



Review

Rethinking local adaptation: Mind the environment!



Matti J. Salmela*

Department of Botany, University of Wyoming, 3165, 1000 E. University Ave., Laramie, WY 82071, USA

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ABSTRACT

Spatial heterogeneity in environmental conditions has led to adaptive genetic differentiation and the development of home-site fitness advantage (local adaptation) among populations of many widespread plant species such as forest trees. Although its overall patterns have been well characterised, earlier studies on adaptation have predominantly used long-term averages of environmental variables to describe local climates. Subsequently, only little is currently known about more complex patterns of variation in potential selective forces and how they affect adaptive processes. Furthermore, we also lack a good understanding of why adaptive traits often vary within populations despite clear evidence of local selection. Because the capacity of a population to respond to changes in its home environment depends on the amount of genetic variation that it contains, an understanding of these patterns is fundamental to predicting how extant populations will cope with climate change. In this paper, I call attention to these two issues and discuss adaptation in heterogeneous environments using studies mainly on Finnish populations of Scots pine (*Pinus sylvestris* L.) as an example. In this geographic area, population means in growth cessation are closely related to the latitude at the population's home site, indicating adaptation to local environments. Yet the trait varies considerably also within populations, with the highest levels of phenotypic variation found in the central part of the latitudinal gradient. Increased variation further north may have a significant genetic component. In stable local environments this would indicate that populations with less variation are more optimally adapted to their home site environments. On the other hand, climate data show that growing season temperature conditions within Finland become temporally more variable towards the north which might contribute to different levels of trait variation. Collectively, these findings demonstrate the weaknesses of focusing only on long-term averages of environmental variables or trait means when examining adaptation in natural populations. Moreover, better integrated analyses of both genetic and environmental variation might help in disentangling the mechanisms that maintain adaptive genetic diversity and adaptive capacity in natural populations of perennial species under changing environmental conditions.

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Contents

1. Introduction	272
2. Materials and methods	273
2.1. Estimating within-population variation in timing of bud set	273
2.2. Spatial and temporal climate variation in Finland	274
3. Results and discussion	275
3.1. Spatial heterogeneity in environment and adaptive genetic differentiation	275
3.2. Temporal variation in environmental factors	275
3.3. Variation in an adaptive trait within populations	276
3.4. Maintenance of adaptive genetic variation within populations	277
3.5. Populations at the northern range limit	278
3.6. Local adaptation and adaptive capacity in complex natural environments	279
4. Conclusions	279
Acknowledgements	280
References	280

* Tel.: +1 307 766 2380; fax: +1 307 766 2851.

E-mail address: msalmela@uwyo.edu

1. Introduction

The amount of genetic variation found in nature has been fascinating biologists for decades, resulting in a large number of studies on its patterns and causes. One evolutionary force that plays a major role in the maintenance of such diversity within and among species is adaptation, the process of genetic divergence that may occur between generations within a population, between different populations or different species in response to an environmental factor and that leads to higher fitness (Stearns, 1992). Evidence of adaptation among plant and animal populations is ubiquitous (Hereford, 2009; Leimu and Fischer, 2008), but the relationship between the environment and variation in adaptive traits is expected to be particularly strong in plants due to their sessile nature (Kawecki and Ebert, 2004). Unsurprisingly, studying adaptation has a long history in plants, and for instance forest geneticists have been pioneers in this field due to the commercial importance of timber production (Linhart and Grant, 1996). In spite of its prevalence, adaptation also clearly has its limits, as evidenced by the limited distributions of species (Bridle and Vines, 2007). One possible reason for range limits is the lack of genetic variation in adaptive traits in peripheral populations that prevents them from expanding to new environments (reviewed in Eckert et al., 2008).

Forest trees are good examples of plant species with wide geographic ranges that occur over environments varying substantially in key variables, for instance temperature and moisture conditions. Such spatial heterogeneity is expected to promote genetic differentiation among populations and the development of local adaptation, a phenomenon in which a population achieves higher fitness than foreign populations at its home site and may also perform worse at environmentally different sites (Fig. 1; Kawecki and Ebert, 2004). Although home-site advantage of local populations can be demonstrated only in reciprocal transplant experiments, alternative methods can also be used to assess adaptive genetic differentiation in response to spatial environmental heterogeneity. In many tree species, patterns of phenotypic variation observed under common-garden conditions have often been found to be associated with environmental factors (reviewed in Howe et al., 2003; Savolainen et al., 2007), and more recently, associations between the home environment and molecular marker polymorphisms have also been discovered (reviewed in Sork et al., 2013).

