--- Introduce local adaptation ----------------------------------------------------------------------------------------------

Adaptation is generally defined as a genetically-based change caused by natural selection [7,8]. 2.

Generally, an adaptation is a phenotypic feature which is functionally designed by past natural selection, and which improves Darwinian fitness relative to alternative features (Williams 1966). 11.

Genotype · environment interaction for fitness is an obvious pre-requisite for local adaptation. 11.

Often show that genotypes are better adapted to their native environments than are genotypes from other populations (Linhart and Grant 1996; Van Zandt and Mopper 1998; Schluter 2000). 6.

Finally, we would like to reiterate that local adaptation as defined above is not a property of individual populations, but of a set of demes (i.e. a metapopulation). Nonetheless, it may be of interest to identify subsets of demes that do show a pattern of local adaptation vs. those that do not, especially if these subsets can be characterized by specific properties such as history, spatial arrangement, habitat size, spatial isolation, or deme size or age (see below). 11.

Theory of local adaptation predicts evolutionary changes in the metapopulation, but not changes in the environment. 11.

Divergent selection is the driving force of local adaptation. 11

Divergent selection leads to local adaptation when environmental heterogeneity is coarse grained relative to gene flow (Bradshaw 1984; Endler 1986), and local adaptation should be more pronounced between populations from more strongly divergent environments (Becker et al. 2006; Hereford and Winn 2008). 6.

Local adaptation to one environment may cause lower relative fitness in alternative environments, resulting in a trade-off or cost of adaptation. These trade-offs are thought to maintain genetic variation among populations within species, leading to morphological or physiological specialization (Futuyma and Moreno 1988; Day 2000; Jasmin and Kassen 2007), and may promote ecological speciation (Rundle and Nosil 2005). 6.

Therefore, the conditions for local adaptation mediated by polygenic traits are most favourable when selection in habitat 1 against genotypes well adapted to habitat 2 and vice versa is strong, but selection against intermediate (recombinant) genotypes is moderate. 11.

Reaching adaptive optima

In contrast, traits that are unconditionally adaptive will tend to become fixed within the species. 11.

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Have shown that spatial heterogeneity facilitates maintenance of polymorphism that shows such antagonistic pleiotropy, provided that density-dependence (population regulation) operates within demes (Christiansen 1975; Pimm 1979; Karlin & Campbell 1981). 11.

local adaptation requires that spatial variation in selection is substantially greater than temporal variation. In particular, latitudinal clines and other forms of spatial variation correlated with environmental factors are often observed for allele frequencies at allozyme loci (reviewed in Eanes 1999). 11.

In the context of local adaptation we are interested in differences in fitness gradients between habitats (e.g. Kalisz 1986; Petit & Thompson 1998; Caruso 2001). 11.

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---mechanisms that bring about local adaptation -------------------------------------------------------------------------

To summarize, ecological factors predicted to promote local adaptation include: low gene flow (i.e. low dispersal or strong habitat fidelity), strong selection against genotypes optimally adapted to other habitats but moderate selection against intermediate genotypes (most likely under moderate differences between habitats with respect to traits under selection), little temporal variation in the forces of selection, small differences between habitats in size and quality (e.g. the amount of resources), and costs of or constraints on adaptive plasticity.

We know much less about the effects of genetic architecture, as even the models with explicit genetics typically assume a simplistic genetic architecture (additivity and unlinked loci). One may expect that loci with large effects may be more important – polymorphism is more easily maintained and greater allele frequency differentiation is possible. Similarly, one could conjecture that linkage will be favourable for local adaptation as it reduces the power of recombination to break up locally adapted gene combinations (for a simple model see Dickinson & Antonovics 1973). Further theoretical work specifically addressing local adaptation mediated by polygenic traits with more complex genetic architecture is needed to substantiate these conjectures and generate new predictions. 11.

Of several forms such an interaction can take, the most important for local adaptation is antagonistic pleiotropy, whereby the alleles have opposite effects on fitness in different habitats. Such antagonistic pleiotropy implies that no single genotype is superior in all habitats, leading to trade-offs in adaptation to different habitats. 11.

Theory suggests that the magnitude of local adaptation will increase with greater genetic variation within populations and with greater environmental and phenotypic divergence between populations (Lande 1976; Endler 1977; Slatkin 1985; Garcia-Ramos and Kirkpatrick 1997).

