

Host race formation in the Acari

Sara Magalhães · Mark R. Forbes · Anna Skoracka ·
Masahiro Osakabe · Christine Chevillon ·
Karen D. McCoy

Received: 23 January 2007 / Accepted: 10 July 2007 / Published online: 3 August 2007
© Springer Science+Business Media B.V. 2007

Abstract Host race formation generates diversity within species and may even lead to speciation. This phenomenon could be particularly prevalent in the Acari due to the often intimate interaction these species have with their hosts. In this review, we explore the process of host race formation, whether it is likely to occur in this group and what features may favour its evolution. Although few studies are currently available and tend to be biased toward two model species, results suggest that host races are indeed common in this group, and more likely to occur when hosts are long-lived. We discuss future directions for research on host-associated adaptations in this group of organisms and the potential relevance of host race formation for the biodiversity of mites and ticks.

Keywords Host race formation · Specialization · Molecular markers ·
Experimental evolution · Genetic diversity · Local adaptation

S. Magalhães (✉)
Instituto Gulbenkian de Ciência, Evolutionary Genetics Group, Rua da Quinta Grande,
6, 2780-156 Oeiras, Portugal
e-mail: smagalhaes@igc.gulbenkian.pt

S. Magalhães
Laboratoire de Génétique et Environnement, Institut des Sciences de l'Evolution,
Université de Montpellier II, Place Eugène Bataillon Bâtiment 22 cc65, 34095 Montpellier, France

M. R. Forbes
Department of Biology, Carleton University, 1125 Colonel By Drive, K1S 5B6 Ottawa, ON Canada

A. Skoracka
Department of Animal Taxonomy and Ecology, Faculty of Biology,
Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland

M. Osakabe
Laboratory of Ecological Information, Graduate School of Agriculture,
Kyoto University, 6068502 Kyoto, Japan

C. Chevillon · K. D. McCoy
Génétique et Evolution des Maladies Infectieuses, UMR CNRS/IRD 2724,
IRD, 911 Avenue Agropolis, B.P. 64501, 34393 Montpellier, France

Introduction

Environmental heterogeneity promotes heterogeneous responses in organisms and thus can generate biodiversity. Population responses to such variation can be organised along a continuum, ranging from the evolution of phenotypic plasticity to speciation (Meyers and Bull 2002). Intermediates along this continuum include genetic polymorphisms among interbreeding individuals and the formation of semi-isolated biotypes or races. The nature of the environmental variation, the history of populations involved, and forces such as drift and gene flow will then dictate whether these intermediates are stable over time or whether they move one way or another along the continuum.

For many species, the environment is largely comprised of another organism, referred to as the host. Temporary adaptation to a given host can promote the maintenance of genetic variation within a species (reviewed in Hedrick 1986), whereas prolonged selection in each host environment may result in permanent genetic divergence among populations inhabiting different host types. Parasites can vary widely in their host use, from strict specialists to wide-ranging generalists. Host races may arise in generalist species in which relatively isolated populations specialize on their host, or in specialist species as a result of host shifts. Specialized populations perform better on their own host species than on others (cost of adaptation; Kassen 2002) and this, in turn, can result in a restriction of gene flow among populations inhabiting these different hosts, even under sympatric conditions. Indeed, host race formation is commonly evoked to explain apparent cases of sympatric speciation (e.g., Filchak et al. 2000; Groman and Pellmyr 2000). When races evolve in allopatry, the restriction of gene flow will be facilitated by geographic distance, thus races may evolve to species more rapidly, especially during secondary contact (Kirkpatrick and Ravigné 2002). Given their multiple origin and their occurrence within the continuum between individual phenotypic plasticity and species, several definitions of host races have been put forward (Jaenike 1981; Diehl and Bush 1984; Dres and Mallet 2002). In this paper, host races are defined as genetically distinct populations specialized on different host species.

The Acari represent an extremely important group of organisms, both in terms of their economical and medical importance and because they comprise a significant amount of the world's biodiversity (<http://tolweb.org/Acari>). These organisms are ubiquitous in nature and have successfully colonised every known terrestrial, marine and freshwater habitat. In many cases, this habitat is, in fact, another living organism and the Acari live in intimate associations with the host organism (Walter and Proctor 1999). Host race formation may therefore be an important force generating diversity in this group. However, to date, studies on this subject are relatively rare and limited to a few model organisms. Here, we evaluate the characteristics of the Acari that may make them susceptible to this evolutionary process. First, we briefly review theoretical concepts linked to the evolution of host races and why we might expect host races to arise in parasitic Acari. We then review current evidence for host race formation in this group, via studies that examine population genetics, parasite ecology, or both. Finally, we suggest how future studies could improve our knowledge of host race formation in the Acari, as well as in other groups of organisms.

