ensuring its persistence into the future.

The state of play

> The population is always running uphill, but the peak is always two steps ahead. All the population ever sees, in effect, is the side of the mountain. Should it stop evolving, it will face extinction. This view is essentially Fisher's description of the deterioration of the environment. It is also closely related to his model on the nature of adaptation that assumes that a population is never exactly at its optimal phenotype. p. 305, J. H. Gillespie (1991).

For the most part, Hendry has argued that local adaptation is widespread, and that most populations are reasonably close to a fitness peak on their adaptive landscape. Theory and empirical evidence, however, suggest that local adaptation is hard to attain and that maladaptation is likely widespread (e.g. Stearns and Sage 1980; Gillespie 1991; Lande and Shannon 1996; García-Ramos and Kirkpatrick 1997; Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997; Crespi 2000; Thompson et al. 2002; Nesse 2005; Roy et al. 2005; Frank 2007; Garant et al. 2007). The reasons for widespread maladaptation are numerous (Haldane 1930, 1956; Barton and Partridge 2000). Adaptation by natural selection is a reactive process that can, at best, only lag changes in the environment. Other constraints include small population size (including its influence on genetic drift), genetic architecture (including pleiotropy and the need for appropriate genetic variation), the evolvability of genetic systems, the dispersal of genotypes, and the highly dynamic nature of the environment. Together, these factors ensure that optima are rarely attained by local phenotypes and that maladaptation is prevalent and persistent.

Environmental gradients and temporal variation are universal and cause adaptive peaks to constantly move. This dynamic nature of adaptive landscapes then drives spatial and temporal variation in selection on local populations. Because the response to selection is delayed, mismatches between the average phenotype in a population and the local optimum are inevitable. These mismatches then cause a decrement in local fitness ("evolutionary load" sensu Lande and Shannon 1996) that defines the level of maladaptation. As I will show, maladaptation may be sufficiently severe that many populations persist as demographic sinks, sustained only by the influx of individuals from source populations. Because all populations and communities are open systems, dispersal and gene flow then constrain local adaptation and ensure persistent maladaptation (i.e. migration load, cf. Lenormand 2002; Hendry and Taylor 2004; Bolnick and Nosil 2007; Moore et al. 2007). The addition of species interactions and the reciprocal selection brought about by coevolution can further hinder local adaptation (Case and Taper 2000; Thompson et al 2002). In the following I will expand on these arguments. Taken together, they provide a strong case for maladaptation as a common state in nature. Moreover, recent theory and experiments reveal that maladapted populations can persist for many generations because of the interaction between immigration and environmental variation. In addition, theory reveals that maladaptation can sustain and

generate new diversity. When placed in the context of rapid environmental change, and the resulting reductions in population size (e.g., Both et al. 2006), the importance of a research program focused on the persistence and evolution of maladaptation is obvious (Crespi 2000).

Defining maladaptation

To identify whether the phenotypes characterizing a population are maladaptive, one must evaluate three conditions (Brandon 1990): (1) the set of phenotypes that have been available for selection, (2) the environment occupied by the population over time and space, and (3) environmentally-mediated mapping of phenotypes onto mean population fitness (often summarized by the *per capita* growth rate). These conditions allow me to identify a strong and a weak definition of maladaptation. In the strong sense, maladaptation is present if the population cannot sustain a positive growth rate in the long term. In the weak sense, maladaptation is present if phenotypes do not maximize local fitness, compared to other relevant phenotypes. In this latter case, a population may maintain positive growth that is nonetheless well below the maximum attainable. An additional measure of relative maladaptation compares the mean fitness of the population with the fitness of the best-adapted phenotype in the population, thus estimating the current evolutionary lag of the population undergoing directional selection (Gandon and Michalakis 2002). The strong definition of maladaptation relates to absolute fitness whilst the weak definition relates to relative fitness.

Maladaptation in nature

Many transplant experiments have been conducted to test for a home site advantage and hence local adaptation. Joe Hereford's unpublished analysis of transplant experiments was cited by Hendry as providing general support for the preponderance of local adaptation. This dataset, however, contains important biases, including experiments conducted across continents and along steep environmental gradients, well beyond the typical dispersal distance of the study organisms. This issue raises the key question of scale. Reciprocal transplant experiments will be most relevant when they are conducted at the scale of dispersal. Clearly, immigrants taken from a great distance are not expected to outperform a local resident. Despite this bias, the frequency of maladaptation in Hereford's analysis was quite high (29% of the estimates), and the magnitude of local adaptation (relative fitness of the native population minus relative fitness of a non-native population) was small given the observed range (0.45 ± 0.03 SE, range −3.0 to 5.0). Ideally transplant experiments should be conducted with replicate populations of varying isolation; local adaptation should be weaker in the case of higher migration and gene swamping (Hendry and Taylor 2004; Bolnick and Nosil 2007).