Population differentiation corresponding to local adaptation is promoted by low dispersal and strong selection (Brown & Pavlovic 1992; Day 2000; Kisdi 2002; Spichtig & Kawecki 2004). However, if selection is very strong (i.e. fitness falls off very quickly as the phenotype deviates from the local optimum), intermediate genotypes have low fitness in all habitats. This makes it difficult for a population initially adapted to one habitat to invade other habitats and evolve into a set of locally adapted demes, promoting the stability of an asymmetric equilibrium with a single phenotype specialized on one habitat (Day 2000; Kawecki 2000, 2003; Ronce & Kirkpatrick 2001; Kisdi 2002). 11.

Finally, local adaptation requires that spatial variation in selection is substantially greater than temporal variation. Both theoretical arguments (Gillespie 1973) and experimental data (reviewed in Kassen 2002) show that temporal variation in selection favours generalist genotypes and thus hinders local adaptation. Thus irrespective of the approach used to study divergent selection, it is desirable to address the issue of its constancy through time. 11.

Nonetheless, many fitness-related characters likely to play a role in local adaptation show polygenic variation. In contrast to single-locus models, the theory of polygenic traits under divergent selection remains relatively unexplored. 11.

Mopper et al. (2000) have demonstrated that older demes of a leaf mining lepidopteran (those on older trees) show more pronounced local adaptation to their individual host trees than young demes, despite being less differentiated from one another in neutral markers. 11.

In this context, a combination of population demography, long divergence times and selection for alternative thermal regimes has apparently resulted in the accumulation of adaptive genetic differences among T. californicus populations and may explain the large difference in innate thermal tolerance observed here. 2.

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---How local adaptation can be constrained --------------------------------------------------------------------------

Because of those other forces, the pattern of local adaptation is not a necessary outcome of evolution under spatially divergent selection. 11.

Local adaptation may be hindered by gene flow, confounded by genetic drift, opposed by natural selection due to temporal environmental variability, and constrained by lack of genetic variation or by the genetic architecture of underlying traits. 11.

If alleles can spread readily throughout the species range (e.g., McDaniel and Shaw 2005), then gene flow can prevent populations within a species from evolving as independent units. 6.

Genetic adaptation between populations of the same species is often opposed by gene flow. In T. californicus, there is abundant evidence that gene flow is extremely restricted over the geographical range of the species [38–40]. 2.

This study also confirms theory that has shown that adaptive divergence not only depends on environmental differentiation and limited gene flow but also may be influenced by genetic drift. 6.

Thus, although divergent natural selection is the driving force, these other forces, in particular gene flow, are integral aspects of the process of local adaptation. 11. ;Thus, restricted gene flow is a pre-requisite for local adaptation. Restricted gene flow (due to low passive dispersal or active habitat choice) also makes the conditions for maintenance of polymorphism more favourable (e.g. Maynard Smith 1966). 11.

Divergent selection is the driving force of local adaptation, but the outcome depends on the interaction between divergent selection and other forces of evolution, in particular gene flow. Therefore, quantitative estimates of gene flow provide important insights in the process of local adaptation. Gene flow is usually estimated indirectly based on differentiation at (presumably) neutral genetic marker loci. 11.

Gene flow is, however, not only a function of dispersal, but also of the success of the migrants in their new habitat. A number of other evolutionary processes will affect the fate of migrants and their offspring, and thus influence the effective gene flow. 11. Genes flow from one deme to another packaged in migrating individuals or propagules (seeds, spores, pollen, etc.), and all genes carried by a propagule initially share the same fate. Because local adaptation is characterized by the inferiority of immigrants relative to locals, effective gene flow is reduced by the presence of locally adapted residents. 11.

A different mechanism influencing gene flow is related to the fact that immigrants are usually rare, so their fitness may be biased by frequency-dependent selection. For example, if different demes have evolved different sexually selected ornament-preference systems, immigrant males will be discriminated against by local females; given that most females will be local, this will create sexual selection against immigrants. The converse is also possible, as females may show preference for males they perceive as unusual (e.g. Sinnock 1970; Ball et al. 2000). In general, frequency dependent selection will tend to obscure local adaptation (if it favours rare genotypes), or to create an appearance of one (if it discriminates against rare genotypes). This calls for studies designed to disentangle local adaptation from frequency dependent selection (e.g. Roy 1998). 11.

