*New Idea*

Ignored patterns in studies of local adaptations: When the grass is greener on the allopatric site

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Abstract

Recently, the focus within microevolutionary studies has been on the ecological divergence of populations. One subset of this research field includes studies on local adaptation. This approach is useful for studying whether or not adaptive spatial variation takes place in a metapopulation context. There is growing body of research studying local adaptations of populations, and much of this has used a formal test for assessing the existence of local adaptation. According to Kawecki and Ebert (2004), the "Local *vs.* foreign" criterion is fulfilled if the local population has higher fitness than other populations in its own locality and "Home *vs.* away" is fulfilled if a population has higher fitness in the sympatric than allopatric environment. Interestingly, interpretation of results not fulfilling these criteria has received scant attention even though the question of how to measure local adaptation is vital for the study field. At present, there is an extensive volume of published results showing other kinds of patterns than those proposed by the "Local *vs.* foreign" or "Home *vs.* away" criteria. Here, we highlight one of these alternative patterns that we believe may have an adaptive background and may show local adaptation not recognized by the above-mentioned criteria.

Keywords: chemical deterrence, ecological divergence, plant-herbivore interactions, local adaptations, ecological speciation, random drift.

Population divergence is the first step towards speciation (Via 2001, Nosil et al. 2009). It can be caused by random processes such as drift, the bottleneck effect or founder effect, but it can be also triggered by selection. The latter, adaptive divergence of populations, results from geographic variation in selective pressures (Mayr 1947, Endler 1986), including both biotic and abiotic variation (Endler 1977, Thompson 1994, 1999). The term "ecological divergence" has been launched to indicate divergence of populations due to variation in ecological conditions (Fox and Morrow 1981, Schluter, 2001, Rundle and Nosil, 2005, Funk et al. 2006). Lately, studies on local adaptations have emphasized the role of selection in generating divergence through adaptations to the local conditions. This refers to situations where the local populations have higher fitness in their own environment than in other environments or higher fitness than allopatric populations in their local environment (Williams 1966, Van Zand and Mopper 1998, Kaltz and Shykoff 1998, Lajeunesse and Forbes 2002, Kawecki and Ebert 2004).

Kawecki and Ebert (2004) clarified the detection of local adaptation by providing two criteria for assessing its existence. The two criteria, "Local *vs.* foreign" and "Home *vs.* away", aim at detecting local adaptation in the outcomes of reciprocal transplant experiments. The main focus of each criterion is different. "Local *vs.* foreign" looks within each site and asks whether the locals always do better. It is fulfilled when a population has higher fitness in its sympatric environment than a population allopatric to this environment (Figure 1a,b).
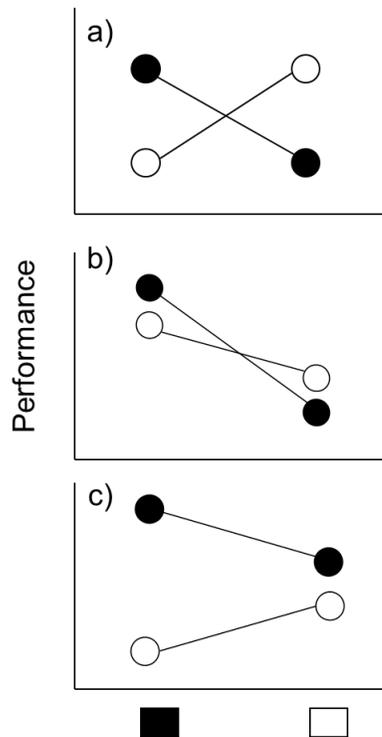
Figure 1. "Local *vs.* foreign" and "Home *vs.* away" criteria in a reciprocal transplant or a reciprocal common garden experiment according to Kawecki and Ebert (2004). Rectangles refer to host populations and circles to herbivore populations, with similar colour referring to sympatric origin. a) Both the criteria are fulfilled for both herbivore populations. b) Only the "Local *vs.* foreign" criterion is fulfilled for both the populations: in both environments the local population has higher fitness. However, one of the environments is better for both populations and therefore the "Home *vs.* away" criterion is fulfilled only for the population marked with black circles. c) Only the "Home *vs.* away" criterion is fulfilled, because both herbivore populations have higher fitness in their sympatric environment than in an allopatric environment. However, the population marked with black circles outperforms the population marked with white circles in both habitats.

"Home *vs.* away" looks across sites and asks whether one always does better at home. It is met when a population has a higher fitness in its sympatric compared with an allopatric environment (Figure 1a,c). The first criterion alone, or together with the second, would show local adaptation. The fulfilment of the second criterion alone (Figure 1c) is assumed to provide less determinate evidence for local adaptation: it does indicate that some populations consistently outperform others, but the

pattern may well be related to mechanisms other than local adaptation.

