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# Sélection, plasticité et dérive façonnent les traits d'histoire de vie chez l'acarien ravageur de cultures *Tetranychus urticae* suite à un changement d'hôte

Cassandra Marinosci

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# THÈSE

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Paléobiologie

Présentée par **Cassandra Marinosci**

**Sélection, plasticité et dérive façonnent les  
traits d'histoire de vie chez l'acarien  
ravageur de cultures *Tetranychus urticae*  
suite à un changement d'hôte.**

Soutenance prévue le 06 Juillet 2016 devant le jury composé de

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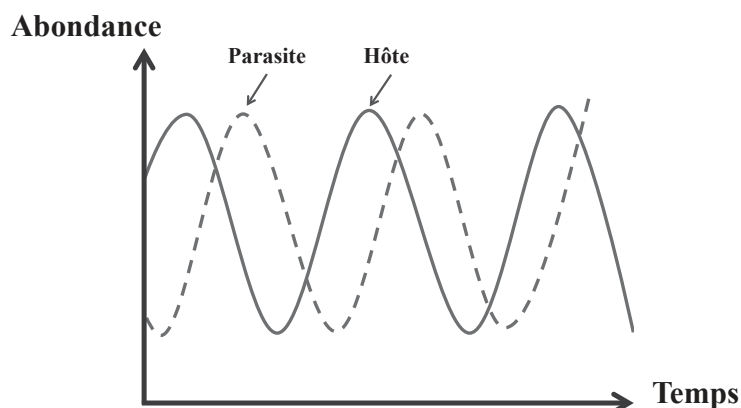
# *Introduction*



## Préambule

Comment expliquer la persistance des organismes suite à un changement dans leur environnement ? Quels sont les mécanismes permettant ou limitant leur maintien au sein de ce nouvel habitat ? Les interactions hôte-parasite, illustrant des relations étroites entre organismes aux intérêts antagonistes, sont de bons modèles d'étude pour décrire et comprendre l'évolution des êtres vivants suite à des changements environnementaux. Pour un parasite, notamment, un changement d'hôte peut représenter un bouleversement radical d'environnement auquel il doit répondre pour subsister.

Par définition, un parasite est un organisme qui exploite un hôte, au détriment de ce dernier, afin d'en tirer les ressources nécessaires pour survivre ou se reproduire. La pérennité du parasite est intimement liée à l'exploitation de l'hôte qui, quant à lui, a tout intérêt à repousser (voire supprimer) son agresseur afin de s'assurer de meilleures conditions de vie. Les objectifs antagonistes de ces partenaires « ennemis » les contraignent à élaborer ou perfectionner des stratégies de défenses et de contre-attaques pouvant entraîner ces organismes dans une course aux armements (Ehrlich et Raven, 1964 ; Thomas *et al.*, 2010 ; Spottiswoode et Stevens, 2012). Ce phénomène de coévolution antagoniste peut se traduire, par exemple, par des fluctuations dans le temps de l'abondance d'un hôte et de son parasite où chacun des organismes tente de s'adapter à l'autre selon le principe du modèle de la Reine Rouge (voir Fig. 1 ; Kaltz et Shykoff, 1998).



**Figure 1. Dynamiques prédites, d'après le modèle de la Reine rouge, au cours du temps d'un parasite et de son hôte au cours de leur coévolution antagoniste.** Les traits continu et pointillé présentent respectivement l'abondance au cours du temps de l'hôte et de son parasite. Les phases d'augmentation de l'abondance d'un organisme correspondent à l'adaptation de l'organisme en question à son partenaire « ennemi ».

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L'étude de la persistance des parasites suite à un changement de leur hôte n'a pas seulement un intérêt en recherche fondamentale pour comprendre des processus tels que l'adaptation, la spécialisation à un nouvel environnement ou encore la spéciation. En effet, la compréhension du maintien de ces organismes face à une modification de leur milieu présente également un enjeu majeur dans le cadre de recherches appliquées notamment pour la gestion de maladies émergentes, d'espèces envahissantes ou encore de ravageurs.

L'adaptation à un nouvel hôte est régulièrement abordée dans le contexte des interactions plante-herbivore car il est possible d'observer une grande variation de la spécialisation à la plante (Gassmann, 2009) pouvant découler d'un processus adaptatif. Les plantes, de par leur statut (quasi) immobile, ont dû développer des défenses efficaces afin d'éviter les attaques du cortège d'herbivores (Fritz et Simms, 1992). A titre indicatif, les plantes peuvent s'associer avec d'autres espèces prédateurs de leurs herbivores, leur échapper dans le temps en accélérant leur développement (par exemple) ou encore se confronter aux phytophages par l'usage de défenses physiques (cuticule épaisse, poils plus ou moins longs) ou chimiques (comme des toxines, des alcaloïdes ou des réducteurs de digestibilité) (Fritz et Simms, 1992 ; Rana *et al.*, 2002). La compréhension de l'adaptation à la plante hôte est ainsi également intéressante à étudier chez les herbivores généralistes car il est possible de se demander si le généralisme de ces organismes est lié à la plasticité phénotypique de leurs traits ou à une évolution génétique rapide et une différenciation des populations sur différents hôtes.

Au cours de cette introduction, nous détaillerons les mécanismes et processus généraux permettant aux organismes de subsister suite à un changement d'environnement, en les illustrant à l'aide d'études s'inscrivant dans le cadre des interactions hôte-parasite. Nous décrirons plus particulièrement les réponses évolutives des parasites suite à un changement de leur hôte. Nous soulignerons également l'apport de l'évolution expérimentale dans ce domaine d'étude. Pour finir, nous décrirons l'organisme modèle utilisé dans le cadre de cette thèse où j'ai utilisé une approche d'évolution expérimentale pour comprendre les mécanismes et limitations de l'adaptation à une nouvelle plante hôte.

## 1. Comment persister suite à un changement d'hôte ?

### 1.1. Une histoire de valeur sélective

La valeur sélective d'un organisme est la mesure de son succès reproducteur dans une condition environnementale donnée. Cette notion implique notamment de mesurer pour chaque organisme le nombre de descendants produits qui survivront et se reproduiront eux-mêmes et donc leur contribution aux générations suivantes. Cette performance d'un organisme varie en fonction de l'adéquation entre le phénotype de l'individu (c'est-à-dire de ses caractères exprimés) et les caractéristiques de l'environnement. Les génotypes ayant une meilleure valeur sélective dans l'environnement contribuent davantage aux générations futures (Darwin, 1859; Futuyma, 2005).

Pour qu'il y ait persistance d'une population d'un parasite donné suite à une modification de son hôte, il faut, dans la population, (i) que des individus acceptent le nouvel hôte, (ii) que, parmi eux, certains individus soient capables de survivre et de se reproduire sur le nouvel hôte et, finalement, (iii) que ces individus deviennent plus nombreux et que la composition de la population change suffisamment rapidement pour qu'elle échappe à l'extinction sur le nouvel hôte. Ainsi, le maintien d'une population de parasite dans un nouvel hôte dépendra de la performance des individus qui composent cette population et particulièrement des différents caractères qui façonnent leur performance.

### 1.2. Les traits d'histoire de vie, composantes de la valeur sélective, et leur évolution en réponse à l'environnement

Les traits d'histoire de vie sont les principaux traits biologiques qui définissent le cycle de vie des organismes. Ils déterminent la performance des organismes, étant liés à ses principales composantes que sont la reproduction et la survie en fonction de l'âge (Stearns 1992 ; Futuyma, 2005 ; Thomas *et al.* 2010). Les traits d'histoire de vie peuvent correspondre à des durées de vie dans différents stades (le temps avant éclosion, le temps de développement avant maturité, la longévité adulte), des probabilités de survivre (survies juvénile ou adulte) ou encore des traits liés à la reproduction (le

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succès d'accouplement et le nombre de descendants produits) (Stearns, 1992). Dans le cas de l'étude de parasites, des traits tels que la virulence, la vitesse de transmission ou encore la résistance aux défenses de leurs hôtes sont autant de caractères qui peuvent affecter la performance des organismes (pour un exemple voir Ebert, 1994).

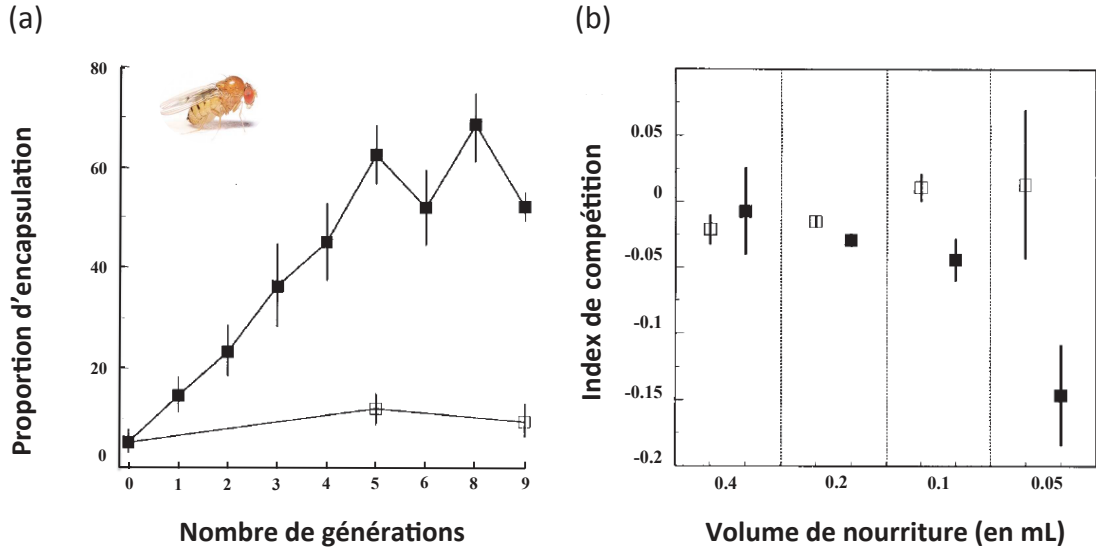
Les traits d'histoire de vie peuvent être considérés comme des points stratégiques du cycle de vie où les ressources disponibles doivent être allouées entre différentes fonctions. On parle de décision d'allocation (Stearns, 1992). Selon les changements induits par leur hôte, les parasites peuvent avoir à répondre aux questions (non exhaustives) suivantes: (i) faut-il se développer plus ou moins rapidement pour augmenter sa probabilité de survie ou de reproduction au sein de l'hôte ? (ii) vaut-il mieux se reproduire tôt ou tard au cours de son cycle de vie afin d'assurer à sa descendance de bonnes conditions de développement ? (iii) faut-il avoir une forte virulence aux dépens de son hôte et de sa propre reproduction ? (Reznick *et al.*, 1990 ; Thomas *et al.*, 2010). Le « choix » d'investir ses ressources dans certains traits dépend de facteurs biotiques et abiotiques environnants et notamment des contraintes environnementales (Stearns, 1992).

Les compromis entre traits d'histoire de vie chez un organisme conditionnent également l'évolution des traits d'histoire de vie en réponse à un nouvel environnement. En effet, il peut exister une covariance entre différents traits d'histoire de vie et l'évolution de l'un de ces traits peut alors affecter (positivement ou négativement) l'expression d'un autre trait (Stearns, 1989). Des mécanismes sous-jacents possibles à ces corrélations génétiques sont la pléiotropie, qui décrit l'action d'un gène sur plusieurs caractères, ou encore des déséquilibres de liaison entre des gènes distincts codant chacun pour deux traits. Les travaux de Kraaijeveld et Godfray (1997) illustrent bien cette notion de compromis entre traits d'histoire de vie chez un hôte, la drosophile, en réponse à son endoparasitoïde *Asobara tabida*. Suite à une exposition prolongée à ce parasite, la proportion de drosophiles ayant un mécanisme de résistance à ce parasite a augmenté chez des drosophiles pré-infestées relativement aux drosophiles non exposées à ce parasite (Fig. 2a). Cependant, lorsque ces deux types de drosophiles sont exposés à des conditions environnementales stressantes (ici une diminution de la ressource alimentaire), la compétitivité des drosophiles ayant développé une



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résistance au parasite se voit diminuer relativement à celle des drosophiles n'ayant pas été sélectionnées pour ce trait de résistance (Fig. 2b).



**Figure 2.** (a) Réponse du mécanisme de résistance de la drosophile (encapsulation) à son endoparasitoïde suite à une exposition à ce parasite sur plusieurs générations, et (b) conséquence de cette acquisition de résistance sur la compétitivité des drosophiles en conditions stressantes (diète alimentaire). Les carrés noirs représentent les réponses des drosophiles ayant évolué en présence du parasite, les carrés blancs correspondent aux réponses de populations ayant évolué sans le parasite.

Ainsi, il a été vu précédemment que les traits d'histoire de vie sont les composantes majeures de la performance et qu'ils peuvent répondre de façons variées à un changement d'environnement. Nous allons à présent décrire un mécanisme à l'origine de la variabilité phénotypique de réponse des organismes à une modification de leur environnement, la plasticité.

## 2. La plasticité adaptative

### 2.1. Qu'est-ce que la plasticité ?

La plasticité phénotypique d'un trait est définie comme la capacité inhérente à un génotype donné de produire différents phénotypes pour ce trait selon son environnement (Bradshaw, 1965 ; Stearns, 1989 ; DeWitt, 1998 ; de Jong, 2005 ; Auld *et al.*, 2010 ; Fragata *et al.*, 2016). La plasticité phénotypique s'oppose au concept de *canalisation* défini par Waddington (1942) selon lequel les organismes produisent le même phénotype, indépendamment de l'environnement dans lequel ils se

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développent. La plasticité phénotypique peut être adaptative, mal-adaptative ou encore neutre si la valeur du phénotype s'éloigne, s'approche ou encore reste à la même distance de l'optimum évolutif dans chacun des environnements (voir Ghalambor *et al.*, 2007). Je m'attacherai au cours de cette introduction à détailler des travaux portant sur la plasticité adaptative, c'est-à-dire la plasticité conférant un avantage sélectif aux organismes au sein d'un nouvel environnement.

La plasticité adaptative est considérée comme un mécanisme clef permettant aux populations de se maintenir suite à un changement dans l'environnement par le biais d'une augmentation de la performance des organismes. La plasticité d'un organisme peut être liée à une capacité à ajuster son comportement, sa morphologie, sa physiologie, en réponse à son environnement immédiat ou alternativement en réponse à l'environnement des parents (on parle alors d'effet parental) (Kuijper et Johnstone, 2016). Un bel exemple de plasticité adaptative est celui présenté par Greene (1989) chez le papillon *Nemora arizonaria*. Au printemps, la chenille de cet herbivore se nourrit principalement de chatons de chêne (des fleurs mâles agglomérées en grappe) faiblement concentrés en tanins. En été, cette chenille restreint ensuite son régime alimentaire aux feuilles de l'arbre qui sont, quant à elles, riches en tanins. Cette chenille est capable de produire deux morphes au cours de son développement; elle imite notamment les chatons et les brindilles de l'arbre selon les parties de la plante dont elle se nourrit au cours de son cycle (Fig. 3). La transition d'un morphe à l'autre est induite par la concentration de tanins de leur aliment (Greene, 1989).

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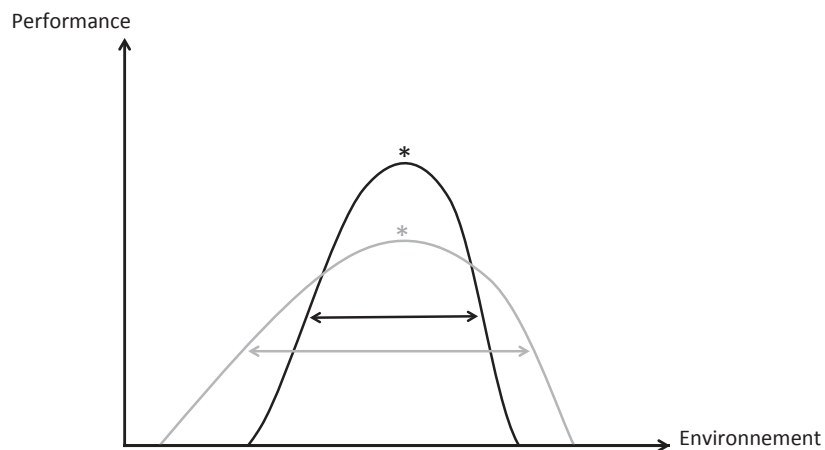


**Figure 3.** Un exemple de plasticité phénotypique au cours des jeunes stades du papillon *Nemoria arizonaria*. Les flèches en rouge indiquent en (a) la présence du morphe printanier imitant la forme des chatons dont il se nourrit, et en (b) le morphe ayant adopté la forme de brindille suite à un changement de régime alimentaire. Le changement est probablement induit par la différence de concentration de tanins dans les organes de la plante (faible concentration de tanins dans les chatons et forte concentration dans les feuilles). Cette plasticité morphologique confère un avantage sélectif aux chenilles qui se trouvent ainsi cachées des prédateurs par l'hôte qu'elles exploitent. Figure adaptée de Greene (1989).