In addition to gene flow, other forms of selection may act against local adaptation. In particular, temporal variation in natural selection favours generalist phenotypes (e.g. Kisdi 2002). Furthermore, temporal fluctuations in habitat quality favour increased dispersal (unless the fluctuations are strongly positively correlated across habitats; e.g. Levin et al. 1984), and thus act against local adaptation. In contrast, spatial environmental heterogeneity favours reduced dispersal and habitat fidelity (e.g. Hastings 1983), which make conditions for local adaptation more favourable. Such feedbacks lead to coadaptation between dispersal rates and traits involved in habitat adaptation (Kisdi 2002). 11.

Low genetic variation due to genetic drift can limit adaptation. Small populations may not be well adapted to their native environment because drift can make it difficult for advantageous alleles to reach high frequency (Whitlock 2003) or because genetic load due to the chance fixation of deleterious alleles leads to low fitness or extinction (Lynch and Gabriel 1987; Lande 1994; Whitlock et al. 2000). Gene flow can also prevent local adaptation by homogenizing allele frequencies and limiting the response to selection within environments (e.g., Stanton and Galen 1997; Hen- dry and Taylor 2004). 6.

The high frequency of local maladaptation suggests that stochastic processes such as genetic drift often limit local adaptation (e.g., Travisano et al. 1995). 6.

Furthermore, a metapopulation may fail to show genetic differentiation for fitness traits because of lack of divergent selection, too much gene flow, or temporal variation in selection, which favours generalist genotypes. 11

Finally, it should be noted that environmental heterogeneity favours the evolution of adaptive phenotypic plasticity. In the absence of costs of and constraints on plasticity, a genotype that in each habitat produces the locally optimal phenotype would become fixed in all demes. 11.

More recently established demes may show poorer adaptation to their habitat than older ones. A beneficial mutation may be spreading in the metapopulation, being already fixed in some demes (which thus would show higher fitness) while absent in others. 11.

Theory of local adaptation predicts evolutionary changes in the metapopulation, but not changes in the environment. We, therefore, propose that a pattern that satisfies the local vs. foreign but not home vs. away criterion (like that in Fig. 1b) offers as much support for local adaptation, as a pattern that satisfies both criteria (like that in Fig. 1a). 11. In contrast, a pattern that satisfies the home vs. away but not the local vs. foreign criterion (Fig. 1c) implies that some demes consistently outperform others in all habitats, in contrast to what the theory predicts. 11.

**The local vs. foreign criterion should be regarded as diagnostic for the pattern of local adaptation. This criterion is directly relevant to the driving force of local adaptation – divergent natural selection – which acts on genetic differences in relative fitness within each habitat. The local vs. foreign criterion addresses the efficacy of divergent selection relative to other evolutionary processes. In contrast, the home vs. away criterion confounds the effects of divergent selection with intrinsic differences in habitat quality. Survival or fertility of a genotype optimally adapted to a poor-quality habitat may still increase following a transplant to a resource-rich habitat, although in the poor habitat this genotype is favoured (i.e. has higher relative fitness than other genotypes) while in the rich habitat it would be outcompeted by other genotypes. 11.**

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---Local adaptation, and temperature; importance ------------------------------------------------------------------------

Understanding how populations adapt to heterogeneous thermal regimes is essential for comprehending how latitudinal gradients in species diversification are formed, and how taxa will respond to ongoing climate change. 2.

The survey of the literature suggests that local adaptation is common and that, on average, a local population has 45% greater fitness than a foreign population. 6. [however, rarely seems to be accounted for within conservation thinking and planning].

Understanding the mechanisms underlying the evolution of thermal tolerance is critical not only for explaining contemporary biogeographic patterning, but also for predicting how climate change and evolutionary adaptation will affect future species distributions [5,6]. 2.

Latitudinal gradients in abiotic factors strongly determine species distributions. Of these factors, temperature is arguably the most important, as its effects are pervasive across all levels of biological organization, from biochemistry of molecular processes to physiology of the whole organism [1–3]. As such, it is expected that organisms adapt to latitudinal gradients by matching their physiological tolerances to the local thermal environment experienced along their range [4]. 2.