The empirical basis of Hendry's argument is also founded on whether directional selection is common and detectable in nature. If populations are maladapted, then phenotypes should be under strong directional selection toward the optimum.

Hendry cites Estes and Arnold's (2007) study as providing support for the existence of local adaptation, yet as Hendry points out, the data are ambiguous. Less than half (46%) of the populations in the dataset are within one phenotypic standard deviation of the optimum, whilst 35% are more than two standard deviations away. To provide some perspective García-Ramos and Kirkpatrick (1997) pointed out that some taxonomists assign a subspecific rank when the morphological difference between two populations exceeds 2.6 standard deviations. Clearly, the jury is still out on whether or not populations are locally adapted according to the analysis of Estes and Arnold (2007).

Source–sink populations and metacommunities

If maladaptation is widespread in nature, then we must explain how it persists over extended spatial and temporal scales. Recent theory demonstrates that maladapted populations may persist for very long periods of time provided they are not too maladapted and that they are connected by a flow of immigrants from elsewhere (Holt and Gomulkiewicz 1997; Gonzalez and Holt 2002). Consider the simplest possible (black-hole) sink population that sends out no emigrants but receives a constant number of immigrants (I), and has a per capita fitness of $R < 1$. That is, $N(t + 1) = RN(t) + I$ and, at equilibrium, we have $N* = I/(1 - R)$. Thus a large sink population can be maintained at equilibrium if there is high immigration and a per capita fitness that is only slightly below replacement (R close 1). In this simple case, I assumed that the environment was constant, yet it is also known that environmental variability influences extinction risk.

Consider therefore a stochastic version of our sink population: $N(t + 1) = R_{(t)}N_{(t)} + I$. Assume that $R_{(t)}$ varies, perhaps because of environmental variation, so that its geometric mean is <1. Roy et al. (2005) showed that the time-averaged arithmetic mean abundance in the sink is

$$\bar{N} = \frac{\text{Cov}(R,N) + \bar{I}}{1 - \bar{R}}$$

where $\text{Cov}(R,N)$ is the temporal covariance between population size and population growth rate. When this covariance is positive, the abundance of the stochastic sink population will be *greater* than its constant equivalent with the same average growth rate. Gonzalez and Holt (2002) provided experimental confirmation from the laboratory by showing that environmental variability can greatly inflate the abundance of maladapted sink populations and aid their long-term persistence. In the above equation, I assumed a constant source population in the landscape. However, Roy et al. (2005) show that the inflationary effect on population densities of environmental variability, captured by the covariance term, can also sustain a metapopulation consisting entirely of sinks. Matthews and Gonzalez (2007) corroborated this theory by demonstrating the persistence of maladapted meta-populations in laboratory microcosms for approximately 100 generations.

The theory just summarized demonstrates that weak maladaptation can persist for arbitrarily long periods of time in variable environments. The conditions for this situation are met easily in nature and some empirical evidence exists from natural
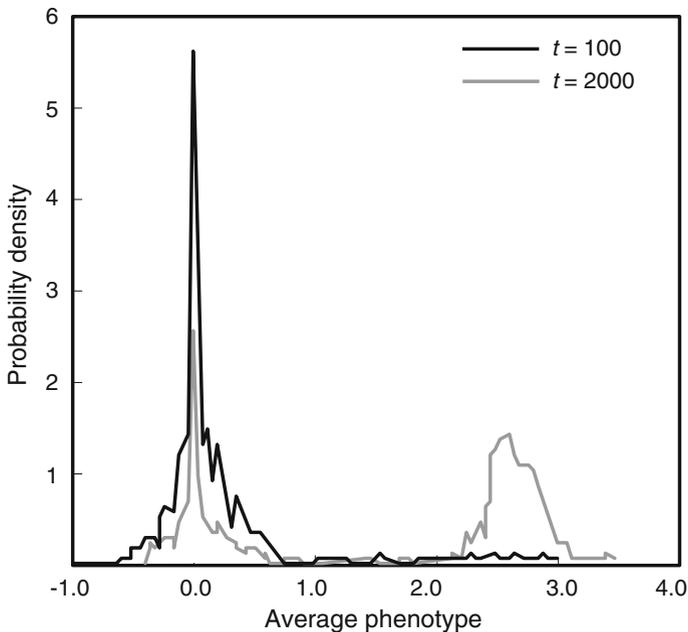
Fig. 4 Evolution in a sink population redrawn from Holt and Gomulkiewicz (2004). Shown is the distribution of mean phenotypes in 400 populations at two different times. After 100 generations most populations are still near the source phenotype (average phenotype = 0). After 2,000 generations, the distribution is bimodal with a large number of 'adapted' populations near the sink optimum ($z = 3$), another set in a 'maladapted' state near the source optimum ($z = 0$), and very few intermediates. Note also that even the adapted phenotypes are displaced from the optimum because of gene flow from the source