Evolution of host races

Host races arise via a process of adaptation combined with restricted gene flow among populations inhabiting different hosts. First, a polymorphism for some trait linked to host exploitation (preference or performance) appears in one or several populations of the same

species. Then, at least one mechanism that limits gene flow arises. There are two non-mutually exclusive and complementary possibilities. First, the evolution of higher performance on one host can entail a cost in performance on the other(s), such that migrants are out-competed by specialist residents (Nosil et al. 2005). In this case, generalist individuals may disperse to the specialist's host type, but will not successfully invade. The second mechanism that can limit gene flow is a genetically-based preference for a particular host type that leads to host-associated assortative mating, effectively reducing encounters among individuals inhabiting different host types. Organisms that prefer a particular host are more exposed to their preferred host, which can then increase the opportunity for selection to operate (host tracking; Whitlock 1996). In this sense, preference can either favour adaptation or reinforce pre-existing adaptations by tightening co-evolution between the host and parasite. Conversely, adaptation to a particular host type can favour the evolution of preference for that host (Rice 1987). If selection for the adaptation results in a reduction in hybrid fitness across habitats, the evolution of assortative mating will be favoured. Therefore, to distinguish host races from a simple population-level polymorphism, one should ideally provide evidence of both some type of host-linked adaptation and of genetic differentiation among the different host-associated populations.

Why expect host race formation in the Acari?

Host races have been documented in numerous parasitic and herbivorous organisms (Berlocher and Feder 2002; Funk et al. 2002). There are several characteristics that may promote the evolution of these host-associated groups, many of which are present in the Acari.

Philopatry

This term refers to a preference to remain at the natal site. An organism can be passively philopatric if it is incapable of dispersing, or it can be actively philopatric, returning to the natal site for reproduction. Passive philopatry is found in many species of the Acari, but it is especially common and strong in gall-making eriophyoid mites, which reproduce in the natal site within a host for many generations (Oldfield 2005). Active philopatry (or homing) has been demonstrated for several tick species (Sonenshine 1991) and may strongly favour assortative mating. When a particular host-type is associated with a given natal site, this can result in host-associated divergence.

Low dispersal ability

Population divergence will be favoured by a lack of active dispersal. In ticks, it is well-documented that active dispersal is limited (e.g., Falco and Fish 1991). When parasites disperse with their hosts, such as ectoparasitic mites (Bohonak 1999) or ticks (e.g., McCoy et al. 2001; Chevillon et al. unpublished), they are likely to encounter the same host type in the new environment. This form of dispersal should therefore not counter-select for specialisation. In herbivorous mites, active dispersal occurs mainly in tetranychids and it is limited to neighbouring plants (e.g., Navajas et al. 2002). Long-distance dispersal can take place passively via wind or phoresy (Kennedy and Smitley 1985), but in this case, mites will have little choice on which host they land and this form of dispersal is likely to be costly. Hence, passive long-distance dispersal is not expected to occur frequently, relative

to active dispersal. Thus, herbivorous mites are probably quite philopatric, which may thus facilitate specialisation (see point 1). When passive long-distance dispersal does occur, new hosts will often be colonised by few individuals (Kennedy and Smitley 1985), which may favour rapid divergence of the population on the new host. Whether this divergence will subsequently result in host race formation depends on the cost of adapting to the newly acquired host.

High intimacy with the host environment

Most parasitic Acari live in strong association with their hosts. However, the intimacy of this association can be variable among host-parasite associations, and its strength can be used as a proxy for how strong host-imposed selection is on the parasite. For example, in hard ticks (Ixodidae), where the blood meal on the vertebrate host lasts several days, evasion of host defences can be a complex process (Brossard and Wikel 2004) and may select for host specificity. In contrast, soft ticks (Argasidae) generally take a series of short, successive blood meals that may help them avoid specific host immune responses and thus enable them to maintain broad host ranges. In mites, the degree of intimacy can range from continuous and strong interactions with the host environment in the case of many animal parasites (Sarcoptidae, Spinturnicidae) to weaker associations in herbivorous mites (e.g., Tetranychidae).

Host-associated mating

The evolution of specialisation is favoured when mating occurs in the host environment. Host-associated mating takes place in many Acari as a by-product of philopatry (see point 1). In addition, many species are known to actively choose their mates (Gotoh et al. 1993; Lesna and Sabelis 1999; Radwan 2004; Vala et al. 2004). This mate choice could then favour a reduction in gene flow among populations infesting different host types. In ticks, host-associated mating depends on the type of life cycle. In one-host ticks, like the southern cattle tick (*Rhipicephalus microplus*), mating occurs on the host whereas in some multi-host ticks, such as *I. ricinus*, it takes place in the abiotic environment.

Reproductive rates

Host race formation can be favoured in parasites with high reproductive rates and short generation times relative to those of the host. This difference in reproductive potential can give an adaptive advantage to the parasite and thus promote host-associated specialisation, provided genetic diversity in the parasite is not limiting (Gandon and Michalakis 2002). The Acari often have shorter generation times than their hosts, as a tick or mite is usually associated with a long-lived animal or plant host. For example, *Rhipicephalus microplus* can have up to four generations per year in a cow herd (Koffi et al. 2006) and some eriophyoid mites, such as *Cecidophyopsis ribis* on currants, *Nalepella* spp on conifers, can have up to seven generations per year on a single host (Castagnoli 1996; de Lillo and Duso 1996).

Evidence for host race formation in the Acari

Researchers have tested the role of adaptation to different hosts in the divergence process in two ways: (1) Genetic studies using molecular markers, and (2) Ecological studies using

reciprocal transplant experiments in field or laboratory populations. Some studies have combined these approaches, but we will tackle the two types of studies independently, as they provide different types of evidence.