Lorsqu'un organisme produit un phénotype qui varie comme une fonction continue des signaux environnementaux, cette fonction est alors appelée norme de réaction (Stearns, 1989 ; Chevin *et al.*, 2010). Une norme de réaction est représentée sur un graphique par une ligne ou une courbe exprimant le phénotype attendu ou observé d'un génotype en fonction d'un facteur environnemental. Il est alors possible, si l'on connaît la relation phénotype – valeur sélective, d'établir des courbes de performance exprimant la valeur sélective en fonction de l'environnement (Huey et Kingsolver, 1989 ; Chevin *et al.*, 2010). Plus cette courbe de performance est large, plus les organismes sont capables de se maintenir au sein d'environnements variés, on parle alors d'organismes généralistes. Inversement, lorsque la courbe de performance forme un pic étroit on parle d'organismes spécialistes capables d'utiliser un ou peu d'environnements (comme illustré dans la Fig. 4).

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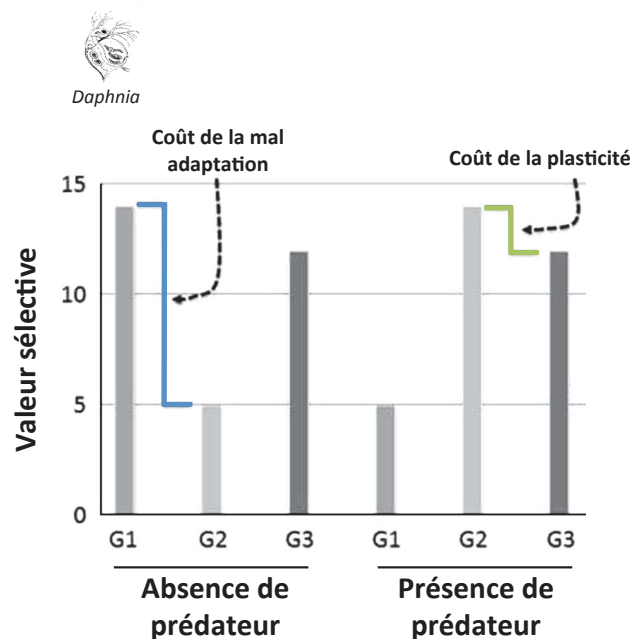
**Figure 4.** Figure présentant les gammes de performance d'organismes généralistes (en gris) ou spécialistes (en noir). Les doubles flèches indiquent la gamme de tolérance à différents environnements chez ces deux types d'organismes et les astérisques indiquent l'optimum des organismes (c'est-à-dire l'environnement pour lequel la performance des organismes est la plus élevée) dont nous discuterons un plus tard au cours de cette introduction.

## 2.2. « Jack of all trades, master of none » : généralistes *versus* spécialistes

L'évolution de la plasticité peut être associée à l'évolution des systèmes généralistes *versus* spécialistes (van Tienderen, 1997 ; Fragata *et al.*, 2016). L'une des hypothèses est que la capacité à exécuter une grande variété de tâches peut être réalisée uniquement au sacrifice de la performance maximale (Huey and Hertz, 1984 ; Chevin *et al.*, 2010). Cela se traduit notamment par une différence entre les performances maximales d'organismes généralistes *versus* spécialistes au sein (voir figure 4). D'où le dicton « Jack of all trades, master of none » traduit littéralement par « Touche-à-tout, maître de rien » (ou « qui trop embrasse mal étreint » en français). Les attendus théoriques sont doubles : (i) des organismes généralistes devraient avoir des performances intermédiaires et plus similaires au travers de différents environnements (par rapport aux spécialistes), et (ii) des généralistes n'évolueraient qu'en milieux hétérogènes. En ce sens, Levins (1966) avait établi qu'en milieu imprévisible des organismes devraient élargir leur niche écologique. De par le fait que la plasticité peut évoluer en fonction des conditions environnantes, il est possible de se demander pour quelles raisons cette aptitude à s'ajuster à l'environnement ne continuerait-elle pas à évoluer jusqu'au point où les espèces excellerait parfaitement dans tous les environnements.

## 2.3. Coûts et limites de la plasticité

Les coûts de la plasticité sont les effets négatifs liés au potentiel plastique des organismes qui se répercutent sur leur performance (DeWitt, 1998; Auld *et al.*, 2010 ; Murren *et al.*, 2015, voir Fig. 5). On peut détecter un coût lié à la plasticité lorsque celle-ci est mal adaptative dans l'environnement concerné (voir Crispo, 2008) ou lorsqu'un organisme plastique a une plus faible performance qu'un organisme non plastique dans un même environnement en produisant une valeur de trait identique à celle de l'organisme non plastique (Murren *et al.*, voir Fig. 5 pour plus de détails).



**Figure 5. Graphique différenciant dans un même environnement donné le coût de la mal adaptation (entre deux génotypes non plastiques dit « fixe ») du coût de la plasticité (entre un génotype « fixe » et un génotype « plastique ») chez la Daphnie.** Les génotypes G1 et G2 sont des génotypes ayant des phénotypes fixes (ou non plastiques) produisant des épines de 200  $\mu\text{m}$  et de 800  $\mu\text{m}$  de longueur, respectivement. G3 a un phénotype plastique produisant des épines de 200  $\mu\text{m}$  à 800  $\mu\text{m}$  en fonction des conditions environnantes (absence ou présence de prédateur). La présence de longues épines confère un avantage sélectif aux individus en présence de prédateur et est coûteuse en l'absence de ce dernier (pour se déplacer notamment). La différence de valeur sélective en l'absence de prédateur entre G1 et G2 (deux organismes non plastiques) présente le coût de la mal adaptation de G2 (qui présente de longues épines, inutiles à l'absence de prédateur et coûteuses qui plus est) tandis que la différence de valeur sélective en présence de prédateur entre le génotype dit plastique (capable d'ajuster la longueur de ces épines) et celui qui est fixe (présentant dans toute situation des épines de longueur égale à 800  $\mu\text{m}$ ) présente le coût lié à l'investissement du génotype G3 dans sa plasticité. Notons également que la différence de valeur sélective entre G1 (non plastique) et G3 (plastique) dans l'environnement avec prédateur présente l'avantage sélectif de la plasticité. Figure adaptée de Murren *et al.* (2015).

Les limites de la plasticité, quant à elles, se manifestent lorsqu'un organisme plastique ne peut pas produire un trait moyen aussi proche de l'optimum (valeur maximale de performance) qu'un organisme au phénotype fixe (ou non plastique).

## **2.4. La plasticité comme tremplin potentiel à l'adaptation**

Malgré les coûts et limites liés à la plasticité, il a été suggéré que la plasticité phénotypique pouvait permettre d'étendre la gamme écologique d'un organisme (revue dans Stearns, 1989). En effet, à l'inverse de l'idée énoncée par Wright (1932), selon laquelle la plasticité peut réduire les effets de la sélection potentielle, la plasticité est capable de générer une opportunité pour davantage de changements génétiques (Price *et al.*, 2003). Ces deux points de vue ne sont pas exclusifs et peuvent s'appliquer à différentes échelles de temps et de situations écologiques. L'idée de Wright est invoquée pour des gammes environnementales déjà rencontrées historiquement par la population, alors que celle de Price concerne des organismes exposés à de nouveaux environnements. De plus, il apparaît que la plasticité adaptative peut également aider au processus d'adaptation en produisant une réponse première rapide aux changements environnementaux et empêchant une extinction trop rapide suite à un changement d'environnement (Chevin *et al.*, 2010).

## **3. Adaptation**

### **3.1. Adaptation vs plasticité**

Comme énoncé précédemment, les parasites peuvent s'acclimater aux changements environnementaux grâce à leur plasticité phénotypique. Cependant, si le changement persiste, on s'attend à observer des changements de fréquences alléliques pour les traits liés à la performance au sein de l'hôte suite à la sélection naturelle. Cette réponse génétique peut remplacer ou se rajouter à la réponse plastique, selon le coût de cette dernière. Pour prédire les réponses adaptatives aux changements environnementaux, il est indispensable de distinguer rigoureusement l'adaptation génétique de la plasticité adaptative (Hansen *et al.*, 2012). Afin de distinguer les réponses plastiques

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de l'évolution génétique, il convient d'utiliser des dispositifs permettant de dissocier plasticité des phénotypes et divergence génétique affectant les phénotypes, comme des expériences en jardin commun par exemple, ou des transplantations réciproques.

## 3.2. Comment mesurer l'adaptation ?

L'analyse conjointe de la variation de traits d'histoire de vie et des marqueurs moléculaires d'un même organisme présent dans des milieux aux conditions environnementales différentes est l'une des approches qui permet d'étudier la divergence génétique ayant conduit à l'adaptation (Jensen *et al.*, 2008). L'étude des traits d'histoire de vie de populations ayant été soumises ou non à un changement d'hôte, mesurées dans des environnements communs, permet de relier les processus d'évolution en réponse au changement d'hôte et leurs conséquences démographiques (Hansen *et al.*, 2012). Certaines études s'attachent à mesurer les réponses de traits à des changements d'environnement (Jensen *et al.*, 2008 ; Magalhães *et al.*, 2007) tandis que d'autres suivent l'évolution de la croissance démographique des populations (notamment chez les micro-organismes, tels que les bactéries, pour lesquels il est plus fastidieux de décrire les traits du cycle) (Elena et Lenski, 2003 mais voir Miskinyte *et al.*, 2013 pour un contre-exemple).

## 3.3. Les limites de l'adaptation

Suite à un changement dans l'environnement, les populations peuvent s'adapter aux nouvelles conditions grâce à l'intervention de la sélection, favorisant certains individus ; cependant l'histoire passée de la population et le hasard sont également deux forces qui peuvent affecter le processus d'adaptation. Lorsque l'environnement change, les populations peuvent subir une diminution de leur taille efficace ( $N_e$  ci-après), c'est-à-dire une réduction du nombre d'individus qui contribuent aux générations futures (Charlesworth, 2009 ; Santos *et al.*, 2013). Ce paramètre tient un rôle clef dans la contribution relative de la sélection et du hasard dans le devenir des populations. Plus les populations ont un  $N_e$  faible, plus elles sont susceptibles de dériver sous l'effet du hasard et la contribution de la sélection dans le processus d'évolution se voit diminuer. A cette réduction de taille efficace de la population peut aussi faire suite une diminution de la valeur sélective des

populations à cause de l'augmentation de consanguinité qui peut entraver leur adaptation (Templeton, 1980 ; Santos *et al.*, 2012, 2013). Parallèlement, les flux de gènes (Lenormand, 2002) et la plasticité phénotypique peuvent aussi limiter les effets de la sélection et ainsi entraver le processus d'adaptation. Toutes ces informations sont difficilement accessibles en milieu naturel et il est d'autant plus difficile d'établir si une valeur sélective élevée est la conséquence de changements génétiques ou encore d'un mécanisme plastique. Pour ces raisons, il est important d'employer aussi d'autres méthodes afin de mieux comprendre comment opèrent les différents processus sur le maintien des populations.

## 4. L'évolution expérimentale, un outil pour l'étude de l'adaptation et de la plasticité

### 4.1. Les avantages de l'évolution expérimentale...

L'évolution expérimentale est un puissant outil en biologie évolutive qui permet de suivre en temps réel les processus évolutifs intervenant au sein de populations expérimentales en réponse à des régimes de sélection imposés par les expérimentateurs (Simões *et al.*, 2009; Kawecki *et al.*, 2012; Santos *et al.*, 2012; Magalhães et Matos, 2012 ; Santos *et al.*, 2013). Cette approche empirique permet d'établir une causalité entre les forces de sélection et les patrons d'adaptation en fournissant des aperçus sur les changements évolutifs qui interviennent (Burke *et al.* 2010). Des changements de performance peuvent être mesurés en comparant la performance des individus des populations ayant évolué dans de nouvelles conditions avec celle des individus de populations témoins (souvent utilisées pour fonder les nouvelles populations) (Kawecki *et al.*, 2012). Pour finir, l'évolution expérimentale est un outil robuste qui peut permettre de dissocier la contribution de la sélection et de la chance dans l'évolution par le biais de répétitions au niveau de la population qui permettent de tester la répétabilité de l'évolution (Garland et Rose, 2009; Kawecki *et al.*, 2012).



## 4.2. ...Et ses limites

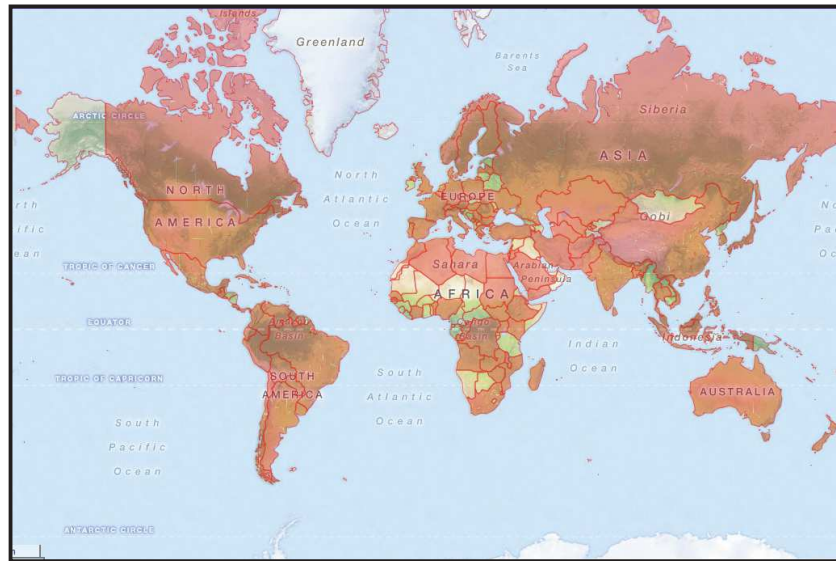
Bien que l'évolution expérimentale contribue grandement aux connaissances dans le domaine de la biologie évolutive, cet outil a également des limites. Notamment il est délicat de vouloir transposer les conclusions issues de ces travaux aux patrons observés en milieu naturel (Fellous *et al.*, 2014) car les populations de laboratoire peuvent répondre à des conditions non désirées (Kawecki *et al.*, 2012). Nous pouvons nous attendre à ce que les populations transférées et maintenues en conditions de laboratoire subissent davantage les conséquences de forts goulots d'étranglement car faisant déjà l'objet d'une sélection au cours de leur transfert de la nature au laboratoire. Ce dernier facteur peut complexifier l'interprétation des résultats et rendre difficile l'estimation du rôle de la sélection exercée sur les patrons observés. Cependant, ces goulots d'étranglement peuvent aussi intervenir en conditions naturelles, en particulier chez des populations généralistes qui peuvent expérimenter plus fréquemment des changements d'hôtes et ceci en lien avec leur gamme d'exploitation.

## 5. *Tetranychus urticae*, un ravageur de culture

### 5.1. Description générale

*Tetranychus urticae*, dit aussi le tétranyque tisserand ou araignée jaune, est un acarien phytophage de la famille des Tetranychidae à répartition cosmopolite comme en atteste la figure 6.

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**Figure 6. Répartition mondiale du ravageur de cultures *T. urticae* d'après les données de Migeon et Dorkeld (2006-2015).** Les aires géographiques en rouge présentent les pays dans lesquels la présence de l'espèce a été recensée sur différentes plantes hôtes.

Bien que de petite taille (de 0,3 à 0,5 mm de long pour les stades adultes), la présence de cet organisme peut être signalée par l'apparition de tâches dépigmentées sur l'appareil foliaire des plantes infestées mais aussi par l'apparition de toiles caractéristiques. En effet, *T. urticae* appartient aux herbivores « piqueur-suceurs » qui aspirent le contenu cellulaire de leur hôte après avoir planté leur stylet dans les feuilles cibles (Helle et Sabelis, 1985). C'est cette action qui occasionne l'apparition de zones jaunâtres sur la plante et qui entraîne, à terme, le dessèchement de la partie endommagée. Au cours de l'exploitation de la plante, cet acarien forme des toiles, servant de barrières de protection contre certains de leurs prédateurs naturels (Sabelis et Bakker, 1992), qui peuvent enserrer les organes vitaux de la plante et ainsi entraver le bon développement de cette dernière.

*T. urticae* est un organisme haplo-diploïde au mode de reproduction de type parthénogenèse arrhénotoque stricte : les mâles sont issus d'ovules (haploïdes) non fécondés et les femelles d'œufs (diploïdes) (ovules fécondés) (Helle et Sabelis, 1985). Une étude de Macke *et al.* (2011a) a mis en évidence que les femelles étaient issues de plus gros ovules, en moyenne, que les mâles. De plus, le sexe-ratio dans la descendance d'une femelle, c'est-à-dire la proportion de mâles dans cette

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descendance, dépend des conditions de compétition locale pour l'accouplement, en accord avec la théorie d'Hamilton (1967) (voir Macke *et al.*, 2011b). Des études ont déjà révélé que ce ravageur de culture a une forte plasticité phénotypique pour certains traits comme par exemple sa dispersion (Bitume *et al.*, 2013, 2014). Le cycle de vie relativement court de *T. urticae* (environ 14 jours du stade œuf au premier événement de reproduction à 20°C) lui confère les caractères d'un redoutable ravageur de cultures capable de rapidement se propager. De plus, sa large gamme de plante hôtes (plus de 1100 espèces végétales en milieu naturel ; voir Migeon et Dorkeld, 2006-2015 ; Grbić *et al.*, 2011) le définit comme un herbivore généraliste ; il occasionne d'importants dommages sur des plantes d'intérêt économique tels que le haricot, la vigne, des solanacées (la tomate, le tabac) (Van de Vrie *et al.*, 1972 ; Navajas *et al.*, 2000 ; Van den Boom *et al.*, 2003). L'étude des mécanismes permettant à cette espèce de subsister sur une nouvelle plante hôte présente ainsi un enjeu agro-économique important.