populations (Virgl and Messier 2000). However, although this theory shows how maladaptation can persist, sustained immigration may provide the opportunity for local adaptation to the sink conditions (Garant et al. 2007). Under what conditions does this occur?

Holt and Gomulkiewicz (2004) reported the results of an individual-based simulation of multilocus evolution in source–sink populations. A fixed number of immigrants per generation were drawn from a stable source population at mutation-selection-drift equilibrium. This study revealed that evolution is "punctuational": the sink population was either strongly maladapted and sustained at low densities by immigration or weakly maladapted and relatively near its optimum (Fig. 4), thus spending very little time in intermediate states. They also found that the harsher the sink environment the less likely it is that adaptive evolution will occur. Critically, the probability of adaptation increased with increasing immigration because this increased the chance a sink population would receive a favorable variant. The strength of this effect, however, will depend on whether or not immigration is stochastic (Gaggiotti and Smouse 1996). In the longer term, however, the role of immigration is reversed and it hampers adaptation once local densities approach the carrying capacity of the sink. There are two reasons for this. First, immigration accentuates intraspecific competition at carrying capacity, which lowers absolute

fitness. Second, immigration introduces suboptimal variants that may mate with locally superior variants.

Urban (2006) introduced evolution into a model of source–sink metacommunities so as to examine whether persistent maladaptation could sustain diversity. In this model, patch and species-specific potential reproductive rates followed a competitive hierarchy whereby species had similar regional fitness when reproductive rates are averaged over all communities (as in Mouquet and Loreau 2002). Each species was composed of variable phenotypes whose fitness, and maladaptation, was determined by the difference between their realized reproductive rate and that which would be obtained at the local optimum. In the presence of migration, superior competitors became locally adapted in source patches, whilst inferior competitors became maladapted because of abiotic patch heterogeneity and competition. The effect of maladaptation on local and regional diversity depended on dispersal rates. Diversity was lowest when dispersal was too low to counterbalance the reduction in reproductive rates due to maladaptation in the sinks. Diversity was greatly enhanced and sustained at intermediate rates of dispersal because the reduction in absolute reproductive rates in intermediate competitors leveled fitness differences amongst them and favoured the persistence of inferior competitors. The decline in fitness due to maladaptation is thus a fitness-equalizing mechanism that can favour coexistence (Chesson 2000). The loss of diversity that accompanies reduced connectivity in this metacommunity is consistent with the experimental results (Gonzalez et al. 1998). Further work is required to establish the importance of maladaptation in the link between species and genetic diversity (Vellend and Geber 2005), but it is clear that maladaptation may not be a hindrance to species diversity and population persistence.

Continuous space

I have thus far discussed populations in discrete sites. Whilst this is an appropriate framework for fragmented and patchy landscapes, many species are distributed almost continuously across space. Several theoretical models have examined maladaptation in this context (Pease et al. 1989; Lenormand 2002; García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997). In the Kirkpatrick–Barton (K–B) model, a species occupies a one-dimensional ecological gradient, along which the phenotypic optimum changes. The mean phenotype of the population determines its adaptation and therefore its growth rate, which then determines its density along the gradient. The main result of interest is that gene flow from populations at the centre of the range can prevent peripheral populations from evolving to their local optima. This maladaptation depresses abundance in peripheral populations and creates sinks. García-Ramos and Kirkpatrick (1997) used a similar model to show that the trait mean in the sink populations may deviate by up to three phenotypic standard deviations from the local optimum, a result consistent with that of Estes and Arnold (2007). Moreover, the steeper the environmental gradient is, the greater the restriction on a species' range. Under some parameter combinations, fully half of the range may be represented by sink populations that persist in a maladapted state and under sustained directional selection.