Studies on host race formation in the Acari were principally found by introducing in Web of Science research engine the keywords “host race formation” and “mite” or “host race formation” and “tick”. Other studies were pointed out by colleagues. We did not include studies in which genetic divergence among populations inhabiting different hosts could be interpreted as isolation by geographic distance (see below).

Genetic studies using molecular markers

Molecular markers can reveal hidden host-associated divergence when different populations are found in sympatry. In this case, it is often assumed that divergence has resulted from some type of host adaptation, even though ideally this should be tested in an independent experiment. When populations exploiting different host types occur in allopatry, genetic divergence, if present, can also be attributed to isolation by geographic distance. To rule out this alternative explanation, and thus demonstrate that the existence of host races is not simply an effect of the geographic distance among parasite populations, it should be shown that the genetic distance among populations from the same host type is lower than that of populations from different host types (e.g. McCoy et al. 2001).

Studies of host race formation in the Acari using genetic markers are presented in Table 1. Unfortunately, there is a very conspicuous phylogenetic bias in these studies. Indeed, of the 12 studies on mites, seven involve mites from the *Tetranychus* genus, of which five are *T. urticae*. In ticks, of the five studies, three were performed on *Ixodes uriae*. This bias hampers any attempt at generalizing the patterns that we might observe. Nevertheless, we opted for analysing the studies obtained anyway, with the hope to lay grounds for future analyses. Based on the studies presented in Table 1, we attempted to answer the following questions: (a) Are certain types of parasites more likely to undergo host-race formation? (b) Are there hosts types that are more likely to induce host race formation? (c) Is the detection of host races contingent on the genetic marker used? In addressing these questions we could not perform a meta-analysis, common in literature surveys, because this method necessitates a common measure for the phenomenon observed, some measure of error and a control group. Most studies (on host race formation, in general, and in the Acari in particular) do not fulfil at least one of these requirements. For example, a common measure of genetic differentiation among populations could be the F_{st} , but its associated variance (F_{st} variation across markers) is seldom given. Moreover, F_{st} among populations inhabiting hosts of the same species, which could be used as a control, is typically lacking. Therefore, we opted for a qualitative analysis of the studies available, if possible accompanied by a Fisher exact test (this test is especially appropriate when sample sizes are small).

Are certain types of parasites more likely to undergo host-race formation?

As outlined above, several parasitic traits are expected to increase the likelihood of observing host races, such as their degree of association with the host or their dispersal abilities. Within the Acari, there is variation for these traits; for example the degree of association with the host can range from very intimate in parasitic ticks or gall-making mites to loosely intimate in other herbivorous mites. Therefore, it is worth asking whether the occurrence of host races varies among parasite species. Studies in Table 1 involve ticks with a very inti-

Table 1 Studies on host race formation in mites and ticks using genetic markers. Alloz.: allozymes; Microsat: microsatellites; mtDNA: mitochondrial DNA

Study	Parasite	hosts	# host species	# pops	Marker	Host races?	REF
1	<i>Tetranychus urticae</i> , mite	Trees, weeds, annual crops	7	2	Alloz	No	Tsagkarakou et al. 1997
2	<i>T. urticae</i> , mite	Trees, annual crops	14	7	Alloz	Yes/No ^a	Tsagkarakou et al. 1998
3	<i>T. urticae</i> , mite	Annual crops, weeds	8	10	Alloz	No	Tsagkarakou et al. 1999
4	<i>T. urticae</i> , mite	Shrubs	2	1	AFLP	Yes	Weeks et al. 2000
5	<i>T. urticae</i> , mite	Annual crops	3	2	AFLP	Yes	Weeks et al. 2000
6	<i>T. turkestani</i> , mite	Annual crops, weeds	9	4	Microsat	No	Bailly et al. 2004
7	<i>T. kanzawai</i> , mite	Shrubs	3	4	Microsat	Yes ^a	Nishimura et al. 2005
8	<i>Panonychus citrus</i> , mite	Shrubs, trees	4	4	Alloz	Yes ^{a,b}	Osakabe and Komazaki 1996
9	<i>Brevipalpus phoenicis</i> , mite	Shrubs, trees	3	3	Microsat	Yes	Groot et al. 2005
10	<i>Abacarus hystrix</i> , mite	Grasses	3	15	mtDNA	Yes	Skoracka and Dabert unpubl.
11	<i>Utonitcola formosa</i> , mite	Mussels	4	4	Alloz	Yes	Edwards et al. 2000
12	<i>Sarcoptes scabiei</i> , mite	Mammals	5	6	mtDNA microsat	Yes ^b	Walton et al. 2004
13	<i>Ixodes uriae</i> , tick	Seabirds	2	6	Microsat	Yes	McCoy et al. 2001
14	<i>Ixodes uriae</i> , tick	Seabirds	6	24	Microsat	Yes	McCoy et al. 2005
15	<i>Ixodes uriae</i> , tick	Seabirds	4	4	mtDNA	No	Kempf & McCoy unpubl.
16	<i>Amblyomma dissimile</i> , tick	Reptiles, amphibians	3	11	Alloz	No	Lampo et al. 1998
17	<i>Rhicephalus microplus</i> , tick	Mammals	2	5	Microsat	Yes	Chevillon et al. Unpubl.