## 5.2. Plasticité et adaptation à la plante hôte

Un grand nombre de travaux ont porté sur la capacité de *T. urticae* à exploiter différentes plantes hôtes. Cela a notamment permis d'établir que ce généraliste pouvait répondre de différentes manières suite à un changement d'habitat. D'abord, certaines populations s'adaptent rapidement à un nouvel hôte (Gould, 1979 ; Fry, 1990 ; Magalhães *et al.*, 2007) alors que d'autres non (Fellous *et al.*, 2014 ; Miyazaki *et al.*, 2015). Ensuite, cette adaptation a différentes conséquences en termes d'exploitation d'autres hôtes. Plusieurs études ont montré que *T. urticae* élargit sa gamme d'hôtes suite à une évolution sur un nouvel hôte (Gould, 1979; Magalhães *et al.*, 2009) tandis que d'autres suggèrent la formation de race d'hôte (Navajas *et al.*, 2000) qui peut restreindre la gamme d'exploitation. Cependant peu d'études portent sur les réponses plastiques de ce phytophage à un nouvel environnement (Agrawal *et al.*, 2002; Magalhães *et al.*, 2011) ainsi que sur les conséquences démographiques liées à la colonisation d'une nouvelle plante hôte.

L'adaptation suite à un changement de plante hôte peut être un processus relativement rapide chez cette espèce (moins de 15 générations après un transfert sur un nouvel hôte comme montré par Magalhães *et al.* 2007). De plus, ce processus d'adaptation à la plante ne cause pas

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toujours une diminution de performance sur l'hôte « ancestral » comme ont pu le montrer Gould (1979), Fry (1990), Agrawal (2000) ou encore Magalhães *et al.* (2009). De nombreuses études ont porté sur la réponse des défenses des plantes de tomate à ce phytophage. Dans celles-ci, on a pu montrer que des attaques par *T. urticae* induisaient les défenses des plantes de tomate (Li *et al.*, 2002 ; Kant *et al.*, 2004). Cependant, il a également été montré que l'induction des défenses de la plante pouvait varier en fonction des souches de *T. urticae* (Kant *et al.*, 2008). Ce type de défenses a probablement évolué au cours de l'interaction de cette plante avec des herbivores afin d'optimiser le système de défense de la plante. Le maintien constant de fortes défenses (telles que les défenses constitutives) serait coûteux pour la plante (Fritz et Simms, 1992 ; Schoonhoven *et al.* 2005), qui ne pourrait allouer les ressources investies dans ce système de protection dans d'autres fonctions comme sa croissance. Il a été montré que l'adaptation de populations de *T. urticae* à la plante de tomate affectait l'expression des gènes de cet acarien codant pour la production d'enzymes de détoxification (Wybouw *et al.*, 2015).

## 6. Objectifs de la thèse

Les travaux de cette thèse s'appliquent à étudier l'évolution des traits d'histoire de vie d'un ravageur de cultures suite à un changement d'hôte dans le cadre d'une approche expérimentale. Plus précisément, dans les chapitres 1 et 2 j'étudie l'évolution sur un même hôte, la plante de tomate, de plusieurs traits d'histoire de vie aux stades juvéniles et adultes, mesurés sur des individus isolés. J'utilise une approche d'évolution expérimentale pour étudier l'adaptation à ce nouvel hôte, en partant de populations d'origines différentes (populations maintenues sur des plantes de concombre dans le chapitre 1 et de haricot dans le chapitre 2) et en répétant les expériences de changement d'hôte. Les expériences menées au cours de ces deux chapitres permettent de dissocier le rôle d'un mécanisme plastique, les effets maternels, et la contribution de l'évolution génétique sur la nouvelle plante hôte, à l'adaptation des acariens mesurée à travers leurs traits d'histoire de vie.

Dans le chapitre 1, les résultats montrent l'importance des effets maternels sur plusieurs traits d'histoire de vie dans un contexte de colonisation d'une nouvelle plante hôte. Cette expérience souligne également des réponses contrastées à différents stades du cycle de vie de cet organisme en

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réponse à l'environnement maternel. De plus, il apparaît que l'histoire évolutive des populations sur différentes plantes hôtes a dans cette expérience un effet faible sur leurs traits d'histoire de vie, hormis sur le sexe ratio.

Au cours du chapitre 2, j'analyse une expérience similaire d'évolution expérimentale correspondant à un changement d'hôte mais avec des conclusions très différentes. Nos résultats nous amènent à discuter comment l'adaptation *via* l'évolution génétique sur le nouvel hôte peut être compromise par des goulots d'étranglement durant la colonisation. Dans cette expérience, je compare les réponses adaptatives à la plante hôte à l'échelle des traits d'histoire de vie à celles obtenues sur des mesures intégratrices de la valeur sélective. Je m'appuie sur des analyses complémentaires sur la diversité génétique des populations afin de mieux inférer sur l'histoire démographique passée de ces populations et expliquer la variation des traits de vie entre celles-ci.

Finalement, le chapitre 3 de cette thèse explore l'un des mécanismes pouvant favoriser la persistance des populations de ce ravageur au cours de son évolution sur la plante de tomate, à savoir la manipulation par les acariens des défenses de la plante et donc de sa qualité comme hôte. Nous étudions les conséquences de la pré-infestation de la plante hôte par différentes populations d'acariens adaptées ou non à cette plante-hôte sur la performance des acariens colonisant ultérieurement la plante. Une fois encore ce dernier chapitre met en avant des réponses contrastées des traits d'histoire de vie (survie ou fécondité) au statut de pré-infestation de la plante, selon l'origine des acariens exploitant ces plantes.

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# *Chapitre 1*

*Des effets maternels peuvent faciliter la  
colonisation d'une plante hôte*



## Effects of host plant on life-history traits in the polyphagous spider mite *Tetranychus urticae*

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**Abstract** - Studying antagonistic coevolution between host plants and herbivores is particularly relevant for polyphagous species that can experience a great diversity of host plants with a large range of defenses. Here, we performed experimental evolution with the polyphagous spider mite *Tetranychus urticae* to detect how mites can exploit host plants. We thus compared on a same host the performance of replicated populations from an ancestral one reared for hundreds of generations on cucumber plants that were shifted to either tomato or cucumber plants. We controlled for maternal effects by rearing females from all replicated populations on either tomato or cucumber leaves, crossing this factor with the host plant in a factorial design. About 24 generations after the host shift and for all individual mites, we measured the following fitness components on tomato leaf fragments: survival at all stages, acceptance of the host plant by juvenile and adult mites, longevity, and female fecundity. The host plant on which mite populations had evolved did not affect the performance of the mites, but only affected their sex ratio. Females that lived on tomato plants for circa 24 generations produced a higher proportion of daughters than did females that lived on cucumber plants. In contrast, maternal effects influenced juvenile survival, acceptance of the host plant by adult mites and female fecundity. Independently of the host plant species on which their population had evolved, females reared on the tomato maternal environment produced offspring that survived better on tomato as juveniles, but accepted less this host plant as adults and had a lower fecundity than did females reared on the cucumber maternal environment. We also found that temporal blocks affected mite dispersal and both female longevity and fecundity. Taken together, our results show that the host plant species can affect critical parameters of population dynamics, and most importantly that maternal and environmental conditions can facilitate colonization and exploitation of a novel host in the polyphagous *T. urticae*, by affecting dispersal behavior (host acceptance) and female fecundity.

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## 1. Introduction

Plants and herbivores exert strong selective pressures upon each other (Schoonhoven *et al.*, 2005), resulting in a coevolutionary arms race (Ehrlich and Raven, 1964; Kant *et al.*, 2008). To cope with attacks by herbivores, plants have evolved physical defenses, such as glandular trichomes, and a large diversity of chemical defenses (Fritz and Simms, 1992; Schoonhoven *et al.*, 2005; Wise and Rausher, 2013). Conversely, herbivores have evolved mechanisms to cope with these defenses, by escaping detection by host plants or suppressing plant defenses (Schoonhoven *et al.*, 2005; Kant *et al.*, 2008; Sarmiento *et al.*, 2011). The herbivore ability to get around host plant defenses is particularly important for polyphagous species, which can feed and reproduce on several plant families (Schoonhoven *et al.*, 2005), relative to monophagous species, which are specialized on a few closely related plant species expected to carry similar defenses. For polyphagous species that can frequently be exposed to new hosts, colonizing a new host plant species often involves tolerating or resisting defenses specific to the new host plant, and thus quickly responding to diverse and possibly strong selection. Responses of herbivore populations to environmental changes, such as a host plant shift, can range from local extinction to adaptation. A related question is how and by which mechanisms can populations of polyphagous herbivores adapt and exploit many host plant species. Addressing this question is not only exciting from an evolutionary perspective, for example, to understand local adaptation processes, but can also provide crucial information for the management of crop pests.

To test for local adaptation of herbivore populations to a given host plant species, a common practice is to compare their fitness components (*e.g.*, life-history traits) on this plant species with those displayed by other herbivore populations that have evolved on a different plant species (Kawecki and Ebert, 2004). It is expected that local genotypes have a higher fitness on their (local) host plant species than do genotypes from a different host plant species. As emphasized by Kawecki and Ebert (2004), experimental evolution is a valuable way to complement research on natural populations using replicated populations in controlled environments and by allowing direct tests for adaptation. This approach allows researchers to establish causality of evolutionary



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processes and adaptation patterns (Kawecki *et al.*, 2012a,b; Magalhães and Matos, 2012), which is impossible with natural populations. Yet, experimental evolution has barely been used to study the adaptation of herbivores to new host plant species (but see Gould, 1979; Fry, 1990; Bolter and Jongasma, 1995; Agrawal, 2000; Fricke and Arnqvist, 2007; Magalhães *et al.*, 2007; Kojima *et al.*, 2010; Fox *et al.*, 2011; Fellous *et al.*, 2014). Moreover, the few studies that used this approach were limited in the number of traits measured and by the fact that plasticity and dispersal processes were usually not simultaneously analyzed.

*Tetranychus urticae* Koch (Acari: Tetranychidae) is a highly polyphagous spider mite that feeds on more than 1100 plant species, of which over 100 are important agricultural crops (<http://www1.montpellier.inra.fr/CBGP/spmweb/>). Recent studies revealed that adaptation of this herbivore to one host plant could facilitate exploitation of other host plant species and therefore broaden its host range (Magalhães *et al.*, 2009; Fellous *et al.*, 2014). Further, adaptation to a new host plant for this species did not always result in its decreased performance on the original host (Gould, 1979; Fry, 1990; Agrawal, 2000; Magalhães *et al.*, 2009). After 15 generations, mite populations evolving and tested on detached leaves of a novel host species (tomato or pepper) performed better on their host than did populations evolving on leaves of another host (cucumber), indicating the occurrence of local adaptation (Magalhães *et al.*, 2007), and adaptation to a specific host plant (here the tomato leaves). In this study, we investigated the responses of *T. urticae* to a host shift, using mite populations maintained on entire plants and tested on detached leaves. As in Magalhães *et al.* (2007), we used populations maintained on cucumber plants in our laboratory. We measured survival, fecundity, changes in the sex ratio (proportion of males), and the host plant acceptance (Via, 1990), which can inform on the dispersal behavior of *T. urticae*. Tests for adaptation were performed on detached leaves to measure life-history traits and to monitor the life cycle of single individuals.

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## 2. Material and Methods

### 2.1. The experimental populations

In May 1994, *T. urticae* mites were collected from a population maintained on cucumber plants (*Cucumis sativus*, variety: Ventura) in a greenhouse in Pijnacker, the Netherlands, then kept on the same variety in a climate chamber at the University of Amsterdam. In September 2007, after they had evolved for circa 480 generations, approximately 5000 mites were sampled from the Amsterdam population to create two populations on cucumber plants at the University of Montpellier, hereafter called “ancestral populations”.

In February 2011, eight independent populations were created from a mixture of the two ancestral populations: four populations each containing 400 females were transferred on the same variety of cucumber plants (hereafter called  $C_i$ , for population  $i$ ) and the other four populations containing, respectively, 400, 400, 260, and 220 females were transferred to tomato plants (*Solanum lycopersicum* species, variety Olympe HF1; hereafter called  $T_i$ ). One month later (circa 2 generations), because  $T_1$  and  $T_2$  experienced a demographic bottleneck, 400 mite females (a mixture of one hundred mites of each  $C_i$  population) were added to each of these populations. All populations were maintained under the same conditions in a single climate chamber at  $25 \pm 1^\circ\text{C}$  with a photoperiod of 14L: 10D and were in different boxes isolated from one another by water (to prevent mites from dispersing). Two to four new plants, depending on the number of old plants, were added every week to each population while old plants were removed. Plants used to maintain mite populations and test for adaptation and maternal effects (see below) were grown from seeds placed during one and a half months in an isolated and herbivore-free room controlled for temperature ( $23 \pm 1^\circ\text{C}$ ) and photoperiod (12L: 12D).

### 2.2. Tests for adaptation and maternal effects

When life-history traits were measured, the C populations had evolved on cucumber plants (in different countries/conditions) for circa 594 generations (17 years and 9 months), and the T

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populations had evolved for circa 570 generations (16 years and 9 months) on cucumber and 24 generations (1 year) on tomato plants. Two temporal blocks of the experiment presented below were performed in January and February 2012; hence, populations had evolved two more generations in the second block compared to the first block. Hereafter the selection regime (SRT for the Selection Regime Tomato, and SRC for the Selection Regime Cucumber) refers to the host plant species (T and C, respectively) on which the populations had evolved the year previous to the experiment.

To study adaptation and maternal effects, mites from each population spent one generation in one of two distinct maternal environments, consisting of either detached cucumber leaf fragments or detached tomato leaves (hereafter the term “leaf” is used to refer to both maternal environments). Thirty adult females were haphazardly sampled from each of the C and T populations and put on either tomato or cucumber leaves of similar sizes (circa 16 cm<sup>2</sup>) and then put in plastic boxes covered with water-saturated cotton to both limit mite dispersal and ensure humidity and thus persistence of leaves. Twenty adult females produced by this first generation were then haphazardly sampled, during 1 day only, from each population in each maternal environment, and put on fresh leaves of the same species as the one experienced by their mothers. Note that because of high mortality in the second block, only thirteen and fifteen adult females for the C2 and C3 populations, respectively, were sampled from the tomato maternal environment. We let females oviposit in groups for 1 day, and twenty-four of the resulting eggs were haphazardly sampled from each population and each maternal environment. Eggs were individually put on a tomato leaf fragment of circa 0.8 cm<sup>2</sup>, hereafter called the testing environment, to measure life-history traits and other fitness components. As monitoring was performed every 2 days and eggs were laid less than 24 h before being isolated, the precision of measures for each trait is less than 2 days. Again, leaf fragments were placed on water-saturated cotton in several plastic boxes. Fresh leaf fragments were provided to individual mites every 4 days. Twenty-four boxes, each containing 16 individuals, were then haphazardly put in a climatic room at 25 ± 1°C with a photoperiod of 14L:10D.

We recorded the status of mites (presence or absence, and alive or dead) on the testing

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environment every 2 days. Once mites had reached adulthood, we could identify their sex and count the number of eggs produced by females. All emerged females remained virgin during the experiment. Of the 768 individuals monitored in the two blocks, we measured life-history traits for 712 individuals (Table 1); fifty-six individuals were removed from the analyses because they were accidentally lost. This monitoring provided for each block the individual following measures: (1) host acceptance at both juvenile and adult stages (*i.e.*, to stay in or leave the testing environment), (2) egg mortality, (3) juvenile mortality, (4) developmental time, that is, the time to reach maturity, (5) sex, (6) time spent as an adult in the testing environment, (7) dispersal time of dispersing juveniles and adults, that is, the time at which they left the testing environment, and (8) fecundity of females, that is, the total number of eggs produced by each female (Table 1).

**Table 1.** Sample sizes at generation 24 for each life-history trait according to the selection regime (SRC and SRT for cucumber and tomato plants, respectively), the maternal environment (MEC and MET for cucumber and tomato leaves, respectively) and the block (B1 and B2).

	SRC		MET		SRT		MET		Total
	B1	B2	B1	B2	B1	B2	B1	B2	
Egg mortality	83	91	85	93	92	91	87	90	712
Juvenile acceptance	75	86	79	93	87	85	83	88	676
Juvenile mortality	70	83	75	86	86	83	79	83	645
Developmental time, Sex ratio and Adult acceptance	56	42	60	64	67	50	68	70	477
Time spent as an adult in the testing environment	56	42	57	64	66	50	66	70	471
Fecundity	44	34	47	44	56	40	62	60	387

All analyses were carried out using the R software (R Core Team, 2013). Analyses of life-history traits were performed by building general or generalized linear mixed models including as fixed effects the selection regime (SR, with two levels), the maternal environment (ME, with two levels), the block (B, with two levels), and the interaction between the selection regime and the maternal environment. The block was included as a fixed rather than a random effect because it

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strongly affected late mite stages. Replicated populations were included as random factors nested within the selection regime. Fixed and random factors were tested by likelihood ratio tests. For all response variables, the best models included a single estimate of the interpopulation variance independently of the selection regime (all P values > 0.18). When analyzing developmental time, adult acceptance and time spent as adult in the testing environment, the factor sex (with two levels) was included in the models. For the analysis of the time spent as an adult in the testing environment and fecundity, the factor adult acceptance (with two levels) was included in the models. We considered binomial distributions for the numbers of dead eggs, dead juveniles, dispersing juveniles, dispersing adults, and males, and thus applied generalized linear mixed models when analyzing variation in these response variables. The time spent as an adult in the testing environment, the logtransformed developmental time and the square-rooted fecundity were assumed to follow normal distributions, and we thus applied linear mixed models for the analysis of these response variables. All models were validated by checking their error structure.