Case and Taper (2000) extended the K–B model to include interspecific competition and coevolution between two or more species. They found that interspecific competition can interact with gene flow such that less extreme environmental gradients are required than those used in the K–B model to generate similar levels of maladaptation. When species ranges meet, interspecific competition induces character displacement, and forces populations farther away from their optimum. Again, deviation from the local optimum reduces population densities, intensifies the asymmetry in gene flow from the centre to the periphery, and hampers local adaptation. Similar results are obtained when the species interactions are extended to include hosts and their parasites (Gandon et al. 1998).

The continuous models of range extent differ from the discrete source–sink models in their prediction of whether dispersal favors or disfavors local adaptation. In the source–sink models, immigration favors demographic persistence and the gene flow it provides enhances the likelihood of adaptation. Only when the sink population has adapted and attained its carrying-capacity does immigration displace the population from its local optimum. This latter effect is the primary mechanism in the continuous range models where gene flow swamps peripheral populations and maintains maladaptation. Both approaches, however, implicate the role of space, dispersal, and gene flow in the widespread maintenance of maladaptation (Haldane 1956).

Mosaics of coevolved maladaptation

The model of Case and Taper (2000) suggests that coevolution may sustain maladaption across a species range. Coevolving populations that engage in antagonistic interactions may not attain adaptive peaks, largely because the selective landscape is under continual change through reciprocal selection between the species (e.g., lag-load; Slatkin and Maynard Smith 1979). Thompson et al. (2002) suggest that geographical structure is the key to maintaining coevolutionary maladaptation across landscapes. Spatial variation in the strength and type of interspecific interactions (e.g. mutualistic vs. parasitic) generates mosaics of coevolutionary selection that, when coupled by gene flow, form complex spatial patterns of adapted and maladapted interactions (see also Gandon et al. 1998; Hoeksema and Forde 2008). For example, selection may locally favor mutualistic interactions, but if neighboring sites favour antagonistic interactions then gene flow may retard the fixation of mutualistic traits by hundreds of generations. Thus, maladaptation is expected to be very strong at the boundary between sites exchanging genes for traits involved in different coevolutionary interactions (Thompson et al. 2002). In addition to suggesting that maladaptation is the norm in non-equilibrium coevolutionary interactions, this work also suggests that the directional selection it causes is a necessary and important component of future evolution.

Darwinian extinction

The ultimate expression of maladaptation is population extinction, and recent theory suggests that natural selection at the individual level can drive the evolution of

sustained decreases in mean population fitness, thus causing extinction (Matsuda and Abrams 1994; Gyllenberg and Parvinen 2001; Dieckmann and Ferrière 2004). This process of Darwinian extinction (Webb 2003) arises because natural selection acts on relative fitness, but changes in population density are determined by absolute fitness. The fate of a population can thus switch when small and slow changes in a trait mean affect the dynamics and induce oscillations and extinction. Examples of this phenomenon are common in predator-prey models where selection for increasing predator attack rate (the trait under selection) increases the amplitude of the oscillations in predator-prey densities and ultimately drive the predator extinct (Rosenzweig 1973; Holt 1985). Selection for anti-predator behaviour amongst prey can have similar outcomes (Matsuda and Abrams 1994). More generally, Allee effects (positive density dependence) can promote Darwinian extinction because evolution can drive densities below a viable threshold. Few examples of Darwinian extinction have been reported from nature but the condition of contemporary evolution coupled to the dynamics of species interactions is now acknowledged to be widespread and is under intensive study in the laboratory (e.g. Yoshida et al. 2003; Fussmann et al. 2007).