^a Only among some host species; ^bbut may be different parasite species

mate association with their host, loosely associated herbivorous mites and two ectoparasitic mites. These studies suggest that host races may arise in herbivorous mites or in parasitic ticks alike and that variation is found even among studies involving the same mite or tick species. For example, of the five studies with *T. urticae*, two revealed host race formation, two did not and one showed mixed results. Therefore, the occurrence of host races seems to be relatively independent of the parasite species involved.

Are there host types that are more likely to induce host race formation?

One of the main factors that may promote host race formation is a difference in reproductive potential of the parasite and its host, which is itself linked to differences in generation times (see above). To investigate whether the host-parasite difference in generation times affects the probability of host-race formation, we selected studies with plants as hosts (as this group encompasses the largest variation in lifespan), and divided them into one group of short-lived annual crops or herbaceous plants and one of long-lived perennials. Next, we calculated the number of host race formation events tested for each host type category. This number is an estimate of the number of events expected if all host species/populations used in the study were susceptible to induce host races. When an expected host-race formation event involved long-lived and short-lived hosts, this event was included in the expected number of both categories. Subsequently, we annotated the number of host race formation events observed in each category of hosts, and compared the proportion of observed vs expected events in each category using a Fisher exact test. Overall, we observe that the probability of host race formation for parasites exploiting perennials is significantly higher than that for parasites exploiting annual crops or herbaceous plants (Table 2, Fisher exact test $P = 0.013$).

In parasites that occur on hosts that are not plants (cf. Table 1), host races were found five out of seven times. However, in this case, all hosts studied had long lifespans, relative to that of their parasites (>10 years versus <3 years, respectively), and we therefore lack a

Table 2 Effect of host life-span on the probability of obtaining host races

Study #	Host-race formation events in parasites exploiting			
	Short-lived hosts		Long-lived hosts	
	expected	observed	expected	observed
1	4	0	2	0
2	12	0	3	1
3	8	0	–	–
4	–	–	1	1
5	3	3	–	–
6	15	0	–	–
7	–	–	3	2
8	–	–	3	2
9	–	–	3	3
10	3	3	–	–
Total	55	6	16	8

The expected and observed numbers of host-race formation events are detailed for parasites exploiting either short-lived (annual) or long-lived (perennial) plants. Correspondence between studies' number and quotations is given on Table 1. Totals are given as very rough estimates under the assumptions of study-cases independence and even probability of host race formation per host-type

comparison with parasites on short-lived hosts. Nevertheless, this analysis suggests that the likelihood of host race formation may indeed depend more on the characteristics of the hosts and those of the association (i.e., the length of time that host and parasite have been in contact or the degree of genetic variability in the parasite versus the host) than on the parasites themselves. However, given the paucity of studies and the above mentioned phylogenetic bias, this hypothesis is quite preliminary and more studies are needed to examine this possibility.

Is the detection of host races contingent on the genetic marker used?

Genetic markers differ in many ways (De Meeûs et al. 2007), and this can affect their suitability to detect incipient phenomena such as host race formation. The most important variable is the number of available polymorphisms, which determines the smallest detectable genetic difference. Thus, it is expected that the most polymorphic markers are the most suitable for detecting host races. However, different marker types may be more or less neutral depending on the degree of selection on the marker itself or selection on adjacent genes. Hence, observed genetic differences may not always reflect neutral divergence. When testing for host race formation, we typically desire neutral markers that provide evidence of population isolation (i.e., limited reproduction between populations). Genetic markers under selection can bias inferences about current gene flow. For example, the same allele (not associated with host adaptation) could be under positive selection in two isolated populations leading to the false conclusion of ongoing gene flow. Thus, markers under selection will only be useful for establishing the presence of host races when their function in the process of host-associated adaptation has been identified.

At present, four different classes of genetic markers have been used to examine host race formation in the Acari (Table 1). Of the six studies using allozyme markers, three did not detect host races, one did and two showed mixed results. Allozymes typically harbour low diversity and at least some loci are likely under selection (De Meeûs et al. 2007). Three studies were performed with mitochondrial DNA, two of which detected host race formation. The polymorphism of mitochondrial markers is very dependent on the species and loci considered, and the neutrality of this genome has been recently challenged (Bazin et al. 2006). Out of the seven studies using microsatellite markers, five detected host races, one did not and one showed mixed results. Although microsatellites are highly variable, the highest degree of polymorphism among individuals is likely to be obtained by AFLPs, as these markers amplify large regions of the genome. Indeed, host-race formation was detected in both studies using amplified fragment length polymorphisms (AFLPs).

Of these two polymorphic marker types, only microsatellites are considered to be reasonably neutral (Jarne and Lagoda 1996). Although the number of studies currently available is too small to conclude on any general pattern, an interesting trend is observed, where the probability of detecting host race formation, ranging from 50 to 100%, increases with the degree of marker polymorphism and the likelihood of neutrality. However, this trend is very incipient, and the Fisher test suggests that the probability of detecting host race formation is in fact independent of the marker used (Unbiased estimate of Fisher exact probability, $P > 0.74$). Clearly, more studies are required to test this hypothesis with sufficient power.