Subsequent to the publication of that paper, these two criteria have been extensively used for detecting local adaptations (reviewed in Greischar and Koskella 2007, Leimu and Fisher 2008, Hoeksema and Forde 2008, Hereford 2009). However, studies often show results incompatible with the criteria. For example, Hereford (2009) found about 30% of studies did not show local adaptation and generally very weak fitness trade-offs between native and foreign environments. With the exception of pinpointing experimental flaws generating misinterpretations (Hoeksema and Forde 2008), there has been surprisingly little discussion on the alternative pathways that could cause these non-matching patterns.

We discuss here one of these patterns and suggest an alternative pathway for inferring the plant-herbivore interactions in such situations. Our aim is to widen the discussion around local adaptations and encourage researchers to reassess the evolutionary patterns behind results that do not fulfil the criteria for local adaptation.

As mentioned above, the actual observations do not always follow the patterns outlined by these criteria. Furthermore, in the search for universal local adaptation, several populations are often used, and the pattern can be met by some of the population pairs but not all. Instead, the pattern may resemble that in Figure 2, where the herbivore (or a parasite or a plant) that originates from the more demanding environment also performs better in the environment where this particular selective pressure is relaxed. To understand this type of unexpected result, we need to consider the nature of both the adaptation and the selective agents. We provide here a hypothetical example that could result in a pattern such as that appearing in Figure 2.

Consider a plant-herbivore interaction including a resistance metabolite that is present in all plant populations but with geographically varying levels. Assume one herbivore population adapts to tolerate a 5% concentration of the resistance metabolite and another population adapts to a concentration of 10% found in their local hosts. Fitness of the former herbivore population should be lower on host plants with the higher than local level of the resistance metabolite. If there is a constitutive cost to maintain the high level of tolerance, the latter population will also be less fit than the former when feeding on plants with low metabolite levels. In this case, the first criterion, "Local *vs.* foreign," by Kawecki and Ebert (2004) would indeed reveal local adaptation. However, we consider the assumption of constitutive tolerance cost unsound in the case where the detrimental effects of the resistance metabolite are the key factor suppressing the performance of the herbivore. As tolerance to toxins or other resistance
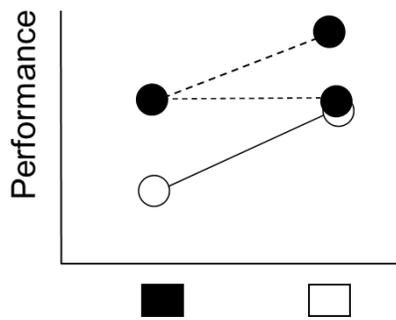
Figure 2. The suggested outcome in studies of local adaptation. The herbivore population that is adapted to a host with low levels of defensive compounds (white circle) can efficiently utilize the host population with low defences (white rectangle) but only poorly utilize the host population with high levels of defensive compounds (black rectangle). The herbivore population that is adapted to high levels of defensive compounds (black circle) can tolerate well the sympatric host, and, in addition, may perform equally well or even better on allopatric hosts with lower levels of defensive compounds. The host populations marked with the black and white rectangles represent the 10% and 5% concentrations of resistance metabolites, respectively, in the example given in the text.

metabolites is likely to evolve gradually (chemical coevolution), herbivores may adapt to efficiently utilize hosts *up to* the local level of the metabolite. In this case, for the population adapted for instance to the concentration of 10%, anything less than (or equal to) 10% of the same metabolite would be easier (or as easy) to digest than the sympatric food. Instead, the population adapted only to up to 5% concentration of the metabolite would have difficulties in digesting anything above this level.

When the herbivore population adapted to 5% concentration feeds on hosts containing 10% of the metabolite, it suffers a lower performance than if fed with the sympatric hosts (Figure 2). Conversely, when the population adapted to a 10% metabolite concentration is fed on hosts containing only 5% of the metabolite, the performance may be equal or even better than on the sympatric food. This would be because tolerating lower concentrations of the harmful metabolite than those to which the herbivore is adapted is not necessarily costly (Fry 1996). On the contrary, resources bound to increased tolerance when feeding on the more demanding host population may now be available for other needs. This brings about an interesting case where a herbivore's adaptation to a local host with a high expression level of a particular trait is manifested as even better performance on allopatric hosts showing a lower expression level of the trait (Figure 2). In this example, both the populations would be locally adapted, but the "Local *vs.* foreign" criterion would fail to identify it. It could be addressed that even though the cost of specialisation—manifested for instance as a decreased ability to consume any metabolite level other than the local one—is often the expected evolutionary outcome of herbivore specialization, it does not seem to occur regularly in nature (e.g. Fry 1996, Koricheva 2002). Thus, cost of specialisation is not likely to reduce the possibility of the occurrence of the pattern described above.