Gonzalez's withering summary

Various lines of evidence thus point to the prevalence of maladaptation in natural populations, both because of factors limiting the evolution of natural populations (e.g., small population sizes and low standing genetic variation), and those that keep them away from local optima or change the adaptive landscape (e.g., environmental variability in multiple dimensions). The results of reciprocal transplants are mixed and often hard to interpret because of biases in the data. Studies of selection find that most populations are more than one phenotypic standard deviation from the optimum, suggesting they are maladapted. All interactions between organisms and their environment occur in space. Models of evolution and adaptation in space typically predict that gene flow (migration load) sustains maladaptation for parameter values typical of natural systems. This outcome is enhanced by interspecific interactions across species ranges, particularly when gene flow sustains nonequilibrium coevolutionary dynamics. In source–sink metacommunities, maladaptation can even foster coexistence by limiting the success of otherwise dominant competitors. Finally, maladaptation can evolve. Individual selection can lead ecological systems down evolutionary cul-de-sacs that ultimately drive their own demise. These findings provide only a glimpse of the relevant literature on maladaptation but they are sufficient to suggest that there really is trouble in Hendry's Panglossian Paradise.

Integration

The foregoing perspectives from an evolutionary ecologist (Hendry) and a community ecologist (Gonzalez) reveal very different views of (mal)adaptation. The key distinctions are that Hendry emphasizes information from phenotypes and

relative fitness in natural populations, whereas Gonzalez emphasizes information from absolute fitness in theory and laboratory experiments. It is also clear that data Gonzalez would interpret as evidence for maladaptation, Hendry would interpret as evidence for adaptation (e.g., García-Ramos and Kirkpatrick 1997; Estes and Arnold 2007). Part of the reason may be that Gonzalez adopts a glass half-empty view of adaptation, where a significant deviation from optimality (the tower is leaning and would fall) is evidence of maladaptation. Hendry, in contrast, adopts a glass half-full view, where evolution in the direction of optimality (the tower has had working church bells for more than 600 years) is evidence of adaptation. Our differences of opinion therefore partly reflect differences in perspective, rather than fundamental disagreements about evolution. Indeed, we now show how our two perspectives can be combined into a common framework based on adaptive landscapes (Fig. 5).

The following integration adopts several basic assumptions. First, the populations do not show density dependence; i.e., when population size is below carrying capacity. This assumption avoids the complication that mean fitness will, regardless of phenotype, approximate unity (i.e., replacement) under reasonably stable, density-limited conditions. This assumption might be relaxed if fitness can be assayed before selection and density dependence act on a given generation. Second, we assume that a single trait determines fitness, thus enabling a simple translation from phenotype to fitness. This translation is more difficult for more traits—but is still possible. Third, we assume a constant variance in phenotypic traits, because our presentation would be otherwise complicated by the variance-induced changes in adaptive landscapes (Schluter 2000; Arnold et al. 2001). This assumption might be relaxed in practice, as long as mean fitness can be calculated for a given phenotypic distribution.