Ecological studies using field or laboratory populations

Ecological studies using field or laboratory populations exploiting different hosts rely on reciprocal transplant experiments to detect host-associated adaptation. Reciprocal

transplants consist of testing the performance of organisms on original and alternative host types. Better performance on the original host compared to the alternative hosts indicates host-linked specialization (Kawecki and Ebert 2004). Ideally, these experiments should control for maternal effects and for the previous experience of organisms if traits are measured in adults. If this is not done, the differences observed may be simply due to phenotypic plasticity and not to a genetically based difference in trait values. In addition, differences in performance may not always correlate with a reduction in gene flow, since adaptation to the different hosts can be maintained in a panmictic population as a genetic polymorphism (Levene 1953). The conditions for the maintenance of this polymorphism are quite restrictive, however (Ravigné et al. 2004; Spichtig and Kawecki 2004), and the occurrence of mechanisms limiting gene flow, such as assortative mating, philopatry, or a cost of adaptation, may result in host race formation. Local adaptation as detected in reciprocal transplants is thus necessary, but not sufficient in itself to establish the occurrence of host races. Therefore, when possible, these studies should be accompanied by analyses using genetic markers and/or by crosses between populations on different hosts.

Field-based experiments attempt to unravel patterns of local adaptation despite the variability inherently associated with natural populations. On the other hand, experimental evolution studies with laboratory populations attempt to follow the process of adaptation to particular host types under controlled conditions. Although frequently carried out under artificial circumstances, these lab-based experiments can help to identify the mechanisms involved in host-associated adaptation and divergence and enable us to estimate the ease at which host races may arise under natural conditions. The main advantage of these studies relative to more direct studies on natural populations is that they allow the experimenter to control the history of the populations (e.g., Magalhães et al. 2007). In this way, the process of adaptation, and not just its result, can be followed. Ideally, however, to obtain meaningful data relative to host race formation, some degree of migration among populations of different hosts should be allowed. That is, experiments should mimic the spatial complexity of natural populations. This has never been done in the Acari, and it is rarely performed in multicellular organisms in general (cf., Garcia-dorado et al. 1991; Tucic et al. 1995).

Results on the survey of ecological studies are given in Table 3. The common measure among studies is a test for host-associated adaptation, as defined above, which is a prerequisite for the occurrence of host race formation. Studies of field populations detected host adaptation more often than experimental evolution studies (five of seven vs. zero of four, respectively). There may be several explanations for this difference. First, laboratory-based studies may over-simplify experimental conditions such that they neglect key factors contributing to adaptation. Another possible explanation is that field-based results may be associated with maternal effects or population history. Indeed, to date, no study involving field populations has controlled for these effects. In contrast, all laboratory-based studies have controlled for maternal effects (Table 3). An alternative explanation is that experimental evolution studies are carried out with annual host species, more amenable to laboratory manipulation, whereas studies on field populations are performed with a variety of hosts (in our survey, only two out of seven involved short-lived hosts). As we have seen above, long-lived host species may be more likely to induce host-race formation, thus explaining the higher proportion of host-linked adaptation found in field studies. Finally, all studies of experimental evolution carried out to date have involved *T. urticae*, a species that is considered as a broad spectrum generalist. This limits our ability to make any general statement on the frequency of host race formation in the Acari using this approach.

Table 3 Studies with reciprocal transplants and/or experimental evolution

Study #	Tick or mite	Species	Host species	# host species	# pops	Trait	LA?	REF
Reciprocal transplants of natural populations								
1	Mite	<i>Panonychus mori</i>	Trees, annual crops	3	3	JS	Yes	Osakabe 1993
18*	Mite	<i>Panonychus citri</i>	Trees	4	1	JS	Yes	Osakabe and Komakazi 1996
19	Mite	<i>Spinturnix myoti</i> , <i>S. andegavinus</i>	Bats	2	2	JS Fec.	Yes	Giorgi et al. 2004
20	Mite	<i>Limnocarex americana</i>	Dragonflies	2	1	JS HR HT	No	Lajeunesse et al. 2004
12*	Mite	<i>Brevipalpus phoenicis</i>	Shrubs, Trees	3	3	JS Fec.	Yes	Groot et al. 2005
21	Mite	<i>Psoroptes ovis</i>	Mammals	9	45	BW HS	No	Pegler et al. 2005
22	Mite	<i>Abacarus hystrix</i>	Grasses	2	2	JS Fec.	Yes	Skoracka and Kuczynski 2006
Experimental evolution								
23	Mite	<i>T. urticae</i>	Annual crops	2	2	JS	No	Gould 1979
24	Mite	<i>T. urticae</i>	Annual crops	2	2	JS Fec	No	Fry 1990
25	Mite	<i>T. urticae</i>	Annual crops	2	2	Fec	No	Agrawal 2000
26	Mite	<i>T. urticae</i>	Annual crops	3	3	JS Fec	No	Magalhaes et al. unpl.