Tropical species are uniformly more heat tolerant than temperate species and, within each latitudinal group, species occurring highest in the intertidal zone have the highest LT50 values. 1

Tropical ectotherms are more threatened by climate change than species from mid-latitudes because tropical species live closer to their upper thermal tolerance limits and, in some cases, live at temperatures above those at which physiological processes exhibit their thermal optima. These authors also emphasize that the range of temperatures experienced by an ectotherm may strongly determine its capacity for coping with rising temperatures (Tewksbury et al., 2008). 1.

Many of these species have evolved for over 15 million years under conditions of extreme and stable cold temperatures. As a consequence of their evolutionary histories – and for the mechanistic factors discussed in the final section of this review – animals of the Southern Ocean are remarkably stenothermal. Many endemic species of the Southern Ocean die of acute heat death at temperatures only a few degrees above their normal habitat temperatures. 1

Moreover, many of these species have extraordinarily narrow ranges over which acclimation can occur (Peck et al., 2009). A study of 13 marine invertebrates from the Antarctic Peninsula found the highest temperatures of acclimation that could be tolerated over periods of months were 1°C to 6°C (Peck et al., 2009). 1.

If these upper temperature limits reflect the genetically fixed abilities of these animals to tolerate high temperatures, some species could be in jeopardy from climate change over the next one or two centuries. 1; A more challenging problem in adapting to climate change arises for species that have lost genetic information required for life at increasing temperatures as a consequence of long evolutionary periods under highly stable conditions of low temperature. 1.

Although a number of physiological systems might be instrumental in causing acute thermal death, any physiological system that collapses rapidly at an organism’s lethal temperature is clearly a sufficient cause of death, whether or not other systems are collapsing simultaneously at these same high temperatures. An obvious candidate for a cause of acute thermal death is cardiac function, which for a number of animals has been shown to decrease precipitously as acutely lethal body temperatures are reached (Hochachka and Somero, 2002). 1. ; Proteins are a highly temperature-sensitive component of organisms and clear patterns of adaptive variation have been discovered in structural and functional properties of proteins from species adapted to different temperatures (Somero, 2004). 1. ; Three types of lesions in DNA may influence how well an ectotherm will be able to respond to rising temperatures. 1.

* First, when protein-coding genes are partially or wholly lost from the genome, the proteome of the organism is correspondingly reduced in complexity. 1.
* Second, mutations that disrupt open reading frames in protein-encoding DNA (pseudogene generation) cause loss of the corresponding proteins from the organism’s proteome. 1.

Third, lesions in gene regulatory regions, whether through loss of DNA or mutations in sequence, that eliminate the capacity to regulate gene expression in response to thermal stress could truncate the ability of organisms to adequately modify the phenotype during acclimatization. 1; thermal mitochondria paper

In the context of climate warming, our results confirm the general prediction that low-latitude populations are most susceptible to local extinction because genetic adaptation has placed physiological limits closer to current environmental maxima, but our results also contradict the prediction that phenotypic plasticity is constrained at lower latitudes. 2.

Studies in other species have shown similar correlation of innate, or environmentally independent, thermal tolerance with latitude (e.g. porcelain crabs [26], marine molluscs [46], amphibians [47] and fruit flies [48]), suggesting that genetic adaptation strongly contributes to large-scale latitudinal gradients observed across species.

An emerging implication of latitudinal gradients of innate thermal tolerance across terrestrial insects [49], also supported by our results in this marine copepod, is that warm-adapted populations from lower latitudes are characterized by thermal limits that are frequently experienced in their local environments, suggesting that southernmost populations might be close to their innate adaptive capacity. 2.

Congeners found highest in the intertidal zone are most heat tolerant, yet, because of the similarity of LT50 and MHT, they face greater threats from warming than less heat-tolerant subtidal species that rarely, if ever, encounter temperatures near their LT50. 1.; Those results imply that warm-adapted taxa from lower latitudes, particularly ectotherms, are most threatened by further increases in temperature because (i) their innate acute thermal limits (LD50 values) lie close to current environmental thermal maxima, and (ii) they have only limited ability to modify heat tolerance through plasticity [6]. 2.; Common garden experiments with populations spanning up to 178 of latitude have shown that survivorship to acute thermal limit decreases with increasing latitude, suggesting that copepod populations are genetically adapted to a latitudinal thermal gradient [32,33]. Transcriptome analysis has shown that expression of orthologous heat-shock proteins strongly differs between a warm- and a cold-adapted population raised in common garden [34], indicating that high inter-population differentiation might facilitate genetic adaptation, via both structural changes in proteins and changes in gene expression. 2.; Across all heat-stress temperatures, northern populations have a lower survivorship than southern populations. 2. That even relatively mild heat-stress (33 and 348C) will cause some mortality in those populations but not in intermediate or lower latitude ones. Showing significant genetic adaptation across conspecific populations. 2. In T. californicus, we find a strong and significant correlation of thermal tolerance, as reflected by LD50, both with mean air temperature (figure 3a) and with latitude (electronic supplementary material, figure S5a). These strong correlations between innate thermal tolerance and habitat measurements strongly suggest that mean temperatures experienced by local populations are a major driver of the large latitudinal gradients of thermal tolerance observed in this species. 2.