## 3. Results

### 3.1. Selection regime

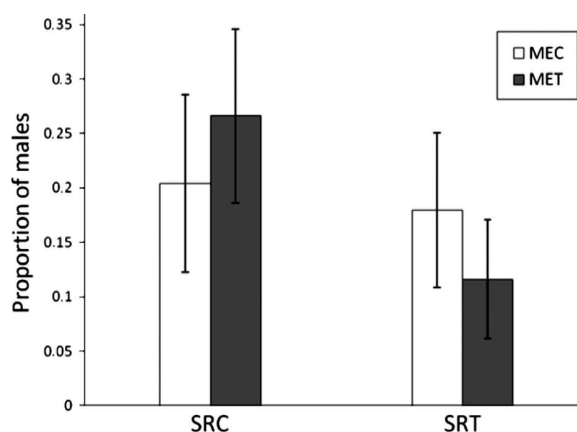
After circa 24 generations of evolution, only the sex ratio of the populations differed between the selection regimes induced by the host plants: females from the populations maintained on tomato plants produced a lower proportion of sons (mean  $\pm$  SE:  $0.15 \pm 0.03$ ) than did females ( $0.24 \pm 0.08$ ) from the populations on cucumber plants, independently of the environment on which they laid eggs (Table 2, Fig. 1). Overall, we found no effect of the selection regime or its interaction with the maternal environment on any of the juvenile or adult traits (Tables 2 and 3).

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**Table 2.** Effects of the experimental design on sex ratio, egg mortality, juvenile acceptance, and juvenile mortality.

Effects	Sex ratio		Egg mortality		Juvenile acceptance		Juvenile mortality	
	$\chi^2$	P-value	$\chi^2$	P-value	$\chi^2$	P-value	$\chi^2$	P-value
SR	<b>4.46</b>	<b>0.03</b>	0.21	0.65	1.82	0.18	1.77	0.18
ME	0.03	0.87	<b>4.38</b>	<b>0.04</b>	2.50	0.11	<b>18.51</b>	<b>&lt;0.0001</b>
SR x ME	3.23	0.08	0.17	0.68	1.16	0.28	0.78	0.38
B	1.54	0.21	3.36	0.07	0.06	0.80	<b>15.94</b>	<b>&lt;0.0001</b>

SR, selection regime; ME, maternal environment; B, block.  $\chi^2$  and P-value are in bold when the P-value <0.05.



**Figure 1.** Sex ratio (proportion of males) of individuals that reached maturity as a function of the selection regime (SRC and SRT for cucumber and tomato, respectively) and the maternal environment (MEC and MET for cucumber and tomato, respectively).

**Table 3.** Effects of the experimental design on adult acceptance, developmental time, time spent as an adult in the testing environment, and fecundity.

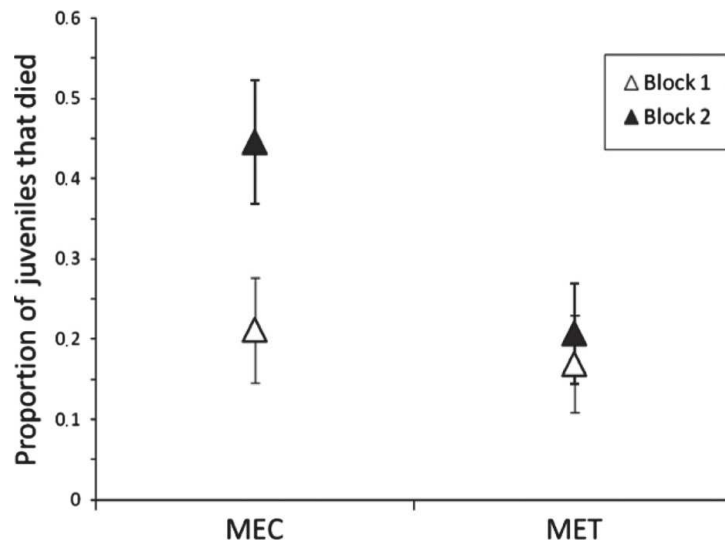
Effects	Adult acceptance		Developmental time		Time spent as an adult in the testing environment		Fecundity	
	$\chi^2$	P-value	$\chi^2$	P-value	$\chi^2$	P-value	$\chi^2$	P-value
SR	1.08	0.30	0.68	0.41	0.42	0.51	0.03	0.87
ME	<b>8.19</b>	<b>0.004</b>	0.50	0.48	1.62	0.20	<b>8.93</b>	<b>0.003</b>
SR x ME	0.02	0.88	0.26	0.61	0.12	0.72	0.14	0.71
B	0.44	0.51	1.40	0.24	<b>30.59</b>	<b>&lt;0.0001</b>	<b>73.5</b>	<b>&lt;0.0001</b>
Sex	0.01	0.91	1.46	0.23	<b>6.21</b>	<b>0.01</b>	–	–
Adult acceptance status	–	–	–	–	<b>20.56</b>	<b>&lt;0.0001</b>	–	–
Female acceptance status	–	–	–	–	–	–	<b>9.16</b>	<b>0.003</b>

SR, selection regime; ME, maternal environment; B, block. The ‘–’ indicates that the variable was not tested.  $\chi^2$  and P-value are in bold when the P-value <0.05.

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## 3.2. Maternal environment

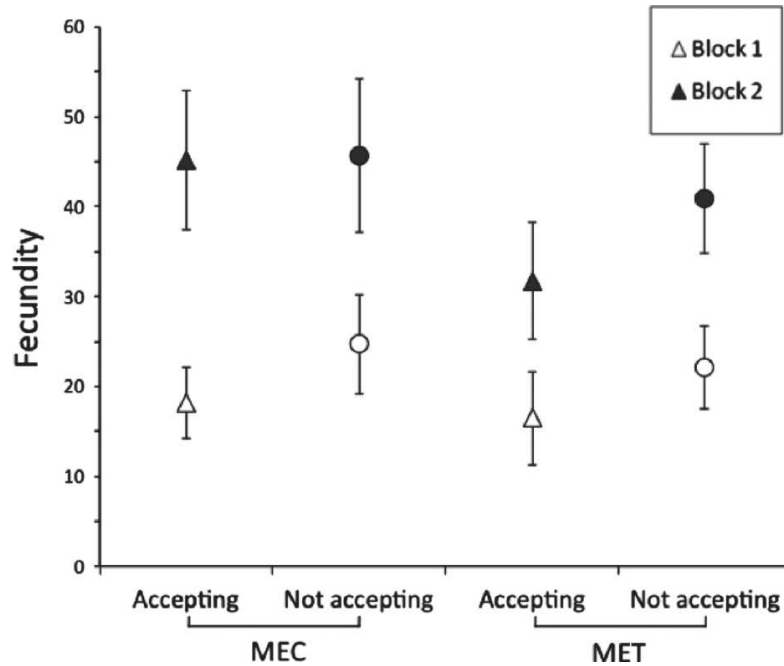
The maternal environment influenced mortality at both the egg and juvenile stages: offspring of females from the cucumber maternal environment had a higher mortality ( $0.07 \pm 0.01$  and  $0.33 \pm 0.03$  for egg mortality and juvenile mortality, respectively) than offspring of females from the tomato maternal environment ( $0.03 \pm 0.01$  and  $0.09 \pm 0.02$  for egg mortality and juvenile mortality, respectively). Note also that juvenile mortality was higher in the second block ( $0.33 \pm 0.03$ ) than it was in the first block ( $0.19 \pm 0.02$ ; Table 2, Fig. 2).



**Figure 2.** Proportion of dead juveniles in the testing environment as a function of the maternal environment (MEC and MET for cucumber and tomato, respectively) and the block (with white for B1 and black for B2); vertical lines correspond to four standard errors.

As adults, individuals (males or females) accepted less the testing environment (acceptance:  $0.43 \pm 0.03$ ) and produced (as females) fewer offspring (fecundity:  $28.08 \pm 1.54$ ) if their mothers were reared on the tomato environment than if their mothers were reared on the cucumber environment ( $0.56 \pm 0.03$  and  $31.34 \pm 1.80$  for adult acceptance and fecundity, respectively; Tables 2 and 3, Fig. 3). The maternal environment therefore acted in opposite directions on juvenile and adult fitness traits.

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**Figure 3.** Fecundity of females in the testing environment as a function of the maternal environment (MEC and MET for cucumber and tomato, respectively), the female acceptance status (with circles for not accepting females and triangles for accepting females), and the block (with white for B1 and black for B2). Vertical lines correspond to four standard errors.

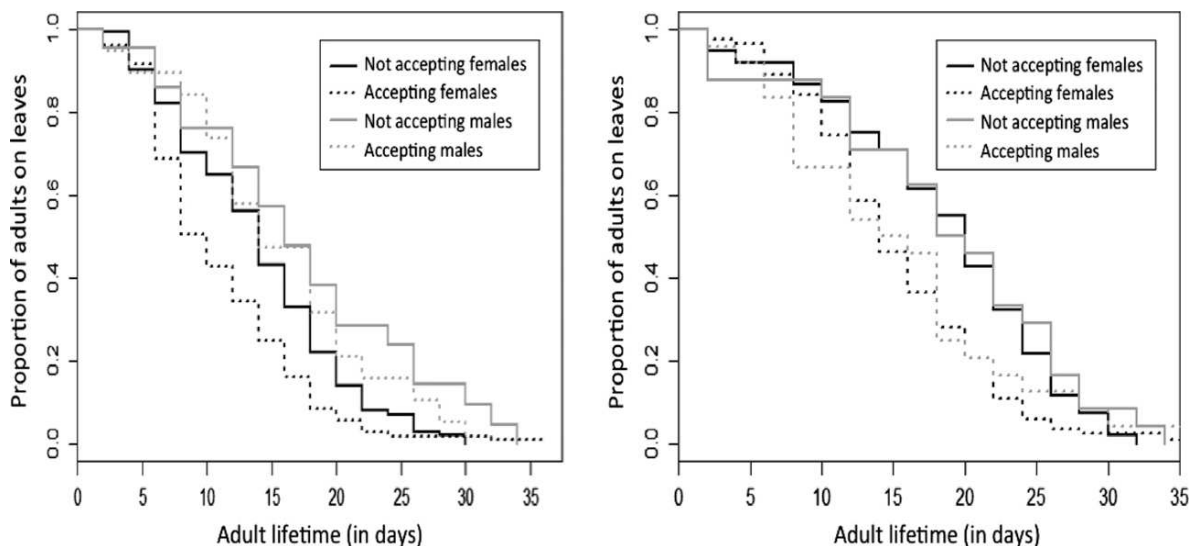
### 3.3. Status of individuals

The adult acceptance status, that is, the choice to stay in or disperse from the testing environment, the sex of the individuals and the block were relevant to describe the time spent as an adult on the testing environment. Independently of the selection regime and the maternal environment, male adults spent more time ( $16.77 \text{ days} \pm 0.92 \text{ days}$ ) in the testing environment than did females ( $14.56 \pm 0.37$ ; Table 3, Fig. 4) and also lived longer than did females (result not shown). Opposite patterns were observed for adult mites on the testing environment, depending on the blocks: adults dispersed at a younger age for the first block (age in days:  $14.46 \pm 0.65$ ) than they did for the second block ( $18.57 \pm 0.73$ ), but they died older in the second block (age at death in days:  $15.26 \pm 0.70$ ) than they did in the first block ( $11.75 \pm 0.59$ ; Table 3, Fig. 4). Female fecundity was influenced by their acceptance status and by the block. Females that dispersed from the testing environment produced more eggs ( $32.72 \pm 1.67$ ) than did females that accepted this environment ( $26.27 \pm 1.62$ ). The fecundity of females was also twice higher in the second block ( $40.53 \pm 1.80$ ) than in the first block



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( $20.20 \pm 1.21$ ), probably because females lived longer in the second block than they did in the first one (Table 3, Figs. 3 and 4).



**Figure 4.** Proportion of live adults in the testing environment through days for blocks B1 (A) and B2 (B). The black lines hold for females, the grey lines for males, the solid lines for adults that accepted the testing environment, and the dotted lines for adults that did not.

## 4. Discussion

In this study, we investigated the evolution of demographic and behavioral traits in response to a host plant shift in populations of a polyphagous mite. The fitness components of these populations were measured while controlling for maternal effects. We did not find signals of adaptation of the populations to the novel host, but detected strong maternal effects and a difference in sex ratio between host plants on which the populations had evolved.

### 4.1. Observed adaptive changes after the host shift

Our experiment reveals that 1 year (circa 24 generations) of evolution of *T. urticae* on tomato plants did not affect their juvenile or adult traits when measured on tomato leaves. As *T. urticae* is an extreme generalist, populations may have been already adapted to both tomato and cucumber plants. However, Magalhães *et al.* (2007), who used the same ancestral population of *T. urticae* and

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also controlled for maternal effects, detected adaptation after 15 generations for mite populations that had evolved and were tested on tomato leaves. These contrasting results may stem from the material used to maintain the populations. Kavousi *et al.* (2009) detected different responses in demographic traits in *T. urticae* when measured on leaf disc versus whole leaves. Adaptation to plants *versus* detached leaves may thus imply different levels of stress and environmental variation require different adaptive processes. Although detached leaves are able to produce chemical defenses (Dicke and Dijkman, 1992), much of the plant response to herbivores is systemic and thus absent in detached leaves. To measure accurately adaptation to novel host plants, populations should be maintained and tested on entire plants, and maternal effects should be controlled for. The present study also shows that the host plant on which the population has evolved influences the sex ratio, measured as the proportion of sons, with females maintained on tomato plants producing a lower proportion of sons than females maintained on cucumber plants. The same effect was observed when sex ratio was measured directly in evolving populations, maintained on either cucumber or tomato plants (unpublished data). The low proportion of males in the populations is thus consistent with the observed and lower density of individuals on tomato plants compared to cucumber plants. The low density of mites on tomato plants can result from several non-exclusive mechanisms: the lack of adaptation to the novel host plant, the low resources provided to mites by tomato plants (as suggested by our personal observations on female fecundity and survival), and the increased dispersal of adult individuals. For *T. urticae*, females have been shown to be the dominant dispersing sex (Kennedy and Smitley, 1985; Bitume *et al.*, 2011); we, however, did not detect differences between male and female dispersal behavior as they left the testing environment equally (circa about 50% of adult mites). The low proportion of males in some populations is also not consistent with the idea that tomato plants may provide fewer resources to females compared to cucumber plants. In *T. urticae* indeed, males result from smaller eggs than do females (Macke *et al.*, 2011), and may thus be less costly to produce in a poor environment.

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## 4.2. Maternal effects increase offspring fitness on the novel host plant

Independently of the host plant species on which the populations were reared, we found that the survival of juveniles from mothers that lived on tomato leaves was near twice higher than was the survival of offspring from mothers that lived on cucumber leaves, suggesting that the tomato was a better previous environment than the cucumber was to then exploit tomato host plant. It has been indeed found that insect individuals produced by mothers experiencing a low-quality environment have a lower performance than do individuals produced by mothers in better-quality environments (Mousseau and Fox, 1998; Franzke and Reinhold, 2012; Kelly *et al.*, 2014). Our results are consistent with those of Magalhães *et al.* (2011) that show that the offspring of mothers reared on pepper, tomato or cucumber leaves had higher performances on these host species than do offspring of mothers reared on bean leaves, which is nevertheless considered as a host plant of high quality for mites (Agrawal, 2000). Our study thus shows that maternal conditions strongly influence the performance of *T. urticae* individuals after a host plant shift could facilitate successful colonization of a novel host plant. Another hypothesis is that mothers from the tomato maternal environment have acquired a better resistance to the constitutive defense of tomato plants, which was transmitted to their offspring. These effects have been shown in *Daphnia* for which offspring that were challenged with the same bacterial strain to that of their mothers showed an increased immune response compared to offspring that were challenged with different strains from their mothers (Little *et al.*, 2003). Similarly, in the milkweed bug arthropod, mothers can store cardenolide, a defensive compound from host plants, and transfer it into their eggs, which are then protected against predation (Newcombe *et al.*, 2013). The maternal conditions also affected the dispersal behavior of the offspring. Independently of the host plant on which their population evolved, *T. urticae* adults produced by mothers from the tomato environment left 1.3 times more the tomato testing environment than did adults from mothers of the cucumber environment. This pattern was independent of the sex of the individuals, and thus highlights that host plant acceptance, that is, a proxy of host plant suitability, by that is similar for males and females. Our results are consistent

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with the observation that the dispersal distance of offspring is strongly affected by maternal and grand-maternal environments (Bitume *et al.*, 2014). We could thus infer that females reared on the tomato common environment produced adults with a dispersal capacity higher than those from females reared on the cucumber common environment, this capacity potentially being adaptive for searching for a more suitable host. An alternative hypothesis would be that mothers reared on tomato laid fewer eggs (personal observations) but were fitter and could disperse at a higher rate than did mothers reared on cucumber plants; this hypothesis cannot be checked as we did not measure individual fitness components in the maternal common environments. Independently of the underlying mechanism, dispersal of adults could prevent resource competition between parents and their offspring or prevent the induction of plant defenses, and thus be adaptive, as only high densities of *T. urticae* (more than 20 mites per leaf) can induce plant defenses (Karban and Carey, 1984; Kant *et al.*, 2004; Sarmiento *et al.*, 2011; Marinosci *et al.*, unpublished manuscript).