We start with a single population and define four major aspects of (mal)adaptation. "Relative fitness (mal)adaptation" (RFMA) is the extent to which the observed mean population fitness ($\overline{W}_{obs}$) deviates from the maximum possible at the local fitness peak ($\overline{W}_{max}$). This difference is akin to Gonzalez's "weak" definition of maladaptation (see above), and it might profitably be standardized by the maximum possible fitness: $(\overline{W}_{max} - \overline{W}_{obs})/\overline{W}_{max}$. "Relative trait (mal)adaptation" (RTMA) is the extent to which the observed mean phenotype ($\overline{Z}_{obs}$) deviates from the mean phenotype that would maximize mean fitness ($\overline{Z}_{opt}$); i.e., $\left|\overline{Z}_{obs} - \overline{Z}_{opt}\right|$. It might sometimes be useful to express this quantity in standard deviation units, so as to control for measurement scales (e.g., Estes and Arnold 2007). "Absolute fitness (mal)adaptation" (AFMA) is the extent to which the observed mean population fitness ($\overline{W}_{obs}$) deviates from unity ($\overline{W} = 1$). This difference is akin to Gonzalez's "strong" definition of maladaptation (see above), and is expressed as $\overline{W}_{obs} - 1$ so that positive values will indicate population growth (source) and negative values will indicate population decline (sink). "Absolute trait (mal)adaptation" (ATMA) is the extent to which the observed mean phenotype ($\overline{Z}_{obs}$) deviates from the mean phenotype that separates positive from negative population growth ($\overline{Z}_{\overline{W}=1}$). We might wish this quantity to be positive when it enables growth and negative when it causes declines. We therefore specify ATMA as either (1) $\overline{Z}_{obs} - \overline{Z}_{\overline{W}=1}$ when $\overline{Z}_{obs} < \overline{Z}_{opt}$ or (2) $\overline{Z}_{\overline{W}=1} - \overline{Z}_{obs}$ when $\overline{Z}_{obs} > \overline{Z}_{opt}$; both assuming a monotonic
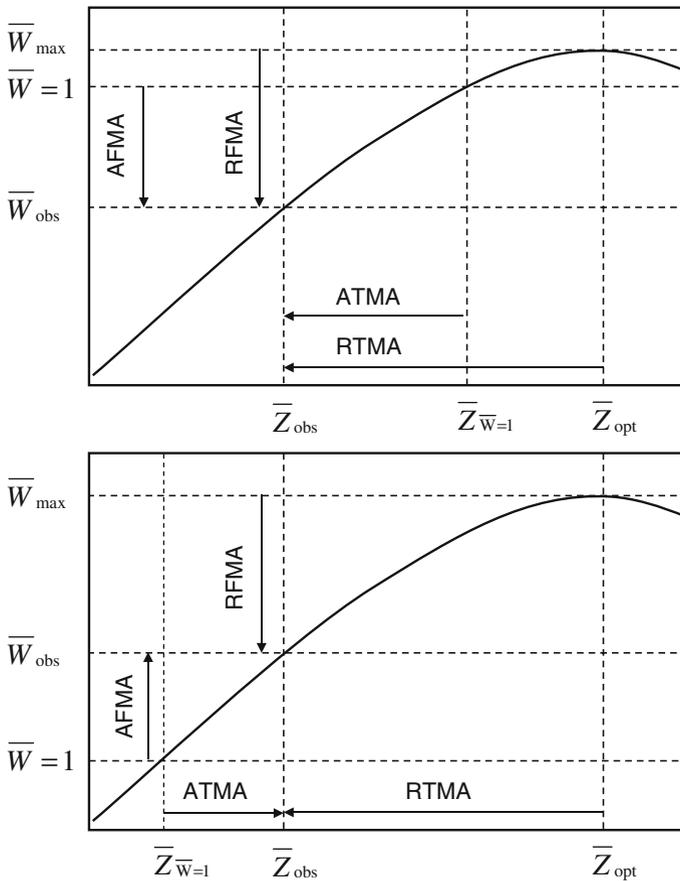
Fig. 5 Different types of (mal)adaptation illustrated on a phenotypic adaptive landscape (solid curve) of mean fitness (y-axis) with respect to mean phenotype (x-axis). Labels along the x-axis (and associated vertical dashed lines) show the observed mean phenotype ($\overline{Z}_{obs}$), the optimal mean phenotype ($\overline{Z}_{opt}$), and the mean phenotype that would correspond to a mean absolute fitness of unity ($\overline{Z}_{\overline{W}=1}$). Labels along the y-axis (and associated horizontal dashed lines) show how these mean phenotypes correspond to mean fitnesses: observed mean fitness ($\overline{W}_{obs}$), maximum mean fitness ($\overline{W}_{max}$), and a mean fitness of unity ($\overline{W}=1$). Also identified are the types of (mal)adaptation discussed in the text: relative fitness (mal)adaptation (RFMA), relative trait (mal)adaptation (RTMA), absolute fitness (mal)adaptation (AFMA), and absolute trait (mal)adaptation (ATMA). The two panels are identical except that a mean fitness of unity is above the observed mean fitness in the upper panel and below it in the lower panel

adaptive landscape with a single peak. Again, standardization by the phenotypic standard deviation will often be useful. (Note that although we have suggested a mixture of mean-based and variance-based standardizations, these are not meant to be definitive.)

We can easily extend some of the above definitions to the case of adaptive divergence between two populations (subscripts 1 and 2) and, although not shown here, to more populations. RFMA is the fraction of the maximum possible total fitness that the two populations actually achieve. This quantity might be calculated