The conjecture that the most warm-adapted species within a genus of marine intertidal invertebrates are likely to be most threatened by climate warming agrees with broad conclusions reached in recent analyses of terrestrial ectotherms from different latitudes (Deutsch et al., 2008; Tewksbury et al., 2008) 1.

Furthermore, size and activity level also have a significant effect on thermal tolerance, with smaller individuals of a species having greater heat tolerance than larger individuals, and more active species having higher tolerance than less active or sessile species. Thus, extinctions from warming may lead to altered ecosystem function due to shifts in size and activity levels of the surviving species (Peck et al., 2009). 1. [leading to potential multi-trophic level interactions via food web alterations]

Understanding how populations adapt to heterogeneous thermal regimes is essential for comprehending how latitudinal gradients in species diversification are formed, and how taxa will respond to ongoing climate change. 2.

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Understanding the mechanisms underlying the evolution of thermal tolerance is critical not only for explaining contemporary biogeographic patterning, but also for predicting how climate change and evolutionary adaptation will affect future species distributions [5,6]. 2.

Divergence of genomic regions involved in thermal tolerance can alter protein expression structure and performance in different environments, affecting individual fitness by natural selection and ultimately leading to fixation of advantageous mutations in populations. This clear link between mutation, gene, function and phenotype, has made studies of genetic divergence appealing and prominent in the adaptation literature [9]. 2.

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The development of these locally adapted populations may be related to the life history of this species, specifically its direct development and limited dispersal capability. In contrast to whelks and other species whose larvae or juveniles have restricted dispersal, species whose larvae spend long periods in the plankton and are distributed over broad ranges of latitude may be less prone to developing locally adapted populations. 1.

--- A. poly and local adaptation ---------------------------------------------------------------------------------------------

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---------Challenges when measuring local adaptation-------------------------------------------------------

**Examples range from major fitness components like juvenile survival or fecundity (e.g. Mopper et al. 2000; Leiss & Muller-Scharer 2001), through life history traits such as age at first reproduction or, for a parasite, infectivity (e.g. Lively 1989; Mopper et al. 1995; Kaltz et al. 1999), to traits such as body size, root growth or number of leaves (e.g. Gomez- Mestre & Tejedo 2003; Berglund et al. 2004) or resistance to local parasites and herbivores (e.g. Roy 1998). A working assumption behind using such traits as measures of performance is that they are monotonically related to fitness, i.e. are under directional selection in all demes. However, fitness-related traits are often under stabilizing selection and/or are trade-off with other fitness components (reviewed in Roff 1992; Stearns 1992). In this case, different intermediate trait values may be optimal in different locations; treating these traits as measures of performance (e.g. the bigger the fitter) may be misleading. However, if the habitat-specific optima of a trait are known, the degree to which each deme matches the optimum for its habitat is highly informative about local adaptation (e.g. Dias & Blondel 1996). Some traits (e.g. juvenile survival or parasite infectivity) will in general be more often under directional selection than others (e.g. root size, phenological traits or parasite virulence). In any case careful consideration should be given to the relationship of a given performance trait to actual fitness. This relationship can often be verified through measurements of selection gradients (see below). 11.**

Many fitness-related traits like the number and quality of offspring are positively correlated with fitness, but trade off with each other, so the effective selection on them is stabilizing. Also, many specific adaptations, like heavy metal tolerance or herbivore resistance, have physiological costs. In environments where these adaptations are not needed these costs translate into a fitness disadvantage (e.g. Strauss et al. 2002), and thus are the reason why such adaptations are local rather than global. 11.