### **4.3. Environmental conditions can affect colonization of a novel host species**

We detected that temporal blocks affected the juvenile mortality, the time spent as an adult in the tomato testing environment, and the female longevity and fecundity. These blocks may reflect one or several uncontrolled environmental variables, such as humidity, temperature, and light in the climate rooms. A previous experiment has indeed found that female fecundities and female longevities decrease with increased temperature (from 25 to 30°C; Riahi *et al.*, 2013). The experimental, that is, environmental, conditions also affected the time at which adult mites left the testing environment, independently of their sex, and the longevity of adults that remained in the testing environment. Extrapolated to natural conditions, these results suggest that host colonization critically depends on environmental conditions by affecting directly female fitness and both male and female dispersal behavior.

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## *Chapitre 2*

*La taille d'une population peut  
compromettre l'adaptation à la plante  
hôte*



**Limits to adaptation when colonizing a new host-  
plant: evidence from experimental evolution in spider  
mites**

Cassandra Marinosci, Ophélie Ronce, Sara Magalhães, Sophie Lefèvre, Elodie Flaven, David  
Carbonell, and Isabelle Olivieri

**Abstract** - Polyphagous species, able to exploit different plants, allow studying dynamics of life history evolution in response to host shifts. In this paper, we use experimental evolution design to test: (i) how life history traits in populations of *Tetranychus urticae*, a generalist species, evolve on a new host-plant; (ii) whether adaptation patterns differ in populations exposed to the new host for different numbers of generations and (iii) how this relates to patterns of neutral genetic variation in such populations. On tomato, individuals from populations that had evolved on that host for approximately 38 and 78 generations showed an increase in juvenile survival and male adult lifespan, relative to individuals from control populations (having not experienced tomato for at least 280 generations). Other traits, such as dispersal and female adult lifespan did not change. Moreover, populations evolving for the shortest number of generations on tomato plants had a higher daily fecundity than populations evolving on tomato for the longest time. As a result, female lifetime reproductive success only increased in the former populations. Populations evolving for the longest time on tomato plants showed a stronger genetic differentiation in neutral markers since their divergence, suggesting that adaptation may have been compromised by drift. Thus, overall, we confirm that both drift and selection shape the evolution of a herbivorous generalist on a novel host.

## 1. Introduction

Polyphagous species are able to exploit a large range of host-plants. This may be achieved through phenotypic plasticity and wide tolerance of herbivore populations to many hosts (Ehrlich and Raven, 1964; Nylin and Wahlberg, 2008), and/or through rapid genetic adaptation and differentiation of host races upon colonization of a new host-plant (Navajas *et al.*, 2000; Magalhães *et al.*, 2007a). A new host-plant may however represent a very hostile environment, in which only few individuals survive, compromising the prospects of adaptation and persistence of the population. Indeed, short-term adaptation to a new stressful environment may come at a cost of strong bottlenecks in population size, leading to random genetic drift and thus increasing consanguinity, possibly depressing population fitness in the long term (Templeton, 1980; Santos *et al.*, 2012; Santos *et al.*, 2013). Concerns about inbreeding depression and genetic load associated with small population size have been mainly discussed in the context of conservation biology in order to prevent the extinction of endangered populations (see Diamond, 1973; Frankham, 1995). We may however expect that consanguinity and drift associated to population bottlenecks are also particularly relevant in the context of host-plant colonization because they can act on population growth by changing life history traits in the new environment (Lee, 2002; Fauvergue *et al.*, 2012).

Even when drift does not affect the adaptation process, different life history traits may evolve at different rates. For instance, recent theory suggests that life history traits expressed early or late in the life cycle may adapt at different paces when populations are shifted to a new environment (Cotto and Ronce, 2014), resulting in different detailed adaptation signatures depending on the number of generations spent on a new host and the stage at which the life history trait is expressed. Such prediction is explained by the fact that life history traits expressed early in the life cycle have a larger impact on fitness and thus are under stronger selection in a new environment than traits expressed late in life (Hamilton, 1966; Rose *et al.*, 2007). More generally, we have still a poor understanding of whether host shifts result in

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similar strategies of adaptation and life history syndromes in independent events of adaptation to the same host-plant, and how often adaptation fails (Fellous *et al.*, 2014).

The system composed of the spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) and the plants it colonizes is ideal to test how selection and drift may shape different life history traits after a host shift. *T. urticae* is a polyphagous spider mite able to exploit hundreds of host-plant species (Grbić *et al.*, 2011). Previous studies on this herbivore revealed that populations respond differently after a host-plant shift. For example, adaptation to a new host-plant in this herbivore species could facilitate host-plant exploitation of other host-plant species and thus broaden its host range (Gould, 1979; Magalhães *et al.*, 2009; Bonte *et al.*, 2010). A few studies also found adaptive learning of host preference (Egas and Sabelis, 2001; Agrawal *et al.*, 2002) or plastic responses to host shifts (Marinosci *et al.*, 2015, Magalhães *et al.*, 2011; Agrawal *et al.*, 2002). In this study, we investigate (1) how evolution of a mite population following a host shift to tomato affects juvenile and adult life history traits, as well as a quantity that we use as a proxy for female fitness (and that we obtain by modelling all the components of fitness jointly), (2) if the 'female fitness' and life history traits evolved similarly in independent experiments of host shift, or differed among populations exposed to the new host for a different number of generations and, (3) if populations lost genetic diversity after the host shift and whether different adaptation signatures may be associated to different rates of changes in genetic diversity, potentially signalling different demographic histories on the new and ancestral hosts.

## 2. Material and methods

### 2.1. Biological model

The two-spotted spider mite *T. urticae* is a small polyphagous mite with an arrhenotokous haplodiploid life cycle: females produce haploid sons parthenogenetically and diploid daughters from fertilized eggs (Helle and Sabelis, 1985). This generalist herbivore is considered as a major pest (Migeon and Dorkeld, 2006-2015), causing severe damages to its

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host-plants (Van de Vrie *et al.*, 1972; Helle and Sabelis, 1985). One reason for this is its short life cycle: less than 15 days at 20°C from egg to egg on a suitable host (Helle and Sabelis, 1985; Riahi *et al.*, 2013). The life cycle can be divided in (i) an egg stage, (ii) a larval stage, with two nymphal stages (protonymph and deutonymph) (hereafter the larval and the nymphal stages are grouped into the juvenile stage), (iii) an adult stage, during which mites can be sexed, reached after a short quiescent period.

### 2.2. Plant cultures

All tomato and bean plants were grown in Montpellier in an isolated and herbivore-free room at 23°C ± 2°C, and with a photoperiod of 12L: 12D. In the experiments and maintenance of mite populations, 45-d-old plants were used, to equalize the effect of plant age on mites.

### 2.3. Mite populations

In October 2000, approximately 5000 individuals of *T. urticae* mites were collected from roses in a garden near Ghent, Belgium. A population was established and maintained on bean (*Phaseolus vulgaris*) potted plants variety 'Prelude' in a climatically controlled room at 25 ± 1°C in Belgium. In November 2008, approximately 800 mite individuals (all stages and sexes confounded) were transferred to Montpellier, France, and a base population was started and maintained under the same conditions with a population size of approximately 2500 mites (see Bitume *et al.*, 2011; Fig 1a). Between April and July 2009, we founded three independent populations on tomato plants (*Solanum lycopersicum*, variety Olympe HF1), by transferring in each population approximately 400 adult females from the base population. Less than two months later, 150 adult females (also from the base population) were added to two of these new populations on tomato to boost the demography on the new host-plant. In February 2011, we created from the base population four independent populations (hereafter called control

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populations, for populations that did not experience tomato plants in the lab) by transferring 400 adult females of *T. urticae* to each of four boxes containing bean plants. At the same time, four additional populations were created on tomato plants by transferring 400 adult females to each new population, corresponding to a mixture of the four control populations in equal proportions. Less than one month later, one hundred adult females from control populations were added to each of these new populations. At the same time, we re-mixed the populations that had been evolving on tomato for at least 20 months, such that all populations would be (re)started simultaneously. To this aim, we created four mixtures (each consisting of approximately 150 to 200 mites) by transferring available mites from the three populations that had been established on tomato plants earlier, in equal proportions. We therefore had populations with three different histories of exposure to tomato (hereafter selection regime, SR): populations that had not experienced tomato as a host-plant in the lab, populations recently transferred on tomato, and populations evolving on tomato for a longer time (Fig. 1a). Hence, we had in total 12 populations with four replicate populations for each selection regime. We assayed life history traits in all these populations in September 2012 (Fig. 1a). Some populations had then been evolving on tomato for 19 months (~38 generations, hereafter Tomato 19 SR) and others for 39 months (~78 generations, hereafter Tomato 39 SR). The control populations (Bean SR) had not experienced tomato plants for at least 144 months before this experiment. All four replicate populations within each selection regime evolved independently and had diverged from each other for the same time. Divergence time among replicate populations was similar for all selection regimes (about 38 generations for the bean SR and the tomato 19 SR and 36 for the tomato 39 SR, see Fig. 1a). Note however that, at the time of divergence, populations in the tomato 39 SR were founded with about half the number of founders in the bean and tomato 19R (as explained above), due to a smaller number of available mites in populations already exposed to tomato, which suggests that founding events could lead a stronger genetic signature in those populations.

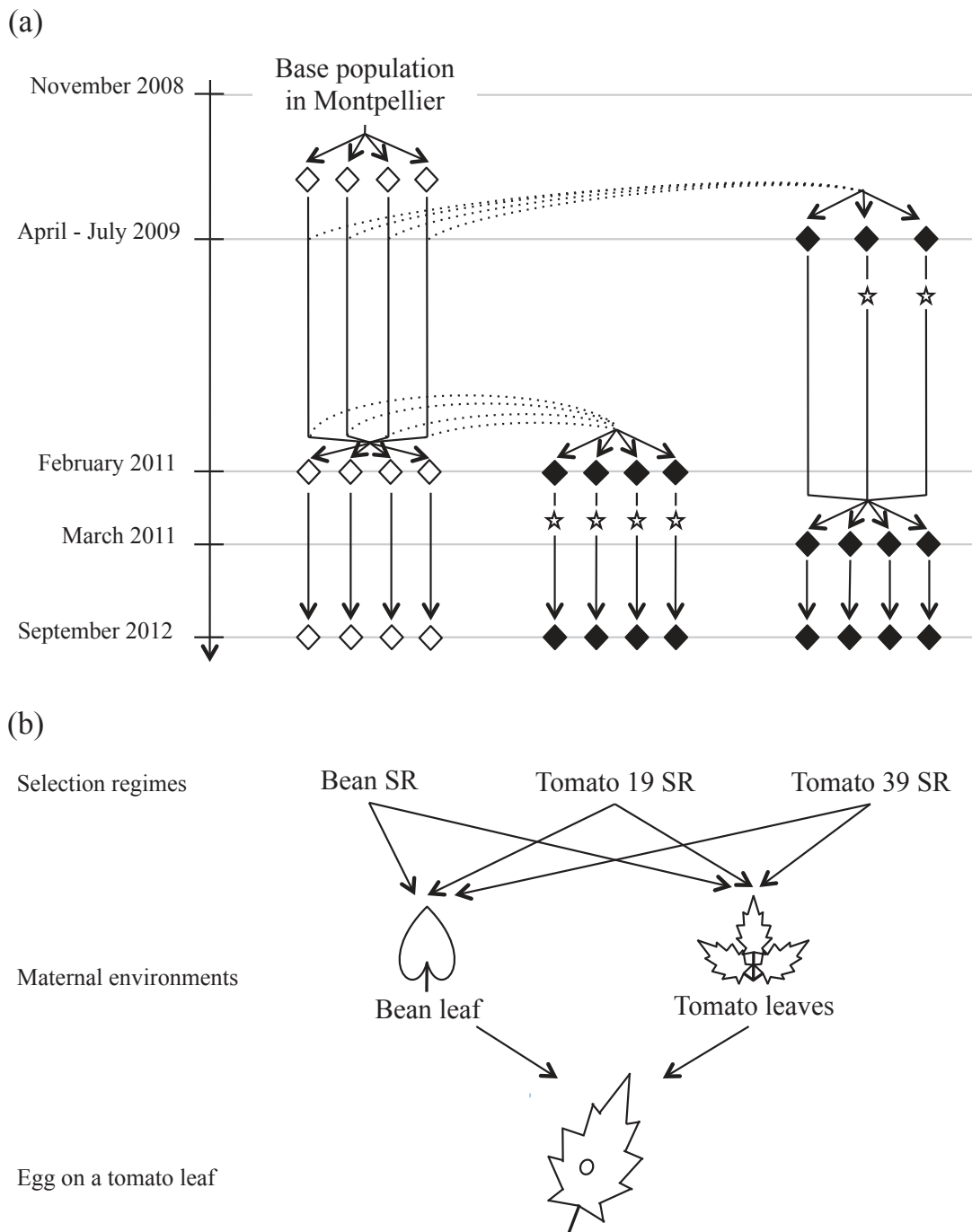
## *Chapitre 2 - La taille d'une population peut compromettre l'adaptation à la plante hôte*

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All mite populations were stored in a climatically-controlled room at  $25 \pm 2^\circ\text{C}$  with a photoperiod of 14L: 10D. Each population was confined to a single translucent plastic box (505 mm length x 310 mm width x 380 mm height). Each of the 12 boxes contained 9 to 12 tomato or bean plants. Every week, rotten plants or plants with no mites were removed from boxes and replaced by young mite-free plants. Only tomato plants were sometimes not colonized by mites, which could mean that these individual plants were of very low quality. The new plants were put in contact with the infested plants to facilitate mite dispersal. Every week, during plant replacements, some water was added at the bottom of boxes to keep plants alive as long as possible. Each lid was cut and the removed part (approximately 490 mm x 200 mm) was replaced by a piece of fine mesh veil, which let the light enter and prevented condensation, while impeding mite dispersal. To strengthen the dispersal barrier, the 12 boxes were put on independent trays with water.



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**Figure 1.** (a) Evolutionary history of the populations used in this study. The white and the black diamonds correspond to populations evolving on bean and tomato plants, respectively. The dashed arrows represent transfer of individuals to the novel host-plant and the solid arrows represent the evolution of populations on their respective host-plant. The white stars indicate the time at which additional individuals from the control populations were added to the populations evolving on tomato plants. (b) Experimental design before measuring individual life history traits on tomato leaf after one generation on either of two maternal environments (bean and tomato maternal environments consisting of one bean leaf and three tomato leaves of the same surface area).

## **2.4. Individual life history traits monitoring on tomato leaves**

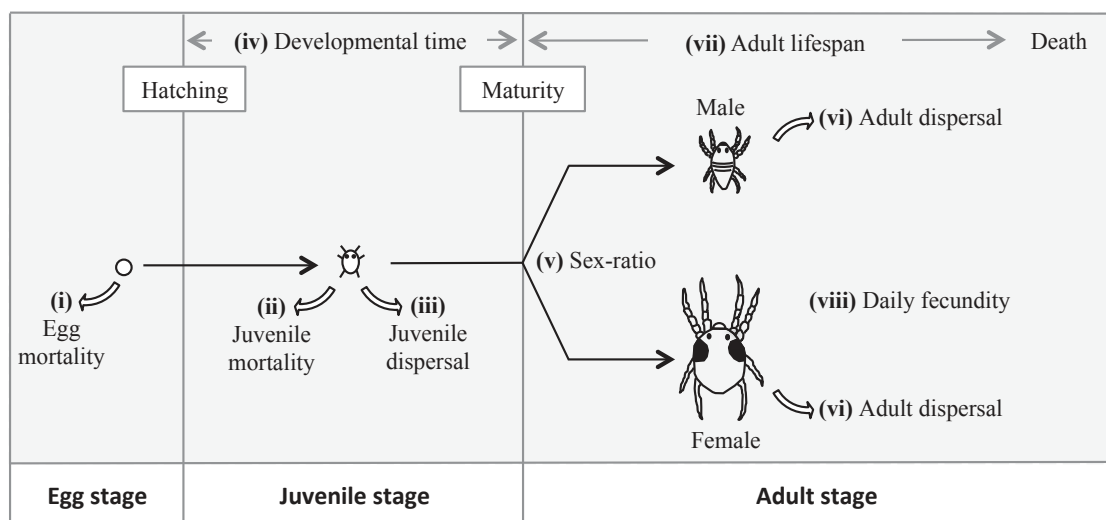
### 2.4.1. Experimental design

To test for adaptation to tomato, we compared life history traits on tomato leaves of individuals from the different selection regimes. To control for environmental effects, mites from each population spent one generation on either three tomato leaves or on one entire bean leaf (Fig 1b). These common environments were of similar size ( $\sim 16 \text{ cm}^2$  of leaves) and placed in boxes with water-saturated cotton to both limit mite dispersal and ensure humidity and thus persistence of plant leaves. We chose to use these two common maternal environments (hereafter called bean ME and tomato ME) to quantify the maternal environment effect on life history trait evolution and thus on host-plant exploitation because they represent both host-plants used. Fifty adult females were haphazardly sampled from each of the 12 populations; 25 mites were placed on bean ME and the other 25 on tomato ME (Fig. 1b). After one generation, we haphazardly collected and grouped 25 mature daughters produced in each ME and placed them in a new environment (that is, fresh leaves) similar to that of their mothers. One day later, we removed from each new environment 21 eggs laid by these females. Each egg was isolated on an individual tomato leaf with a surface area of  $\sim 1.5 \text{ cm}^2$ , placed in a plastic box with water-saturated cotton. In total, fourteen boxes were used and each box contained 36 tomato leaves. Once eggs reached maturity, mites were transferred with a brush to a new tomato leaf every four days until death. The boxes were placed in an incubator maintained at  $25 \pm 1^\circ\text{C}$  with a photoperiod of 14L: 10D.