as the sum of absolute fitness in the two populations divided by the sum expected at the optimum. Assuming a normal distribution, this might be approximated as $\left(\overline{W}_{\text{obs1}}N_1 + \overline{W}_{\text{obs2}}N_2\right)/\left(\overline{W}_{\text{max1}}N_1 + \overline{W}_{\text{max2}}N_2\right)$ where N_i might refer to the number of individuals in each population in the present, thus ignoring any adaptation-driven changes in population size. Alternatively, N_i in the denominator (the case of perfect adaptation) could be those attained under optimality, thus including any adaptation-driven changes in population size. This latter parameterization is obviously more difficult, particularly under density dependence. RTMA might be the observed difference in mean phenotype between populations expressed as a proportion of the divergence expected at optimality: $\left(\overline{Z}_{\text{obs2}} - \overline{Z}_{\text{obs1}}\right)/\left(\overline{Z}_{\text{opt2}} - \overline{Z}_{\text{opt1}}\right)$ (see also Moore et al. 2007), and this can be expressed in standard deviation units. Note that this particular equation is specific to the situation where $\overline{Z}_{\text{opt1}} \geq \overline{Z}_{\text{obs1}} \geq \overline{Z}_{\text{obs2}} \geq \overline{Z}_{\text{opt2}}$, as should be common. AFMA might be the average fitness deviation from unity across both populations. Assuming a normal distribution, this might be approximated as $\left(\left[\overline{W}_{\text{obs1}} - 1\right]N_1 + \left[\overline{W}_{\text{obs2}} - 1\right]N_2\right)/(N_1 + N_2)$. Positive values here indicate a system-wide positive rate of growth and negative values indicate a system-wide negative rate of growth. Extensions to divergence between populations are most complicated for ATMA, and so we do not here provide any details.

Quantifying (mal)adaptation in nature

The initial motivation for this paper was the authors' difference of opinion regarding the prevalence and strength of adaptation in nature. Having now formally defined various aspects of local adaptation, we can consider how these might be estimated. With these procedures in mind, we can revisit some of the previously-presented evidence to see if any resolution is yet possible.

Relative trait (mal)adaptation (RTMA) is the difference between the mean phenotype of a population (a quantity easily measured) and the locally-optimal mean phenotype (corresponding to the local fitness peak). This optimum might be estimated in several ways. First, one might examine multiple populations in similar environments to identify those that are least subject to constraints on adaptation. Mean phenotypes in these presumed-optimal populations can then be the basis of comparison for assessing maladaptation in other populations (e.g., Stearns and Sage 1980; Riechert 1993; Bolnick and Nosil 2007). A similar approach can be taken to quantifying RTMA for populations paired in different environments (i.e., adaptive divergence: Moore et al. 2007). This general approach is not perfect, of course, because it requires assuming that similar phenotypes would be optimal in all populations, when instead selection may vary in ways that are cryptic to the researcher. More powerful inferences are therefore possible if a constraint to adaptation (e.g., gene flow) is removed to track convergence on the expected optimum (e.g., Riechert 1993). A second approach to estimating optimal phenotypes is to use measurements of directional and stabilizing selection to estimate distances to local optima (Estes and Arnold 2007). The only meta-analysis of RTMA thus far performed used this method to conclude that 46% of the estimates were within one standard deviation of the inferred optimum and 65% were within two standard

deviations (Estes and Arnold 2007). Even ignoring concerns with the estimates themselves, a remaining hurdle is uncertainty as to what distribution of RTMA values might be interpreted as evidence for strong, or weak, adaptation (see above).

Relative fitness (mal)adaptation (RFMA) is the difference between observed mean fitness and the mean fitness of a comparable population at the local optimum. Reciprocal transplants can certainly be used to show that adaptation is greater for local than foreign individuals (see above), but this comparison cannot directly reveal how well each population is adapted to its home environment. For this, one first needs an estimate of mean population fitness, which is difficult to obtain but nonetheless possible through detailed demographic data (Hairston et al. 2005; Saccheri and Hanski 2006; Kinnison et al. 2008). One next needs an estimate of mean fitness at the local optimum, which might be obtained through two approaches. One is to estimate the shape of the adaptive landscape (see below) and to then extrapolate from observed mean fitness to that expected at the inferred optimum. Another approach is to track the trajectory of fitness change in populations introduced to new environments, or from which constraints (e.g., gene flow) have been removed, thus allowing projections to the expected equilibrium. It is here important to remove the confounding effects of changing density, which might be achieved by comparing the fitness of ancestors and descendents in the descendent population's home environment. This sort of work has been done in the laboratory (e.g., Lenski and Travasino 1994) but has only recently been attempted in the wild—and then at only a single time step (Kinnison et al. 2008). At present, we therefore have no idea of the distribution of RFMA in nature.