LA: local adaptation; JS: juvenile survival; Fec: fecundity; HR: hatching rate; BW: body width; HS: hair size; HT: hatching time. Note that some studies are also included in the survey of studies using molecular markers (12 and 18, marked with an asterisk)

Conclusions and perspectives

Given their global distribution, extreme biodiversity and overwhelming abundance, as well as their inherent biological traits, the Acari can be considered as an ideal model group for studying the evolution of host race formation. The present survey showed that host races are relatively frequent in this group; of the 17 studies with molecular markers, 12 identified host races and 5 of the 11 reciprocal transplant experiments showed local adaptation. Our survey has revealed a strong bias toward a few model organisms in tests of host race formation in the Acari. Despite this bias, it seems that parasite characteristics are not strongly associated with the likelihood of host race formation, as illustrated by the disparate results obtained for a single parasite species, *T. urticae*. In addition, results suggest that host races are more likely to evolve when long-lived organisms are used as hosts. However, this analysis was limited to plant hosts as no studies have yet examined short-lived animal host species (i.e., with similar life-span than their parasites). It is therefore necessary to use systems involving a greater variety of animal host types in order to draw a clear conclusion about the importance of host longevity (or other host characteristics) for host race formation. From the available studies, it seems that the likelihood of host race formation may lie less with the parasite itself and more with the characteristics of the hosts along with those of the association (e.g., difference in generation times). Replicate studies of novel systems with known population histories should be performed to examine this possibility.

From a methodological viewpoint, we noted a potentially interesting pattern in the detection of host races using different types of genetic markers, even if this pattern was rather incipient. Indeed, the probability of detecting host races seems to depend on the polymorphism and degree of neutrality of the markers themselves. The use of different types of markers within a given system would enable us to determine whether this pattern holds. In addition, the contribution of ecological studies to our understanding of host race formation would greatly benefit from tests that control for maternal effects and that use parasites other than *T. urticae*.

Of the characteristics susceptible to induce host-race formation outlined in the introduction, we have only examined two in the current survey: the degree of intimacy with the host and the generation time of the host (linked to relative reproductive rates). Experimental evidence for the other characteristics (philopatry, dispersal rates and assortative mating) is usually not quantitative and a larger diversity of species groups that encompass a greater variability in these characteristics will be necessary to test their general importance. In other words, these characteristics are known to exist in the Acari but whether they play a role in the formation of host races in this group remains an open question. Our understanding of this phenomenon would therefore greatly benefit from coupling ecological and behavioural processes with patterns of genetic distances among populations in the field and by including these results in a more general study of host race formation across a variety of biological groups.

Given that host race formation is associated with a reduction in gene flow, genetic divergence among populations inhabiting different host types may result in the permanent isolation of these populations. In this sense, the formation of host races is considered to be an essential step toward speciation, and particularly so for parasitic organisms (including herbivorous arthropods). Given the paucity and bias in the studies available, the actual contribution of host race formation to acarine biodiversity is as yet difficult to evaluate. Moreover, even with good databases, the role of host race formation in the process of speciation is not easily determined. For example, it is possible that speciation events occur too quickly, such that the intermediate stage of host races will not be observed. On the other

hand, host races may represent transient entities in generalist species that rarely move toward the species state (Navajas 1998). Hence, patterns of host race formation cannot easily be extrapolated from those of niche breadth. For example, Futuyma (1976) found that lepidopteran species inhabiting woody plants were more generalist than those dwelling on grasses, a pattern that apparently contrasts with that observed here. However, generalist species may actually be a recompilation of as yet unidentified host races, whereas specialist species may be the recent result of host race formation. Therefore, the connexion between the formation of host races and the formation of species necessitates more thorough analyses. It is clear, however, that studies on host race formation using mites or ticks have an enormous potential to contribute to our understanding of fundamental phenomena such as specialization and speciation.

Acknowledgements This paper was inspired by a symposium on Host-Race Formation, organised by KM and SM at the International Congress of Acarology held in Amsterdam in August 2006. Comments by Isabelle Olivieri were highly appreciated. SM was funded by a grant from the Portuguese Science Foundation (FCT-BI 15997). KM and CC were supported by the CNRS and the IRD, and by funding from the BRG (project n° 53), the French Polar Institute (IPEV programme n°333) and the ANR (project Jeunes chercheurs-jeunes chercheuses “VectorAdapt”). MRF was supported by a NSERC (Natural Sciences and Engineering Research Council of Canada) discovery grant. CC received funding by the French Ministry of Ecology (InvaBio program). This is publication ISEM–2007–063 of the Institut des Sciences de l’Evolution, Montpellier.