Every two days during egg, juvenile and adult stages, we checked and recorded the mite state (alive or dead), and its presence on the tomato leaf (mites sometimes left the leaf and died in the water) (Fig. 2). This last state is hereafter called dispersal status (although it might be unrelated to dispersal under natural conditions) and corresponds to the choice of staying (status = philopatric) or leaving (status = dispersing) the tomato leaf. From these observations,

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we estimated the dates of transition ( $\pm$  two days) from the egg to the juvenile stage, and from the juvenile to the adult stages (*i.e.*, hatching and maturity, respectively; Fig. 2). Once mites had reached adulthood, we identified their sex and counted the number of eggs produced by females every four days. Note that all emerged female stayed virgin during the experiment. Out of the 504 individuals initially put on tomato leaves, we monitored the life cycle of 492 individuals and measured their life history traits; 12 eggs placed on tomato leaves were never found back and were thus excluded from the analysis.



**Figure 2.** Steps at which individual life history traits were measured during the life cycle of *T. urticae* (see the numbering in bold), from the egg stage to the death of individuals. ‘Hatching’ and ‘Maturity’ define the transitions between the egg stage and the juvenile stage and between the juvenile stage and the adult stage, respectively. Black arrows indicate when individuals successfully pass from one stage to the next one (from egg to juvenile and from juvenile to adult). White arrows correspond to individuals that died or left the leaf before having successfully achieved their whole life cycle at (i) the egg stage, (ii) the juvenile stage, or (iii) the adult stage. Grey arrows indicate life history traits that are measured in time units.

We analysed eight life history traits for each population on tomato leaves: (i) egg mortality, through the proportion of unhatched eggs, (ii) juvenile mortality, through the proportion of individuals that died at the juvenile stage (thus the number of individuals that died on the tomato leaf or in the water as juveniles over the total number of hatched eggs), (iii) juvenile dispersal, *i.e.*, the proportion of juveniles that left the tomato leaf, (iv) the (coarse)

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developmental time, that is the time in days elapsed from hatching to maturity, (v) adult sex ratio, that is the number of males among individuals that reached adult stage, (vi) adult dispersal, (vii) adult lifespan in days, that is the time elapsed from maturity to death (by including adults that naturally died on the tomato leaf and adults that left the tomato leaf and thus died in the water), (viii) daily fecundity, that is the total number of eggs produced by virgin females per day. Table 1 presents the sample sizes for each life history trait by SR (bean, tomato 19 and tomato 39) and by ME (bean and tomato).

**Table 1.** Sample sizes for each life history trait according to the selection regime (SR) (bean, tomato 19 and tomato 39) and the maternal environment (ME) (bean or tomato).

Life history traits	Bean SR		Tomato 19 SR		Tomato 39 SR		Total
	Bean ME	Tomato ME	Bean ME	Tomato ME	Bean ME	Tomato ME	
Egg mortality	82	83	82	84	80	81	492
Juvenile dispersal	78	72	72	70	67	62	421
Juvenile mortality							
Developmental time	21	17	42	39	29	33	181
Sex ratio	21	17	42	37	29	31	177
Adult lifespan							
Adult dispersal							
Daily fecundity	16	5	29	20	24	14	108

### 2.4.2. Statistical analysis

#### *Life history traits*

All analyses were carried out using the R software (R Core Team, 2013). The analysis of life history traits was performed by building general or generalised linear mixed models including as fixed factors the SR (with three levels: bean, tomato 19 and tomato 39), the ME (with two levels; bean and tomato) and the interaction between these factors (hereafter called SR x ME).

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Populations, nested within the selection regime, were included as random factors. We kept for each life history trait this model structure as a basis (*i.e.*,  $\text{response} \sim \text{SR} + \text{ME} + \text{SR} \times \text{ME} + (1|\text{Pop})$ ). We excluded the random factor box from all models because we found no significant variance associated to this factor. For some traits (developmental time, adult dispersal and adult lifespan), we added sex (with two levels, male or female) as a covariate and all possible interactions with the previous defined fixed factors. All effects involving sex were tested and only those with a significant effect at the 5% level were kept in the model. We applied generalised linear mixed models with a binomial distribution to the following variables: egg mortality, juvenile mortality, juvenile dispersal, adult dispersal and sex ratio. For the developmental time, we applied a generalised linear mixed model with a Poisson distribution. We validated these models by verifying that residuals were not overdispersed (*i.e.*, that the combined residuals are not much larger than the residual degrees of freedom). Finally, the adult lifespan and the daily fecundity followed a normal distribution. We checked and validated these models by testing normality of the residuals. We used likelihood ratio tests for the phase of model selection and to test the significance of effect of factors on life history traits. When we found a significant effect of an interaction between a factor and SR (*e.g.*, SR x Sex), we analysed the effect of the SR on the response variable within each level of the other factor (*i.e.*, by sex here). When the SR had a significant effect on a life history trait, and to determine which level was significantly different from others, we applied contrasts on this response variable and compared bean SR *versus* tomato 19 SR, bean SR *versus* tomato 39 SR and tomato 19 SR *versus* tomato 39 SR. Within each selection regime, replicate populations were treated as a random factor.

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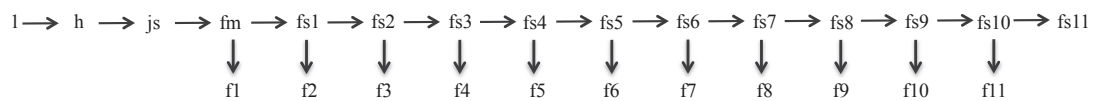
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### *Integrative fitness measure*

We conducted an aster life history analysis, which allows to jointly analyse data on survival and reproduction, each having different probability distributions, and explicitly model the conditional relationships between different life history traits (Geyer *et al.*, 2007; Shaw and Geyer, 2010). We applied aster analysis to detect if there is an effect of SR, ME, and their interaction, on female lifetime reproductive success on tomato leaves, which was estimated as the total number of new eggs produced per egg (*i.e.*, if the egg was a male its female lifetime reproductive success was zero). These factors were included as fixed factors in the model. We did not include population as a random effect in this analysis because variation among replicate populations were estimated to be small in our analyses of individual life history traits (see Results) and random effects sometimes cause estimation problems in aster analyses (see however Geyer *et al.*, 2013 for implementation of random effects in aster models). By using an unconditional aster model, we obtained an integrated measure of female fitness, including survival at young stages (*i.e.*, at egg and juvenile stages), probability to be female, survival as adult (for females only) and (female) fecundity. This analysis modelled the dependence of later expressed components of fitness (*e.g.*, fecundity) on those expressed earlier (*e.g.*, female survival). We describe the life history of an individual, starting at the egg stage, and computing the number of eggs produced by this individual during its lifetime with the graphical model shown in Fig. 3. Each monitored egg initially put on a tomato leaf was in the same state, thus this initial state (or root node in aster terminology) is associated to the constant variable 1 (as in Fig. 3). The graphical model includes five types of transitions in the life cycle: hatching rate (called *h*), juvenile survival (called *js*), maturing as a female (called *fm*), female survival (*fs*) through 11 intervals, and fecundity associated to each of ten intervals of the female survival (from *fm* to *fs10*) (Fig. 3). Although we defined eleven intervals for female survival and fecundity, for the model to converge, we had to assume that intervals of female survival followed the same probability of transition and also that female fecundity at each age was

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derived from the same distribution (we therefore do not model senescence in fecundity and survival). We modelled the transition between the egg stage and the juvenile stage (*i.e.*, the hatching rate), the juvenile survival rate, the transition between the juvenile stage and the emergence of adult females (*i.e.*, the female maturation rate), and the female survival, using Bernoulli distribution. The fecundity of each female at each stage was modelled using a Poisson distribution.



**Figure 3.** Graphical model for aster analysis of lifetime reproductive success. The single root node corresponds to the egg state;  $h$  denotes a hatched egg;  $js$  denotes an individual that has survived the juvenile period;  $fm$  represents a recently-emerged female;  $fs_i$  represents an adult female that is alive at the end of the census interval  $i$ ;  $f_i$  represents the number of eggs laid between census  $i-1$  and census  $i$ .

To study the effect of the interaction SR x ME but also of these two factors (independently) on total fitness, we compared first the models with and without the interaction and then the models with and without the factor of interest (*i.e.*, SR or ME) by using likelihood ratio tests. When the SR had a significant effect on the lifetime reproductive success, and to determine which level was significantly different from the others (*e.g.*, bean SR *versus* tomato 19 SR, bean SR *versus* tomato 39 SR, and tomato 19 SR *versus* tomato 39 SR), we applied the same model and methods to the datasets only containing the relevant treatments. These independent analyses did not correct for the number of tests.

### 2.5. Genetic analyses

Evolution of life history traits on different hosts may be influenced by drift. In our experiment, replicate populations within each selection regime have diverged and evolved separately from each other for approximately the same number of generations (~36 generations) whatever the selection regime. Evolving on different hosts may however exert different constraints on

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population size and strong selection on the new host may have further reduced the effective population size. We may thus expect different populations from different selection regimes to lose diversity at neutral markers and accumulate neutral differences between them at different rates depending on their effective size during divergence. The number of founders and their origin furthermore differed in tomato 39 SR lines compared to bean SR and tomato 19 SR lines, as they were founded from populations having already evolved on tomato for several generations and with a smaller number of mites. We expect populations of smaller size and/or having experienced stronger bottlenecks to harbour lower levels of diversity and to be more differentiated from each other. Genetic variability, measured as the expected heterozygosity, and the genetic differentiation of populations, measured by  $F_{ST}$ , were estimated using microsatellite markers. For that purpose, in February 2014 we haphazardly collected 24 adult females from each population of the bean SR, the tomato 19 SR and the tomato 39 SR to estimate and compare genetic diversity of populations from these selection regimes.

Females from these populations were individually placed in a tube with 96% ethanol and conserved at -24 °C before DNA extraction. DNA was extracted from mature females by using the Dneasy Cell and Tissue Kit (Qiagen) and the protocol described in Boubou *et al.* (2011). To measure genetic diversity of each population, 15 microsatellite markers were used in three multiplexes (TuCA25, TuCA83, Tu01, Tu27, Tu35b and TuCT18 within Tupmix1; Tupm08, TuCA02, TuCT67 and TuCT09 within Tupmix2; Tupm02, Tupm07, Tupm09, TuCT04 and Tu16 within Tupmix3, for more details see Bitume *et al.*, 2013). STRAND software was used to determine individual genotypes (Veterinary Genetics Laboratory, University of California; <http://www.vgl.ucdavis.edu/STRand>). Readings were made by two different users. Allele binning was based on raw size using Autobin (an Excel macro available at <http://www6.bordeaux-aquitaine.inra.fr/Production-scientifique/Logiciels/Autobin>; for more details see Guichoux *et al.*, 2011) to detect discrete size variants. We estimated the expected heterozygosity within populations and the  $F_{st}$  among populations of the same selection regime



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by using the program GENETIX version 4.05. Genetix produces confidence intervals of  $F_{st}$  by bootstrapping over loci. To compare the genetic diversity of populations with different selection regimes, we applied an ANOVA on the expected heterozygosity.

### 3. Results

#### 3.1. Life history traits on tomato

The variance associated to populations within the same selection regime was very small for all life history traits (except for the sex ratio, Table 2).

##### 3.1.1. Juvenile traits

The maternal environment did not affect juvenile traits (see statistical results in Table 2). Two juvenile traits evolved in response to the selection regime: egg and juvenile mortality (Table 2). There were only slight differences in egg mortality between populations having evolved on different host-plants. The proportion of unhatched eggs in populations having been transferred recently on tomato plants (tomato 19 SR) was marginally higher (from raw data:  $0.08 \pm 0.03$ ) than that in control populations (bean SR) ( $0.03 \pm 0.03$ ; bean SR *versus* tomato 19 SR:  $P=0.09$ ), while other contrasts were not significant (Fig. 4a). In contrast, juvenile mortality on tomato plants was significantly lower for populations that had evolved on tomato than for control populations (Table 2; Fig. 4b): when feeding on tomato, 75% of individuals died as juveniles in the bean SR, compared to 43% for mites collected in populations recently transferred on tomato plants (bean SR *versus* tomato 19 SR tomato:  $P<0.001$ ), and 52% for mites collected in populations evolving for a longer time on tomato plants (bean SR *versus* tomato 39 SR tomato:  $P<0.001$ ). Juvenile mortality was similar in populations evolving on tomato for a different number of generations (tomato 19 SR *versus* tomato 39 SR:  $P=0.46$ ). We did not detect any difference in juvenile dispersal and developmental time according to the

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selection regime, the maternal environment or the interaction between these two factors (Table 2, Fig. 4c and 4d).

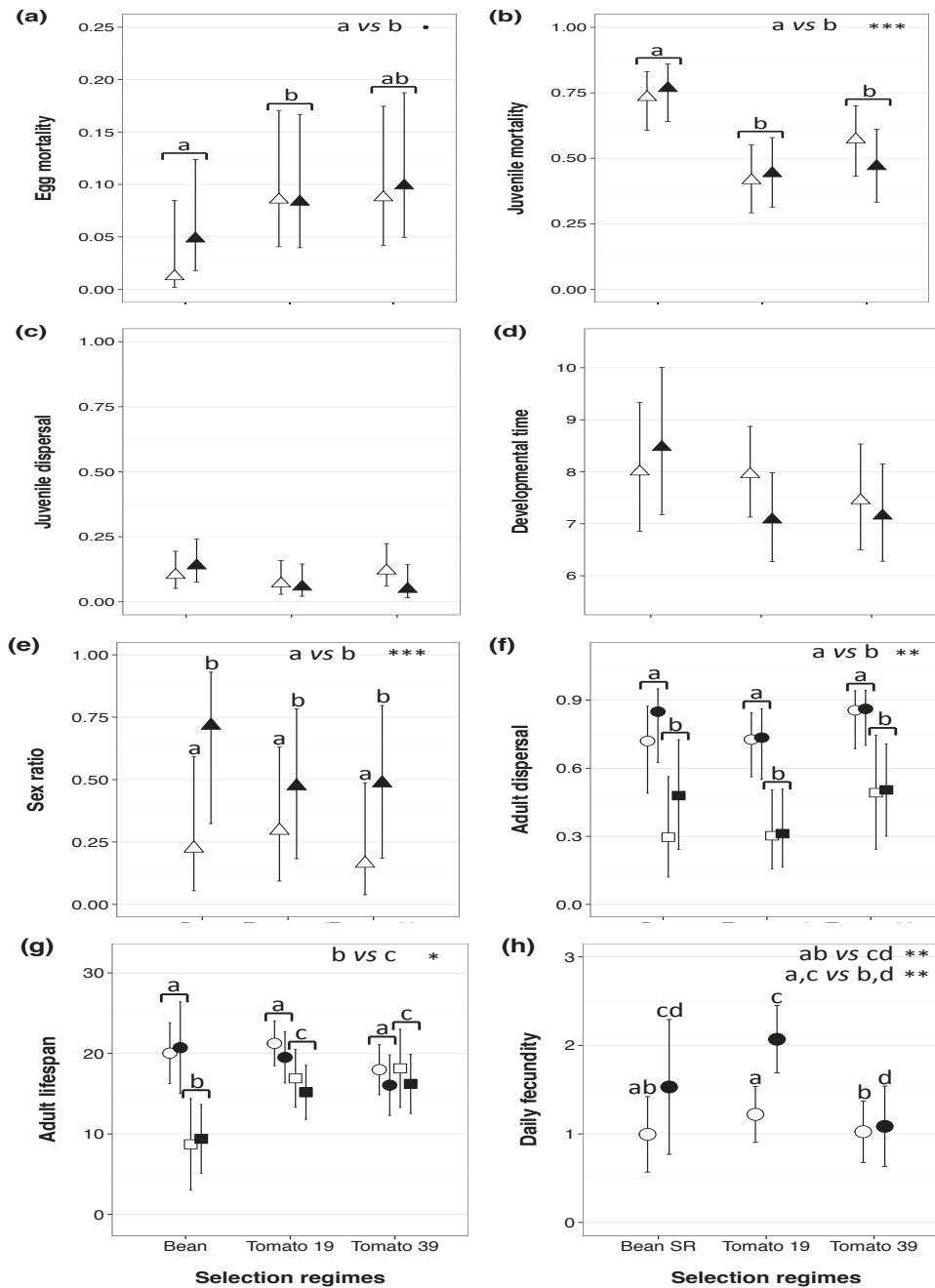
**Table 2.** Statistical analysis of spider mite life history traits on tomato leaves. The ‘-’ indicates that the variable was not in the model for the analysis of the corresponding life history traits. The ‘NT’ indicates that the factor was not tested in the model because there was a significant effect of an interaction including this factor. SR indicates the selection regime; ME the maternal environment; SR x ME corresponds to the interaction between these factors; Sex x SR corresponds to the interaction between sex and selection regime and Pop corresponds to replicated populations within the same selection regime. The P-values (P) are in bold when they are less than 0.05.  $\sigma^2$  indicates the variance associated to the replicated populations on corresponding life history traits.