Absolute fitness (mal)adaptation (AFMA) can be quantified by measuring the per-capita growth rate of natural populations, while accounting for immigration and density dependence. This is no small feat, of course, but can be done with enough effort (Hanski and Saccheri 2006). More simply, one might qualitatively determine whether AFMA is positive (growth) or negative (decline) by eliminating immigration and then tracking changes in population size. This mimics the approach taken in some field studies of habitat fragmentation (Gonzalez et al. 1998) but it has not yet been generally applied. It would here be important to track population trajectories for an extended period of time because immigration may be the reason why a population is maladapted in the first place (Kirkpatrick and Barton 1997). If so, it may take some time for ongoing adaptation to enable population growth. The proportion of populations that might persist under such manipulations is unknown but it certainly isn't zero given the persistence of taxa on isolated islands with little or no immigration (e.g., atolls, small lakes without streams, mountain tops). At present, however, we have no direct insight into the distribution of AFMA in nature.

Absolute trait (mal)adaptation (ATMA) is the most difficult aspect of (mal)adaptation to estimate because it requires knowledge not only of fitness in a well-adapted population but also of the contributions of various traits to fitness. Estimation would therefore require integration of the approaches suggested above. We are not aware of any studies quantifying ATMA in nature.

As the foregoing summary reveals, it is possible to estimate the four aspects of local adaptation in nature, although too few studies have formally done so to yet allow generalizations. Once more such studies have been performed, it should be

possible to determine distributions of these estimators across natural populations. Any desired translation of such quantitative distributions into qualitative statements about whether or not adaptation is common or strong would require the development of some objective criteria for what constitutes "common" or "strong."

Adaptive landscapes in nature

As for the foregoing suggestions indicate, quantifying aspects of (mal)adaptation amounts to quantifying aspects of adaptive landscapes. The Holy Grail of understanding (mal)adaptation is therefore a full description of the adaptive landscape and the position of populations on this landscape. This is, of course, not a simple task. A first step is to estimate individual fitness across a wide range of trait space in various accessible environments (e.g., habitats, resources). This can be accomplished through the examination of natural phenotypes and artificially-generated phenotypes (e.g., phenotypic manipulations and hybridization) in a range of possible environments/resources (e.g., through habitat manipulations, reciprocal transplants, and performance assays in the lab). A second step is to translate the resulting individual fitness landscape into an adaptive landscape—by applying reasonable phenotypic variances (Schluter 2000). As a third step, we have stressed the importance of evaluating such landscapes in the context of absolute (rather than relative) fitness. This might be done by determining absolute fitness at one or more locations (e.g., existing populations) on a landscape and extrapolating to the rest of the landscape by reference to relative fitness.

No study has yet presented formal adaptive landscapes for natural populations. Some have come close, however, including (1) Schluter and Grant's (1984) prediction of mean population density for hypothetical populations of Darwin's finches with different beak sizes, (2) O'Neil's (1999) individual fitness landscapes for flowering traits in *Lythrum salicara*, (3) Svensson and Sinervo's (2000) individual fitness landscapes for egg size and hatching date in experimentally manipulated populations of side-blotched lizards, and (4) Benkman's (2003) individual fitness landscapes for real and hypothetical beak shapes in crossbills. In these cases, the resulting landscapes were used for understanding adaptive radiation (Schluter and Grant 1984; Benkman 2003) or for demonstrating current adaptation (O'Neil 1999; Svensson and Sinervo 2000). When expressing these landscapes in terms of absolute fitness, an additional use is the prediction of population growth or decline under environmental change (e.g., climate) or phenotypic change (e.g., hybridization, gene flow, domestication). Importantly, all of these inferences require information on phenotypes and fitness in nature, highlighting the importance of retaining a phenotypic perspective in the face of increasing emphasis on genomics.

Conclusion

Although both Hendry and Gonzalez are prepared to acknowledge the other's eloquence and strength of conviction, neither author has substantially changed his position. Hendry still feels that local adaptation is prevalent and strong, whereas

Gonzalez still feels it is uncommon and weak. It is now clear, however, that much of this disagreement boils down to different metrics of adaptation (traits and relative fitness for Hendry versus absolute fitness for Gonzalez), as well as differences in perspective (the tower stood for 600 years versus the tower is leaning and would fall). Each author does see considerable value in the other's viewpoint, which therefore led to our attempt at integration. This integration naturally points to a consideration of how we might better define and quantify various aspects of (mal)adaptation in nature. Our proposed metrics have been calculated only rarely, and so we are left uncertain as to whether we should even agree to disagree about the prevalence and strength of adaptation. One thing we can agree on, however, is that more studies should quantify the *degree* of maladaptation for traits and for fitness (Crespi 2000; Nesse 2005; Moore et al. 2007).

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