Forest genetic literature is filled with examples of how large-scale spatial differences in the environment have shaped the patterns of genetic variation within species. When environmental conditions vary at a very fine local scale, adaptive genetic differentiation in quantitative traits may develop also among different microhabitats (Campbell, 1979). However, despite the fact that climate fluctuations characterise all natural environments (e.g. Stenseth et al., 2002; Vasseur and Yodzis, 2004), local environments in studies on adaptation have generally been described by long-term averages of climate variables such as temperatures or rainfall; in other words, local environments have been considered to be rather fixed and non-overlapping so that selection is thought to operate towards static and distinct phenotypic optima in each population (e.g. Barton, 1999; Le Corre and Kremer, 2012, Fig. 1). As a result, the potential effects of temporal environmental fluctuations and spatial differences in their level on the genetic makeup of populations have received little attention in empirical studies of multiple populations. So far, ecological studies on plants and animals have been better at characterising the effects of temporal environmental heterogeneity and as a consequence have found links to various population and community-level processes such as population size fluctuation, timing of reproductive events, and species interactions (reviewed in Post and Stenseth, 1999; Ruokolainen et al., 2009; Stenseth et al., 2002). Further, it has been found that the

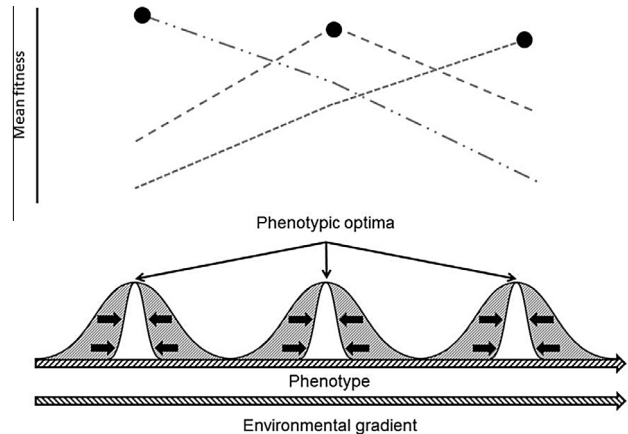


Fig. 1. The classical view of local adaptation. In this simple example, three populations are found in contrasting environments with different selection pressure and phenotypic optima. This has led to genetic differentiation in trait means among populations. Variation is found also within each population (striped areas) for instance due to mutation and gene flow. Natural selection (black arrows) eliminates individuals from the populations that are too far from the fixed phenotypic optima. Thus, adaptive traits are expected to show variation mainly among populations. The lines in the upper part of the figure describe the mean fitness of each population at the home site (black spheres) and also in the other two environments. In this case local adaptation has developed in parallel with genetic differentiation because the populations survive best in their respective home environments.

combination of ecophysiological traits associated with higher fitness in plants may differ among climatically variable years (Kimball et al., 2012). In species with non-overlapping generations in temporally variable environments, evolutionary biology and genetic models generally predict the development of mechanisms allowing a genotype to produce a wide range of phenotypes in response to changes in the environment, either via bet-hedging (random responses) or phenotypic plasticity (systematic responses; e.g. Bull, 1987; Kawecki and Ebert, 2004).

The ability of a population to adapt to changes in its home environment depends heavily on the amount of adaptive genetic diversity in traits under selection (Falconer and Mackay, 1996). Because natural selection is generally expected to result in the loss of genetic diversity in traits under selection as non-optimal phenotypes are removed from the populations (Falconer and Mackay, 1996, Fig. 1), local adaptation is sometimes considered to limit the potential of populations to adapt to a changing environment (e.g. Bennington et al., 2012). In recent years, changing environmental conditions and the resulting threats to the survival of extant populations have resulted in increased interest to study also if and how genetic variation is maintained in natural populations (Hoffmann and Sgró, 2011).

In contrast to theoretical predictions, it is commonly found that in the wild even the most strongly selected traits contain significant amounts of genetic variation (Barton and Keightley, 2002). Yet demonstrating the cause(s) of abundant genetic variation in natural populations has proven a challenging task, even in theoretical studies. According to models that have been developed to address the question, variation within populations may arise for instance from new mutations entering a population and selection removing them (Bulmer, 1989), genetic differences in response to different environments (i.e., genotype \times environment interactions; Gillespie and Turelli, 1989), or variable responses of different age classes to temporally variable selection (Ellner and Hairston, 1994). Empirical work on the importance of different factors in nature remains rare, but quantitative genetic experiments on a variety of study organisms such as *Arabidopsis*, fruit fly, and forest trees have shown that different environments can trigger the

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