Life history traits	SR	ME	SR x ME	Sex	SR x Sex	Pop
Egg mortality	$\chi^2=6.05$ <b>P=0.05</b>	$\chi^2=0.44$ P=0.51	$\chi^2=1.57$ P=0.46	- -	- -	$\sigma^2=0$
Juvenile mortality	$\chi^2=12.34$ <b>P=0.002</b>	$\chi^2=0.05$ P=0.83	$\chi^2=1.62$ P=0.44	- -	- -	$\sigma^2=0.07$
Juvenile dispersal	$\chi^2=2.89$ P=0.24	$\chi^2=0.22$ P=0.64	$\chi^2=2.51$ P=0.29	- -	- -	$\sigma^2=0$
Developmental time	$\chi^2=2.47$ P=0.29	$\chi^2=0.93$ P=0.33	$\chi^2=1.57$ P=0.46	- -	- -	$\sigma^2=0$
Sex ratio	$\chi^2=0.98$ P=0.61	$\chi^2=15.83$ <b>P &lt; 0.0001</b>	$\chi^2=2.68$ P=0.26	- -	- -	$\sigma^2=0.32$
Adult dispersal	$\chi^2=3.94$ P=0.14	$\chi^2=0.31$ P=0.58	$\chi^2=0.81$ P=0.67	$\chi^2=55.15$ <b>P &lt; 0.0001</b>	- -	$\sigma^2 = 2.06e-15$
Adult lifespan	NT	$\chi^2=1.14$ P=0.29	$\chi^2=0.59$ P=0.74	NT	$\chi^2=9.24$ <b>P=0.01</b>	$\sigma^2=0$
Daily fecundity	$\chi^2=6.74$ <b>P=0.03</b>	$\chi^2=8.30$ <b>P=0.004</b>	$\chi^2=4.26$ P=0.12	- -	- -	$\sigma^2=0$

### 3.1.2. Adult traits

The maternal environment affected the sex ratio of the progeny of mothers, as well as the daily fecundity of their daughters (Table 2). Mothers that experienced a tomato environment produced a higher proportion of males ( $0.53 \pm 0.11$ ) (Fig. 4e), and daughters with a higher daily fecundity on tomato ( $1.65 \pm 0.35$ ) (Fig. 4h), than mothers experiencing a bean environment (proportion of males and daily fecundity of  $0.25 \pm 0.09$  and  $1.10 \pm 0.18$ , respectively).

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**Figure 4.** Evolution of (a) egg mortality, (b) juvenile mortality, (c) juvenile dispersal, (d) developmental time, (e) sex ratio, (f) adult dispersal, (g) adult lifespan and (h) daily fecundity, in response to the selection regime (SR) (bean, tomato 19 and tomato 39) and the maternal environment (ME) (bean and tomato). The figures present the predicted data (mean values  $\pm$  CI) from the models. Symbols in white and black represent bean and tomato ME, respectively. The figures (f) and (g) also present the effect of sex on adult dispersal and adult lifespan, respectively. Squares (figures (f) and (g)) represent data on adult virgin males and circles (from figures (f) to (h)) represent data on adult virgin females. Life history traits for which sexes were confounded (figures from (a) to (e)) are represented by triangles. The symbols ‘.’, ‘\*’, ‘\*\*’ and ‘\*\*\*’, associated to fixed factors, indicate the significance of corresponding effects on life history traits. In (h) the symbol associated to ab vs cd presents the significance of the maternal environment effect whereas that associated to a,c vs b,d presents the contrast between tomato 19 SR and tomato 39 SR.

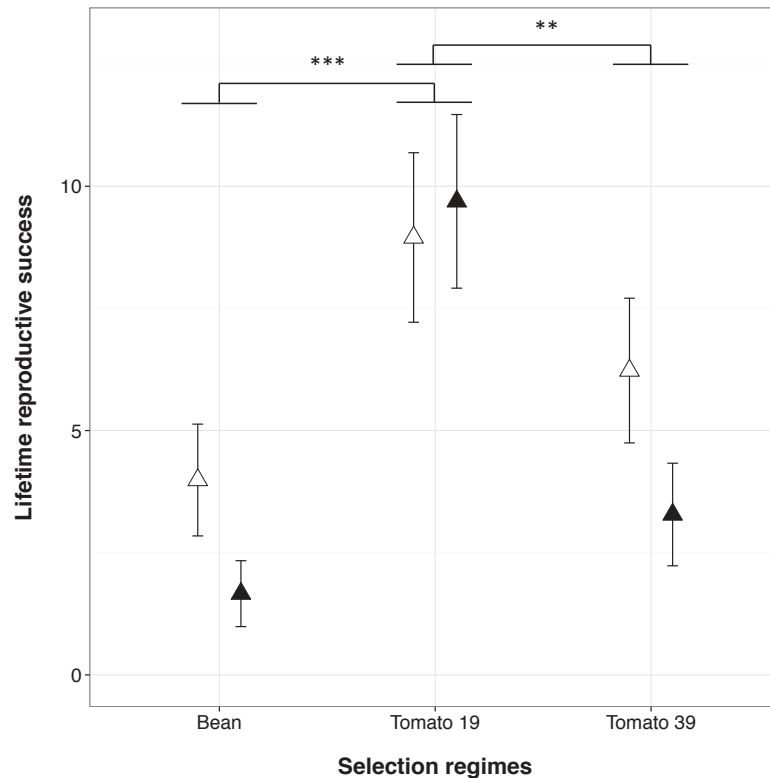
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The selection regime also affected the daily fecundity of females independently of the maternal environment. The daily fecundity of females from the tomato 19 SR was higher ( $1.57 \pm 0.30$ ) than that of females from the tomato 39 SR ( $1.05 \pm 0.23$ ; tomato 19 SR *versus* tomato 39 SR:  $P=0.005$ ) (Fig. 4h), while other contrasts were not significant. The selection regime affected differently adult lifespan in males and females (Table 2). Adult males from the bean SR lived a shorter time on tomato leaves (in days:  $9.18 \pm 3.04$ ) than adult males from the tomato 19 SR ( $15.93 \pm 3.24$ , bean SR *versus* tomato 19 SR:  $P=0.02$ ) and also than adult males from the tomato 39 SR ( $16.67 \pm 3.63$ , bean SR *versus* tomato 39 SR:  $P=0.02$ ) (Fig. 4g). Female adult lifespan was however not significantly different across populations evolving on different host-plants (Fig. 4g). The proportion of dispersing females was nearly twice as high (78% of females dispersed) than the proportion of dispersing males (40% of males dispersed from the tomato leaves) but was similar for the different selection regimes and maternal environments (Fig. 4f).

### 3.2. Aster analysis of female lifetime reproductive success

There was a significant effect of the SR on the female lifetime reproductive success ( $P<0.0001$ ). Both ME ( $P=0.19$ ) and the interaction SR x ME ( $P=0.12$ ) had no significant effect. The female lifetime reproductive success of populations from the tomato 19 SR was twice as high as the one from the bean SR (Fig. 5,  $P<0.0001$ ). Conversely, the female lifetime reproductive success of the populations evolving on tomato plants for the longest generation time (tomato 39 SR) was only marginally significantly different from those of the populations from the bean SR ( $P=0.09$ ) and was lower than that from the tomato 19 SR ( $P=0.005$ ).



**Figure 5.** Female lifetime reproductive success, or total offspring produced by female contributing to the population growth rate as predicted by aster, according to the selection regime (bean, tomato 19 and tomato 39 SR) and the maternal environment in which mothers developed (white and black triangles present the bean and the tomato ME, respectively). The figure presents the predicted data (mean values  $\pm$  CI) from the model. The symbols ‘\*\*’ and ‘\*\*\*’ indicate significance (at the 0.05 and 0.001 levels, respectively) of the selection regime effect on lifetime reproductive success.

### 3.3. Genetic diversity and genetic differentiation

Genetic diversity decreased in populations from the bean SR ( $0.52 \pm 0.02$ , for the average of the expected heterozygosity of the four control populations  $\pm$  std), to populations from the tomato 19 SR ( $0.47 \pm 0.04$ ), to populations from the tomato 39 SR ( $0.41 \pm 0.06$ ; more details in Appendix, Table 1). The diversity of the bean SR did not significantly differ from that of the tomato 19 SR ( $P=0.14$ ), which itself only marginally differed from the tomato 39 SR ( $P=0.06$ ), but the diversity within populations of the bean SR was significantly larger than that of the tomato 39 SR ( $P=0.005$ ).

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The  $F_{st}$  among populations increased from the bean SR (equal to 0.02 between pairs of bean SR populations, with confidence interval [0.006 - 0.047]), to the tomato 19 SR (0.18 [0.118 - 0.238]), to the tomato 39 SR (0.29 [0.234 - 0.376]) (for further details see Appendix, Table 2). Since the confidence intervals are almost not overlapping, no test is necessary: the three  $F_{st}$  are significantly different.

### 4. Discussion

In our study, we found that mites adapted rapidly to a novel host-plant (*i.e.*, within 38 generations). However, adaptation was compromised in populations evolving on tomato for a longer period (*i.e.*, 78 generations). This may be related to the fact that tomato is a stressful environment for spider mites. Indeed, the establishment of populations on tomato plants in this study was challenging for *T. urticae*, as is reported in the literature (Fry, 1989; Marinosci *et al.*, 2015). Mortalities and/or weak fecundity necessitated additional transfer of individuals from the control populations less than two months after creation. The strong juvenile mortality recorded for control populations on tomato (more than 70% of individuals died at the juvenile stage) during the experiment was also consistent with the idea that tomato plant is a stressful environment for this mite species (*e.g.*, Agrawal *et al.*, 2002). In the context of host-plant colonization, new environmental conditions may exert strong constraints on populations. In the short term, this may lead to a strong decrease in population size potentially entailing drift and compromising adaptation in the long term.

#### 4.1. The maternal environment does not necessarily facilitate host colonization

Females experiencing a tomato environment produced more offspring on that host-plant than on bean. A contradictory response was found in Marinosci *et al.* (2015) with different populations, suggesting a maladaptive plasticity of this trait in response to tomato maternal

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environment relative to cucumber maternal environment. In contrast, Magalhães *et al.* (2011) found with these two last maternal environments (cucumber and tomato) the reverse pattern, that is an adaptive plasticity of the fecundity in response to tomato. This last result was also detected in Agrawal *et al.* (2002). Such adaptive plasticity (here maternal effects) might facilitate the colonization of this stressful host-plant, because it will allow for more mites to survive in the new environment. This will lead to larger population sizes, hence more individuals upon which natural selection can operate (Lee, 2002; Price *et al.*, 2003; Chevin *et al.*, 2010). Conversely, adaptive plasticity may also reduce the selection differential among individuals in a population, leading to a lower rate of adaptation (DeWitt *et al.*, 1998; Chevin *et al.*, 2010). Genetic assimilation describes the process through which adaptive plastic changes for a trait evolve into fixed genetic differences for that trait in a new environment. This process may be operating in spider mite populations adapting to novel hosts. However, other studies found that the set of genes that modify their expression when mites are placed on tomato were found to show little overlap with those changing in evolved lines (Dermauw *et al.*, 2013), a result also found in other systems (Wertheim *et al.*, 2011).

In contrast, mothers growing on tomato also produced a higher proportion of sons than mothers growing on bean, which is not expected to result in a higher population growth rate. These results differ from those of Marinosci *et al.* (2015), who found no effect of maternal environment on sex ratio when contrasting cucumber and tomato environments. Because male eggs are on average smaller than female eggs (Macke *et al.*, 2011), it is possible that, in our study, females in a hostile tomato maternal environment produced smaller eggs, hence a higher proportion of male offspring. A biased sex ratio on tomato may explain why male lifespan improved after several generations on the new host, and not female lifespan, as more numerous males were exposed to selection on tomato.

In contrast with the findings of Marinosci *et al.* (2015), we found, in the present study, no improvement of early traits such as egg hatching rate and juvenile survival on tomato, when mothers were raised on tomato. Although we found strong maternal effects on both daily fecundity and offspring sex ratio, we did not detect any effect of the maternal environment on

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overall fitness. This is probably due to the fact that these two effects cancel each other out. Indeed, a tomato maternal environment will result in a higher oviposition rate, but a higher proportion of those eggs will be males, which effectively do not count for fitness in the aster analysis (and for population growth rates in general).

### 4.2. The response to selection varies with the trait measured

Seven of the eight measured life history traits of mites showed similar patterns of evolution after a host shift to tomato. Replicated populations transferred to tomato plants at the same time were furthermore remarkably similar, as shown by very small estimates of variance associated to the populations. These results globally suggest a convergent response of individual life history traits after a host shift. In particular, survival of mites at different stages (juvenile and adult male stages) increased in all populations evolving on tomato plants. In this mite species, a similar improvement on juvenile survival was also found in different populations evolving on tomato plants for a small number of generations (Fry, 1990; Magalhães *et al.*, 2007b, Wybouw *et al.*, 2015). Moreover, we did not detect differences in juvenile and adult male survival between populations exposed to tomato plants for different numbers of generations, which could indicate that the evolution of these traits had already reached a plateau after 19 months (~38 generations) on the new host, a result also found in Magalhães *et al.* (2009). This suggests a rapid adaptation to a novel host, as also recorded previously in *T. urticae* on other host-plants (Gould, 1979; Agrawal, 2000; Bonte *et al.*, 2010). In contrast, the proportion of unhatched eggs was slightly higher in populations evolving on the novel host than in control populations (the difference being significant only for the populations recently evolving on tomato). Unfortunately, only one other study on experimental evolution on novel host-plants has measured this trait, so it is difficult to assess the generality of this interesting result. Some traits did not respond to the host selection regime in any population (sex ratio, dispersal at juvenile and adult stages, developmental time and female adult lifespan). Other studies also report a lack of response of dispersal (Marinosci *et al.*,



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2015), developmental time and of longevity after a host shift (Magalhães *et al.*, 2007b; Bonte *et al.*, 2010). Marinosci *et al.* (2015) however found that females from populations having evolved on tomato produced more daughters than females from control populations having evolved on cucumber, which contradicts the sex ratio result of the current study. Finally, daily fecundity, a relevant component of fitness (Stearns, 1992; Futuyma, 2005), differed in our study between populations evolving on tomato plants for different number of generations. In particular, daily fecundity of individuals from populations having evolved on tomato for 38 generations was higher than that of individuals from control lines and from lines having evolved on tomato for 78 generations. This trait had similar values in the two latter sets of populations. Studies on experimental evolution of spider mites also show mixed results concerning this trait, with some showing a clear response (Magalhães *et al.*, 2007b, Bonte *et al.*, 2010), whereas others showing no change (Fellous *et al.*, 2014, Marinosci *et al.*, 2015, Miyazaki *et al.*, 2015).

Several causes may underlie these contrasting responses on different life history traits. First, the optimum for some life history traits in the previous environment may be more or less related to the optimum in the new environment. This will result in some traits being under strong selection when the switch occurs, but not others. Second, a lack of genetic variance for some traits may hinder response to selection during the evolution on tomato. Magalhães *et al.* (2007b) found no genetic variation in developmental time, which may explain the absence of response to selection on a novel host in this life history trait. The same lack of genetic variation could have occurred here (note that it is also possible that our window of observation for this trait may have been too large to detect a change). Another possibility is that trade-offs between different life history traits will constrain the simultaneous evolution of two or more traits (Stearns, 1992). For instance, egg mortality could have increased because of trade-offs between egg size and egg number. Indeed, bigger eggs in *T. urticae* are more likely to hatch than smaller ones (Macke *et al.*, 2011). It is thus possible that the increased oviposition rate observed in females evolving on tomato came at a cost of egg size, and hence hatching rate. Although hatching rate and egg size are probably relevant traits for fitness, they have not been

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specifically measured in earlier experimental evolution studies, hence this potential trade-off remains to be investigated. Still, Macke *et al.* (2012) found a negative correlation between egg size and number in the offspring of virgin females, suggesting that this trade-off may indeed exist. Finally, the absence of responses in traits expressed later during life cycle (*e.g.* female adult lifespan) may be due to a decrease in selection (which acts more efficiently on early traits) as suggested by theoretical studies (Hamilton, 1966; Stearns, 2000; Rose *et al.*, 2007; Cotto and Ronce, 2014). Indeed, the new host-plant may exert different selection pressures on different life history traits leading to changes only in those with the highest contribution to fitness, which is likely to be the case of juvenile survival. In line with this, Magalhães *et al.* (2007b) found that the lack of response of adult longevity could not be explained by the absence of additive genetic variation for this trait, suggesting that the trait was under weak selection.

Considering female lifetime reproductive success (from egg to egg) integrating the effects of variation in different life history traits, this study shows clear signs of rapid adaptation to a new host-plant, but only in mite populations having recently evolved on tomato plants. This result of rapid adaptation is consistent with past findings in that species (adaptation to tomato plants was reported after less than 30 generations on this host, see Magalhães *et al.*, 2007b; Wybouw *et al.*, 2015). Contrary to our expectation, female lifetime reproductive success did not significantly improve in populations that had spent the longest time growing on the new host, with fitness on tomato comparable to that of control populations not selected on this new host. This suggests that adaptation to a new host failed in these populations, as was also sometimes documented in this species (Fellous *et al.*, 2014; Miyazaki *et al.*, 2015; Díaz-Riquelme *et al.*, 2016), or that the increase in performance was transitory.