References

- Agrawal AA (2000) Host-range evolution: Adaptation and trade-offs in fitness of mites on alternative hosts. *Ecology* 81:500–508
- Bailly X, Migeon A, Navajas M (2004) Analysis of microsatellite variation in the spider mite pest *Tetranychus turkestani* (Acari: Tetranychidae) reveals population genetic structure and raises questions about related ecological factors. *Biol J Linnean Soc* 82:69–78
- Bazin E, Glemin S, Galtier N (2006) Population size does not influence mitochondrial genetic diversity in animals. *Science* 312:570–572
- Berlocher SH, Feder JL (2002) Sympatric speciation in phytophagous insects: Moving beyond controversy? *Annu Rev Entomol* 47:773–815
- Bohonak AJ (1999) Effect of insect-mediated dispersal on the genetic structure of postglacial water mite populations. *Heredity* 82: 451–461
- Brossard M, Wikel SK (2004) Tick immunobiology. *Parasitology* 129 (Suppl):S161–S176
- Castagnoli M (1996) Ornamental coniferous and shaded trees. In: Lindquist EE, Sabelis MW, Bruin J (eds) *Eriophyoid mites: their biology, natural enemies and control* (World Crop Pests). Elsevier Science B.V., Amsterdam, pp 661–669
- De Lillo E, Duso C (1996) Currants and berries. In: Lindquist EE, Sabelis MW, Bruin J (eds) *Eriophyoid mites: their biology, natural enemies and control* (World Crop Pests). Elsevier Science B.V., Amsterdam, pp 583–591
- De Meeûs T, McCoy KD, Prugnolle F, Chevillon C, Durand P, Hurtrez-Boussès S, Renaud F (2007) Population genetics and molecular epidemiology or how to “débusquer la bête”. *Infect Genet Evol* 7(2):308–332
- Diehl SR, Bush GL (1984) An evolutionary and applied perspective of insect biotypes. *Annu Rev Entomol* 29:471–504
- Dres M, Mallet J (2002) Host races in plant-feeding insects and their importance in sympatric speciation. *Phil Trans R Soc Lond B* 357:471–492
- Edwards DD, Labhart M (2000) Genetic differences among host-associated populations of water mites (Acari: Unionicolidae: Unionicola): allozyme variation supports morphological differentiation. *J Parasitol* 86:1008–1011
- Falco RC, Fish D (1991) Horizontal movement of adult *Ixodes dammini* (Acari: Ixodidae) attracted to CO₂-baited traps. *J Med Entomol* 28:726–729
- Filchak KE, Roethele JB, Feder JL (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* 407:739–742

- Fry JD (1990) Trade-offs in fitness on different hosts—Evidence from a selection experiment with a phytophagous mite. *Am Nat* 136:569–580
- Funk DJ, Filchak KE, Feder JL (2002) Herbivorous insects: model systems for the comparative study of speciation. *Ecology* 116:251–267
- Futuyma DJ (1976) Food plant specialization and environmental predictability in Lepidoptera. *Am Nat* 110:285–292
- Gandon S, Michalakis Y (2002) Local adaptation, evolutionary potential and host-parasite coevolution: interactions between migration, mutation, population size and generation time. *J Evol Biol* 15:451–462
- Garcia-dorado A, Martin P, Garcia N (1991) Soft selection and quantitative genetic variation—A laboratory experiment. *Heredity* 66:313–323
- Giorgi MS, Arlettaz R, Guillaume F, Nussle S, Ossola C, Vogel P, Christe P (2004) Causal mechanisms underlying host specificity in bat ectoparasites. *Oecologia* 138:648–654
- Gotoh T, Bruin J, Sabelis MW, Menken SBJ (1993) Host race formation in *Tetranychus urticae*—genetic differentiation, host-plant preference, and mate choice in a tomato and a cucumber strain. *Entomol Exp Appl* 68:171–178
- Gould F (1979) Rapid host range evolution in a population of the phytophagous mite *Tetranychus urticae* Koch. *Evolution* 33:791–802
- Groman JD, Pellmyr O (2000) Rapid evolution and specialization following host colonization in a yucca moth. *J Evol Biol* 13:223–236
- Groot TVM, Janssen A, Pallini A, Breeuwer JAJ (2005) Adaptation in the asexual false spider mite *Brevipalpus phoenicis*: evidence for frozen niche variation. *Exp Appl Acarol* 36:165–176
- Hedrick PW (1986) Genetic-polymorphism in heterogeneous environments—A decade later. *Annu Rev Ecol Syst* 17:535–566
- Jaenike J (1981) Criteria for ascertaining the existence of host races. *Am Nat* 117:830–834
- Jarne P, Lagoda PJJ (1996) Microsatellites, from molecules to populations and back. *Trends Ecol Evol* 11:424–429
- Kassen R (2002) The experimental evolution of specialists, generalists, and the maintenance of diversity. *J Evol Biol* 15:173–190
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecol Lett* 7:1225–1241
- Kennedy GG, Smitley DR (1985) Dispersal. In: Helle W, Sabelis MW (eds) *Spider mites—their biology, natural enemies and control*. Elsevier, Amsterdam, pp 233–242
- Kirkpatrick M, Ravigne V (2002) Speciation by natural and sexual selection: models and experiments. *Am Nat* 159:S22–S35
- Koffi BB, de Meeùs T, Barré N, Durand P, Arnathau C, Chevillon C (2006) Founder effects, inbreeding and effective sizes in the Southern cattle tick: the effect of transmission dynamics and implications for pest management. *Mol Ecol* 15:4603–4611
- Lajeunesse MJ, Forbes MR, Smith BP (2004) Species and sex biases in ectoparasitism of dragonflies by mites. *Oikos* 106:501–508
- Lampo M, Rangel Y, Mata A (1998) Population genetic structure of a three-host tick, *Amblyomma dissimile*, in eastern Venezuela. *J Parasitol* 84:1137–1142
- Lesna I, Sabelis MW (1999) Diet-dependent female choice for males with ‘good genes’ in a soil predatory mite. *Nature* 401:581–584
- Levene H (1953) Genetic equilibrium when more than one ecological niche is available. *Am Nat* 87:331–333
- Magalhães S, Fayard J, Janssen A, Olivieri I (2007) Adaptation in a spider mite population after long-term evolution on a single host plant. *J Evol Biol* doi: 10.1111/j.1420-9101.2007.01365.x
- McCoy KD, Boulinier T, Tirard C, Michalakis Y (2001) Host specificity of a generalist parasite: genetic evidence of sympatric host races in the seabird tick *Ixodes uriae*. *J Evol Biol* 14:395–405
- McCoy KD, Chapuis E, Tirard C, Boulinier T, Michalakis Y, Le Bohec C, Le Maho Y, Gauthier-Clerc M (2005) Recurrent evolution of host-specialized races in a globally distributed parasite. *Proc R Soc Lond Ser B-Biol Sci* 272:2389–2395
- Meyers LA, Bull JJ (2002) Fighting change with change: adaptive variation in an uncertain world. *Trends Ecol Evol* 17:551–557
- Navajas M (1998) Host plant associations in the spider mite *Tetranychus urticae* (Acari: Tetranychidae): insights from molecular phylogeography. *Exp Appl Acarol* 22:201–214
- Navajas M, Perrot-Minnot MJ, Lagnel J, Migeon A, Bourse T, Cornuet JM (2002) Genetic structure of a greenhouse population of the spider mite *Tetranychus urticae*: spatio-temporal analysis with microsatellite markers. *Ins Mol Biol* 11:157–165
- Nishimura S, Hinomoto N, Takafuji A (2005) Gene flow and spatio-temporal genetic variation among sympatric populations of *Tetranychus kanzawai* (Acari: Tetranychidae) occurring on different host plants, as estimated by microsatellite gene diversity. *Exp Appl Acarol* 35:59–71