Trade-offs associated with local adaptation were stronger when environmental differences between populations’ native sites were larger. 6. Costs of adaptation will increase when a population adapts to environments that are drastically different from its ancestral environment. 6.

which individual demes show local adaptation can be correlated with their characteristics such as size, age, demography, isolation, and habitat quality. 11.

Traits mediating local adaptation should show genetically based phenotypic differences between demes evolved in different habitats, the phenotype being understood broadly to include physiological and biochemical characteristics and patterns of gene expression. However, not all genetically based phenotypic differences between demes must be adaptive. Instead they may represent the costs of adaptive traits, mediated by pleiotropic effects of underlying genes. They may also be because of genetic hitchhiking of genes linked to those favoured by divergent selection. Finally, such differences may be produced by processes not related to local adaptation (such as drift or evolution of alternative coadapted gene combinations). 11.

Finally, different demes may have reached alternative adaptive peaks of different height, i.e. if they have evolve alternative epistatic gene combinations that result in different fitness. Thus, the absence of the pattern does not necessarily mean that the, process of divergent natural selection is not operating. Studying the processes driving, hindering, and interacting with, local adaptation would help to understand why local adaptation is apparent in some metapopulations but not in others. This involves asking questions and testing hypotheses about ecological factors responsible for divergent natural selection, traits under selection and their genetic architecture, gene flow, and processes affecting immigrants (such as heterosis or outbreeding depression). 11.

Because organisms have to survive to reproductive age in order to produce offspring, fecundity or population growth may capture more of the underlying variation in fitness, resulting in more accurate estimates of selection and local adaptation. Alternatively, past selection may have eliminated variation in traits that influence survival, resulting in little contemporary viability selection. Future studies should include the most comprehensive measure of fitness possible, given that the fitness metric influences the interpretation of experiments. 6.

The average magnitude of local adaptation depended on the measure used to quantify fitness. Local adaptation measured with viability as fitness was smaller than with fecundity or composite fitness (fig. 2), suggesting that the overall magnitude of local adaptation would have been greater had more studies included fecundity or a composite measure of fitness. 6.

Therefore, loci with large effects on fitness should disproportionally contribute to local adaptation (Macnair 1991). This is indeed the case in the classic examples of local adaptation of plants to sites contaminated with heavy metals (reviewed in Macnair 1987, 1991). 11.

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---How to examine local adaptation---------------------------------------------------------------------------------------

First, the key comparison from the viewpoint of local adaptation is between the relative fitness of local vs. immigrant genotypes within each test habitat, not between the performance of a given genotype at home and away. Second, the unit of biological eplication is a deme, and more than two demes need to be studied to distinguish the pattern of local adaptation from other forms of deme · test habitat interactions. 11.

In each habitat the local deme is expected to show higher fitness than demes from other habitats. In contrast, the home vs. away criterion emphasizes the comparison of a deme’s fitness across habitats: local adaptation would be said to occur if each deme had a higher fitness in its own habitat (at home) than in other habitats (away). 11.

**The local vs. foreign criterion should be regarded as diagnostic for the pattern of local adaptation. This criterion is directly relevant to the driving force of local adaptation – divergent natural selection – which acts on genetic differences in relative fitness within each habitat. The local vs. foreign criterion addresses the efficacy of divergent selection relative to other evolutionary processes. In contrast, the home vs. away criterion confounds the effects of divergent selection with intrinsic differences in habitat quality. Survival or fertility of a genotype optimally adapted to a poor-quality habitat may still increase following a transplant to a resource-rich habitat, although in the poor habitat this genotype is favoured (i.e. has higher relative fitness than other genotypes) while in the rich habitat it would be outcompeted by other genotypes. 11.**

In general statistical terms, local adaptation implies a specific form of deme · habitat interaction: mean deme fitness should be systematically higher for the sympatric deme · habitat combinations (i.e. a deme is tested in its habitat of origin) than in the remaining, allopatric cases. 11.

The magnitude of differences between the home environments of populations in reciprocal transplant studies had a small but significant positive effect on the magnitude of local adaptation, suggesting that greater local adaptation results from greater differences between environments. Phenotypic differences between populations were not associated with the magnitude of local adaptation. Finally, local adaptation often resulted in trade-offs, though the magnitude of the cost of local adaptation was small. 6.

Nonetheless, replication at the level of the deme is needed to demonstrate local adaptation on the basis of the fitness pattern alone. 11

However, the frequency of maladapted populations reported here suggests that foreign population advantage may not be rare. It appears that selection acts on most measurable phenotypic traits (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001) and can often be exceptionally strong (Hereford et al. 2004). 6.