The pattern where the population locally adapted to the more demanding host/environment performs equally well or better in an allopatric, less demanding site (Figure 2) may apply to many cases. First, populations of the moth *Thaumetopoea pityocampa* are distributed over areas having both the soft- and tough-needled *Pinus* species. *Thaumetopoea pityocampa* populations sympatric to soft-needled *Pinus* species perform well only with the local host, whereas those sympatric to the tough-needled *Pinus* species perform equally well or better on the allopatric host (Zovi et al. 2008). Second, Agrawal (2000) studied adaptation of the spider mite *Tetranychus urticae* to a poor-quality novel host (cucumber plant) and found that after five generations on the cucumber, the mites showed increased performance not only on the cucumber but also on the main host, the cotton plant, compared with the population maintained solely on the cotton plant. Finally, the pattern may be found not only in plant-herbivore interactions but may fit in local adaptation to abiotic conditions also. Of the three studied locations of the perennial weed *Ruellia nudiflora* (Acanthaceae), the northernmost site was the driest and induced the lowest performance for each plant population (Ortegón-Campos et al. 2009). Fulfilling the "Local *vs.* foreign" criterion, this (i.e. the local) population had higher performance than the others in its sympatric environment. However, this population from the most severe site also showed the highest performance in the less severe locations ("Home *vs.* away" not fulfilled for this population) and actually had higher fertility in the allopatric sites with, for instance, higher amount of rainfall. Instead, the other two populations originating from the less severe sites performed worse in the more demanding northern site (Ortegón-Campos et al. 2009).

In all of these cases, the "Local *vs.* foreigner" criterion is fulfilled for the most demanding environment (superiority of the sympatric population), but due to the superiority of this population in general, the "Home *vs.* away" criterion is not fulfilled for this population, nor is the "Local *vs.* foreigner" fulfilled for the other populations. Thus, in these cases adaptation to the more demanding host/environments also improves performance on the less severe hosts/environments.

Instead, in the marine isopod herbivore *Idotea balthica,* three populations performed best on a host population with a high amount of sugars and a low content of phenolic resistance compounds (Jormalainen et al. 2008). Accordingly, the isopod population from this location had the lowest performance on the allopatric host with lower levels of sugars and higher levels of phenolic compounds. In this case, local adaptation to the less severe host would be seen as lower performance in the allopatric environments, but not as superior performance in the sympatric environment, as this environment is also the least severe for the other populations; the other populations would perform better with this less severe allopatric host than with their own sympatric host as found in the other examples.

We suggest that this "Greener on the allopatric site" pattern occurs commonly in nature. It may be of particular importance in herbivore adaptations to plant resistance but potentially also more generally in local adaptations to both biotic and abiotic selective agents. Thus, it could well be worth analysing whether herbivore performance is consistently lower on more demanding hosts and higher or similar on hosts more poorly defended than the herbivore's sympatric host. This type of adaptation process also helps in understanding the pattern shown in Figure 1c, where one population constantly outperforms others; the population adapted to tolerate high levels of resistance metabolites may have a high performance over a range of host populations.

In conclusion, we seek to promote here discussion on the studies of local adaptations. At the present, there is a wealth of empirical studies about local adaptations, and it could be the right time to critically reassess their evolutionary messages. How do the local adaptations finally evince themselves, and—instead of neglecting a big portion of the results—how do we interpret the evolutionary patterns shown by those studies not fulfilling the commonly accepted local adaptation criteria?

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Response to referee

We agree with Parachnowitsch (2013) about the importance of meta-analyses and different summary statistics for studying the generality of local adaptations, but we also strongly suggest that in addition to focusing on "Local *vs* foreign" and "Home *vs* away" criteria (Kawecki and Ebert 2004), there should be more discussion about the different results that could be considered local adaptations. At the very least, the evolutionary trajectory behind the results not meeting the criteria should be discussed rather than neglected. One possibility is to re-interpret the earlier studies in order to better understand how general or rare the "Greener on the allopatric site" hypothesis (or "Allopatric site advantage" hypothesis *sensu* Parachnowitsch) suggested above actually is.

As Parachnowitsch (2013) suggested, the key to understanding adaptation is to recognize the selective agents causing the observed evolutionary patterns. Parachnowitsch's response guided us to realize that the process of "Greener on the allopatric site" could be

manifested especially in those cases in which the selective agent is abiotic. If the selective agent is an abiotic factor, such as drought, alkalinity or pH, adaptation to the maximal value of the constant selective pressure can be reached given sufficient genetic variation. Instead, biotic selective agents such as host plant chemistry in plant-herbivore interactions co-evolve with the interacting party as suggested by the Red Queen hypothesis. This causes constant changes in the selective agent, thus preventing fixation of any specific level of herbivore's adaptation. In this case, the opportunity for selection, as discussed by Parachnowitsch, could be an ongoing process. However, this is not say that biotic selective pressures could not lead to local adaptations as, for instance, in plant-herbivore interactions the evolutionary potential of the herbivore may be higher than that of the plant, and the herbivore can therefore be expected to evolve more rapidly and became locally adapted (Kaltz and Shykoff 1998, Bergerlson et al. 2001).

We encourage researchers to challenge our "Greener on the allopatric site" hypothesis by providing either non-adaptive explanations for the pattern or experimental or meta-analytical evidence for its generality. Further, we hope that this paper inspires researchers to consider their results again and look for fulfillment of this alternative criterion.

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