- Nosil P, Vines TH, Funk DJ (2005) Perspective: reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution* 59:705–719
- Oldfield GN (2005) Biology of Gall-inducing Acari. In: Raman A, Schaefer CW, Withers TM (eds) *Biology, ecology and evolution of gall-inducing arthropods*. Science Publishers, Enfield, USA, pp 35–57
- Osakabe M (1993) Divergence of the northern and southwestern populations of *Panonychus mori* Yokoyama (Acari, Tetranychidae). In *Japan in host-range and reproductive compatibility*. *Appl Entomol Zoolog* 28:189–197
- Osakabe M, Komazaki S (1996) Host range segregation and reproductive incompatibility among *Panonychus citri* populations infesting *Osmanthus* trees and other host plants. *Appl Entomol Zoolog* 31:397–406
- Pegler KR, Evans L, Stevens JR, Wall R (2005) Morphological and molecular comparison of host-derived populations of parasitic Psoroptes mites. *Med Vet Entomol* 19:392–403
- Radwan J (2004) Effectiveness of sexual selection in removing mutations induced with ionizing radiation. *Ecol Lett* 7:1149–1154
- Ravigne V, Olivieri I, Dieckmann U (2004) Implications of habitat choice for protected polymorphisms. *Evol Ecol Res* 6:125–145
- Rice WR (1987) Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evol Ecol* 1:301–314
- Skoracka A, Kuczynski L (2006) Is the cereal rust mite, *Abacarus hystrix* really a generalist? Testing colonization performance on novel hosts. *Exp Appl Acarol* 38:1–13
- Sonenshine DE (1991) *Biology of ticks*, vol 1. Oxford University Press, Oxford
- Spichtig M, Kawecki TJ (2004) The maintenance (or not) of polygenic variation by soft selection in heterogeneous environments. *Am Nat* 164:70–84
- Tsagkarakou A, Navajas M, Lagnel J, Pasteur N (1997) Population structure in the spider mite *Tetranychus urticae* (Acari: Tetranychidae) from Crete based on multiple allozymes. *Heredity* 78:84–92
- Tsagkarakou A, Navajas M, Papaioannou-Souliotis P, Pasteur N (1998) Gene flow among *Tetranychus urticae* (Acari: Tetranychidae) populations in Greece. *Mol Ecol* 7:71–79
- Tsagkarakou A, Navajas M, Rousset F, Pasteur N (1999) Genetic differentiation in *Tetranychus urticae* (Acari: Tetranychidae) from greenhouses in France. *Exp Appl Acarol* 23:365–378
- Tucic N, Milanovic D, Mikuljanac S (1995) Laboratory evolution of host plant utilization in the bean weevil (*Acanthoscelides obtectus*). *Genet Sel Evol* 27:491–502
- Vala F, Egas M, Breeuwer JAJ, Sabelis MW (2004) *Wolbachia* affects oviposition and mating behaviour of its spider mite host. *J Evol Biol* 17:692–700
- Walter DE, Proctor HC (1999) *Mites: ecology, evolution and behaviour*. University of New South Wales Press and CAB International
- Walton SF, Dougall A, Pizzutto S, Holt D, Taplin D, Arlian LG, Morgan M, Currie BJ, Kemp DJ (2004) Genetic epidemiology of *Sarcoptes scabiei* (Acari: Sarcoptidae) in northern Australia. *Int J Parasit* 34:839–849
- Weeks AR, Van Opijnen T, Breeuwer JAJ (2000) AFLP fingerprinting for assessing intraspecific variation and genome mapping in mites. *Exp Appl Acarol* 24:775–793
- Whitlock MC (1996) The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *Am Nat* 148:S65–S77