The small amount of variation in local adaptation explained by environmental and phenotypic differences suggests that it may sometimes be difficult to identify the environmental gradients on which local adaptation occurs or that differences in the expression of phenotypic traits may not be associated with differences in relative fitness. I found that environmental and phenotypic divergence explained little variation in the magnitude of local adaptation (figs. 3, 4). Though environmental variation is not a direct measure of divergent selection, stronger environmental differences might be expected to result in more divergent selection (e.g., Schluter and Grant 1984), and divergence between populations in at least some phenotypic traits should be associated with local adaptation (de Jong 2005). Many of the phenotypic traits in the data were related to size, which is often positively correlated with fitness (Kingsolver et al. 2001; Hereford et al. 2004). 6.

The lack of a significant relationship between local adaptation and phenotypic divergence may not be due to a lack of selection on these traits. Instead, differences in the expression of these traits may not contribute to differences in relative fitness. Individuals may be able to grow to large sizes in novel environments but may not be able to get the same fitness benefit from large size in novel environments that they could gain in their native environment. 6.

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---What the presence of local adaptation means ----------------------------------------------------------------------

The study of local adaptation offers the more feasible alternative of comparison between local populations, which have evolved under different conditions. In the absence of divergent (i.e. spatially heterogeneous) natural selection, genetic differentiation in fitness-related traits is expected to be obliterated by gene flow. Therefore, local adaptation in a set of demes connected by gene flow must be due to ongoing (or very recent) natural selection related to differences in environmental conditions experienced by different demes. 11.

Therefore, the existence of a pattern of local adaptation despite gene flow certifies to the strength of natural selection imposed by particular environmental factors. Second, it is sometimes possible to infer the age of a deme from geological or historical data; this allows one to estimate the rate of adaptive evolutionary change (e.g. Stearns 1983; Gomi & Takeda 1996). Third, local adaptation has been recognized as an important mechanism maintaining genetic variation (reviewed by Felsenstein 1976; Hedrick et al. 1976; Hedrick 1986). Finally, a number of scenarios for allopatric and sympatric speciation (reviewed by Schluter 2001; Turelli et al. 2001; Via 2001) assign local adaptation a crucial role in initiating the divergence of incipient species. 11.

If selection against intermediate genotypes is weak, intermediate generalist phenotypes are likely to be favoured, leading to loss of genetic variance and little differentiation (Spichtig & Kawecki 2004). If it is too strong, the population is likely to be trapped in a source-sink situation with little differentiation among demes (in a single- locus model this case corresponds to loss of polymorphism because of excessive marginal underdominance for fitness averaged between habitats; Christiansen 1974). An asymmetric equilibrium is also promoted by differences in size and quality of habitats, so local adaptation is most likely when such differences are small (Kawecki 1995, 2000, 2003; Ronce & Kirkpatrick 2001; Kisdi 2002). 11.

Even if the genes responsible for local adaptation remain unknown, useful information about the genetic aspects of traits mediating local adaptation can be learned with the methods of quantitative genetics. First, how much additive genetic variation for this trait exists and how is it distributed within vs. among demes? The former indicates the ability of the trait to respond to selection (for estimation see Falconer & Mackay 1996; Lynch & Walsh 1998, part III). The latter, which can be quantified as Qst (Merila & Crnokrak 2001; McKay & Latta 2002), measures the degree of genetic differentiation of quantitative traits between populations. Traits under strongest divergent selection are expected to have the highest Qst, which is another way of identifying traits mediating local adaptation. 11.

As discussed above, adaptive plasticity may be seen as an evolutionary alternative to local adaptation. 11. **However, plasticity may also be a maladaptive by-product of environmental influences on physiology. Selection will counteract such maladaptive plasticity, so local adaptation will in this case be manifested as reduction of phenotypic differences between demes living in different habitats. Selection will thus be divergent at the genetic level, but not at the phenotypic level, and will thus not be detectable as a difference in fitness gradients. This type of local adaptation has been termed countergradient variation (Conover & Schultz 1995). 11.**

Understanding how populations adapt to heterogeneous thermal regimes is essential for comprehending how latitudinal gradients in species diversification are formed, and how taxa will respond to ongoing climate change. 2.

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