Possibly, fitness may have improved in all populations and our analysis has failed to detect this change. Indeed, our fitness model using the aster framework does not integrate potentially relevant fitness components of mite populations such as the male contribution to the overall fitness. By analysing individual life history traits, we clearly showed that males from populations evolving on tomato plants lived longer on this host-plant than those from the

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control populations. Furthermore, female fecundity was measured on adult virgin females, hence our fitness measure does not take into account female fertilization by males and its putative effect on female fecundity and survival. More generally, all life history traits were measured on isolated individuals on a restricted environment (*i.e.*, a tomato leaf) and thus did not integrate possible interactions between mite individuals but also with a more complex environment, (the whole tomato plant) that could affect the expression of life history traits. In line with this possibility, a previous study showed that *T. urticae* traits differed depending on whether they were measured on whole tomato leaves or on leaf discs (Kavousi *et al.*, 2009). It should be noted, however, that it is not clear why these possible explanations should apply to populations having been for more generations on tomato, and not to those evolving on that host for fewer generations.

### 4.3. Impact of demography on life history traits and fitness

In this study, populations evolving on tomato plants showed signatures of increased genetic drift compared to control populations having evolved and diverged on bean plants: genetic diversity was lower and genetic differentiation between replicate populations was higher, in populations evolving on tomato. In addition, populations having evolved for a longer time on tomato plants revealed higher genetic differentiation among replicate populations and a lower genetic diversity relative to populations transferred more recently on this host suggesting a stronger genetic drift despite the same time since the divergence of populations. This pattern is also consistent with the fact that the former replicate populations were founded with a smaller number of individuals.

Populations exposed to tomato for a longer time may never have significantly improved their female overall fitness on this host-plant. They would have succeeded in maintaining themselves in this environment by slightly enhancing their female lifetime reproductive success (we only found a marginal improvement) relative to that of females from control populations. Possibly, contingent experimental circumstances constrained population

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size and the ability to respond to selection in our first transfer to tomato more than in the second experimental transfer.

Alternatively, populations having evolved for the longest time on tomato plants may have first rapidly adapted to this host-plant before experiencing a fitness decrease during their evolutionary history due to the accumulation of mutations. This fitness deterioration could be associated with longer-term effects of decreased population size during evolution on tomato plant, a stressful environment. Indeed, our molecular data is compatible with strong drift in populations evolving for more than 39 months on tomato plants. It is interesting to note that, less than six months after the genetic analysis, populations evolving for the longest generation time on tomato finally went extinct (after ~128 generations on tomato plants), while those transferred on tomato more recently persisted. This suggests that the patterns observed are not linked to the number of generations spent on tomato *per se*, but to either different founding effects (as in Simões *et al.*, 2008) or a different impact of drift on those populations.

Adaptation to a stressful environment causing a population crash is the result of a race between evolution and demographic decline (Gomulkiewicz and Holt, 1995; Gonzalez *et al.*, 2013). Evolutionary rescue models and experiments (reviewed in Carlson *et al.*, 2014) showed that some populations adapt fast enough to be rescued by evolution before becoming extinct whereas others fail to adapt quick enough and become extinct because of demographic and genetic problems associated with small population size (Willi *et al.*, 2006). A small population size is known to compromise adaptation to a novel environment because of inbreeding depression, mutation accumulation depressing mean fitness and loss of adaptive genetic diversity due to random genetic drift (Weber and Diggins, 1990). For example, Oakley (2013) showed, in an endangered plant species, that founders originating from populations with small census size had a low fitness after transplantation in a novel habitat. Lachapelle *et al.* (2015) described, in replicate populations of unicellular alga, that adaptation to a novel environment was not repeatable for populations under a critical effective size, because of genetic drift.

## Conclusions

This work underlines the relevance of both adaptive and non-adaptive evolutionary processes on changes in life history traits and overall fitness after a host-plant shift in a phytophagous species. Evolution of spider mite populations on a novel host seems to be shaped both by selection and drift, with remarkably convergent adaptive patterns for some traits in all populations and suggestive evidence for strong drift impeding adaptation for other traits in some populations. Some aspects of adaptation were thus very repeatable (including across different experiments of adaptation to tomato from different base populations) and others more variable and contingent on demographic history. Interestingly, these patterns differed depending on the life history traits examined. It remains to be investigated why the evolution of some traits, such as daily fecundity, may be more sensitive to demographic history than others, as for example juvenile survival. Our results nonetheless suggest strong caution when deducing adaptation from the examination of single life history components and illustrate the value of contrasting evolutionary responses at the level of traits and that of an integrative fitness measure (Bonte *et al.*, 2010; Cameron *et al.*, 2013). Measuring, modelling and analysing relevant integrative fitness components measures can be difficult but should be attempted when studying adaptation to a new environment. Our results suggest that future insights on crop pests should also consider the constraints that these organisms may encounter after colonization of a novel host in order to better understand which events may prevent host-plant adaptation and thus limit culture damages.

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### Acknowledgments

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## *Chapitre 3*

*Un mécanisme potentiel d'adaptation  
à la plante hôte*



## Does the effect of plant pre-infestation on herbivore performance depend on past evolutionary history?

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**Abstract** - Plants evolve physical and chemical defences in response to attacks by herbivores. In turn, herbivores develop mechanisms to cope with these defensive compounds such as tolerance and/or manipulation of the level of plant defences. The latter can improve herbivore performance by improving host-plant quality. It is as yet unclear, however, on which of these mechanisms adaptation of generalist herbivores to a new host relies. Moreover the effects of such mechanisms on host exploitation by conspecifics remain to be elucidated. We tested this using experimental evolution of the spider mite *Tetranychus urticae* on tomato. For that, we measured life history traits (female survival and oviposition rate) in populations adapted to tomato and in control populations evolving on the ancestral host, bean, when placed on leaves from tomato plants that had received one of three treatments: (i) no previous infestation (clean plants), (ii) previous infestation by tomato-adapted populations, and (iii) previous infestation by control populations. We found that females from the populations evolving on tomato had a higher oviposition rate on this host than females from the control populations irrespective of the treatment received by the plants. This suggests that populations adapted to tomato have evolved tolerance to plant defence. Surprisingly, we found that females from all populations survived less on tomato plants pre-infested by mites from the tomato-adapted populations than on plants previously infested by control populations. This suggests that host-plant quality may be more degraded by adapted populations, leading to a higher mortality of females. This work suggests that in this species, phytophagous populations adapt to a novel host mainly by evolving tolerance to plant defences but also that host-plant adaptation can affect the outcome of future colonization events.

## 1. Introduction

When an herbivore colonizes a novel host-plant, the new environment may be harsh. Indeed, the novel host-plant may be strongly constraining if other species (*e.g.*, potential predators and/or competitors) already use it (Kaplan, 2012; Xiao *et al.*, 2014), or if the novel environment quality is unfavourable to the species. To avoid herbivory, plants may use different defensive strategies such as physical structures (wax, trichomes, thorns) or chemical defences. These defences can be constitutive (always present on the plant) or inducible, *i.e.*, released upon attack by parasites (Karban and Myers, 1989; Fritz and Simms, 1992; Schoonhoven *et al.*, 2005; Alba *et al.*, 2011; Walters, 2011). An abundant literature describes the composition of secondary chemical compounds involved in host-plant defence as the main mechanism shaping the evolution of plant-herbivore interactions (Brattsten *et al.*, 1977; Berenbaum, 1995; Becerra, 1997). As a response to the toxic compounds in their diet, phytophagous species have developed abilities (more or less specialised) for detoxification of phytochemical compounds (Brattsten *et al.*, 1977; Berenbaum *et al.*, 1986; Musser *et al.*, 2002, 2012; Villarroel *et al.*, 2016). In turn, plants have evolved refinements of their defensive systems, resulting in arms races between herbivores and their hosts (Ehrlich and Raven, 1964; Becerra, 1997; Schoonhoven *et al.*, 2005).

Herbivorous generalists, defined as phytophagous species with large host-plant ranges (Bernays and Graham, 1988; Schoonhoven *et al.*, 2005; Ali and Agrawal, 2012), are good biological models to study the mechanisms underlying the adaptation of herbivores to a novel host. Indeed, because they occur on different host-plants, a particular population is not expected to be fully adapted to all host-plants in the range of the species (Via, 1990; Drès and Mallet, 2002; Ali and Agrawal, 2012). Therefore, such populations can be used to test short-term adaptation processes (Gould, 1979; Fry, 1989; Magalhães *et al.*, 2007). How such adaptation affects the interaction between such herbivores and plants is however still poorly understood (but see Wybouw *et al.*, 2015). In particular, it is unclear whether this adaptation is related to the evolution of the ability to tolerate the defences on that host or if adapted individuals have evolved means to evade or manipulate plant defences.

Some herbivorous species are known to manipulate plant defences. For example, the



caterpillar *Helicoverpa zea* can reduce the toxic nicotine of tobacco plants by releasing salivary compounds and consequently having a better performance on this host (Musser *et al.*, 2002). In the group of herbivores composed of spider mite species, studies have reported both interspecific (Sarmiento *et al.*, 2011; Godinho *et al.*, 2016; de Oliveira *et al.*, 2016) and intraspecific (Takabayashi *et al.*, 2000; Kant *et al.*, 2008; Wybouw *et al.*, 2015) variation in the ability to trigger host-plant defences. Indeed, Sarmiento *et al.* (2011) found that undamaged tomato plants produced higher levels of defensive compounds (*i.e.*, proteinase inhibitors) than plants infested by the spider mite *Tetranychus evansi*. This finding contrasted with previous knowledge on most herbivores, including the closely-related *Tetranychus urticae*, which is known to induce plant defences (see Li *et al.*, 2002; Kant *et al.*, 2004). Concomitantly, mite performance (oviposition rate) of both *T. urticae* and *T. evansi* was lower on plants previously infested with *T. urticae* than on control plants, but performance on plants infested by *T. evansi* was higher than in both clean and *T. urticae* infested plants. Similarly, Godinho *et al.* (2016) found that plants infested by *T. ludeni* produced fewer proteinase inhibitors than control plants, and thus affected positively the performance of other spider-mite species. In addition to these variations in plant defences manipulation among related mite species, variation also has been found within a same species. For example, Takabayashi *et al.* (2000) found that two mite strains (red and green) of *T. urticae* induced different levels of volatile compounds on tomato plant, involved in indirect defences (by attracting herbivore predators), for the same mite density. Kant *et al.* (2008) showed that two of three *T. urticae* strains tested in their study induced tomato plant defences whereas another one did not. Furthermore, the susceptibility of mite strains (inferred by mite fecundity measures) to defence levels in tomato was variable, with fecundity on plants infested with conspecifics varying according to the mite strain tested (Kant *et al.*, 2008). This last work did not elucidate the causes of such variation between strains (but see Wybouw *et al.*, 2015). We here hypothesize that the evolutionary history of different mite populations (*e.g.*, selection imposed by different environments in which populations previously evolved), and in particular past exposure to the host, could explain variation in manipulation and resistance ability.

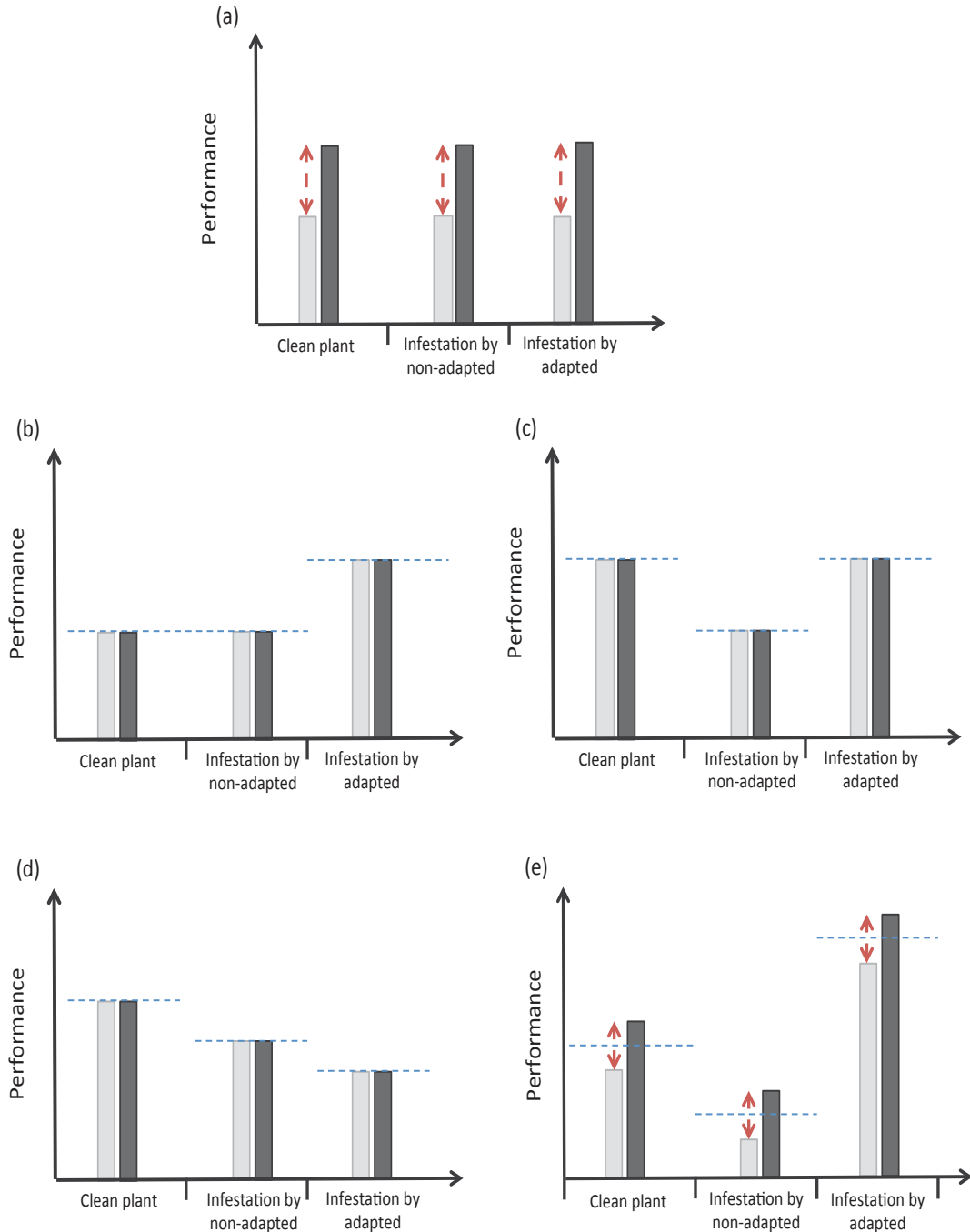
Several studies have documented rapid adaptation of *T. urticae* to several host-plants (Fry, 1990; Magalhães *et al.*, 2007; but see Fellous *et al.*, 2014; Marinosci *et al.*, in prep.). Of all the interactions of *T. urticae* with its host-plants, that with tomato is the best described. Indeed, attacks by *T. urticae* can induce plant defences in tomato plants (Li *et al.*, 2002; Ament *et al.*, 2004; Kant *et al.*, 2004). More recently, Wybouw *et al.* (2015) found that genes involved in constitutive and inducible defences pathways were downregulated when plants were infested by tomato-adapted populations in comparison with control populations, suggesting a manipulation of plant defences by adapted mites. However, the consequences of such manipulation for the performance of mites further infecting the plants was not tested. One could hypothesize that mite populations adapted to tomato may have evolved higher tolerance to their host specific defences, resulting in their performance on tomato plants being higher but also less sensitive to the infection status of the plant than for mites not adapted to this host. Downregulation of plant defences specifically by adapted mites as found by Wybouw *et al.* (2015) would suggest that performance of all mites, but especially that of non-adapted mites, most sensitive to such defences, may be increased on plants infected by tomato-adapted populations in comparison to plants infected by naïve mites. Conversely, efficient exploitation of host-plants by adapted mites may decrease their quality, decreasing performance of all mites further exploiting the host. To test these ideas, we use mite populations having evolved on tomato for 88 generations and control populations, derived from the same ancestral populations, having evolved on bean plants for 336 generations. Previous assays (Marinosci *et al.*, in prep.) have shown that the populations having evolved on tomato had indeed higher female lifetime reproductive success on that host than control populations. We investigate the effect of previous infestations of tomato plants by mites from these tomato-adapted populations and from non-adapted populations on the performance of both adapted and non-adapted populations.

## 2. Materials and methods

### 2.1. Expectations

When attacking tomato plants, mites that have evolved on this host may affect the performance of conspecifics in different ways (Fig. 1). If mite populations do not interfere with plant defences, we expect that the average performance of females from each population (adapted or non-adapted populations) is the same irrespective of the treatment imposed to the tomato plant (see Fig. 1a). In this same case, if adapted populations have acquired the ability to tolerate tomato plant defence during their evolutionary history, we expect a higher performance of tomato-adapted populations than of bean-adapted populations on all plant treatments (Fig. 1a). In contrast, if, during their evolution on tomato plants, populations have acquired the ability to modify host-plant quality for mites (through the downregulation of plant defences), the pre-infestation by these populations could improve female performance on the host relative to those of females on plants previously infested by non-adapted populations (e.g., in Fig. 1b,c). Figure 1b describes patterns expected in a scenario where non-adapted populations do not decrease host-plant quality compared to clean plants, while adapted population decrease the level of defences below their constitutive level. In contrast, Figure 1c considers that mite performance is lower only on plants previously infested by non-adapted populations, if only these ones decrease the host-plant quality by inducing tomato plant defences while adapted populations go undetected. Note that populations adapted to tomato may also degrade host-plant quality, for instance if they cause greater damages to the tomato plant, due to a higher ability to exploit this host (Fig. 1d). In this case, we would expect the opposite pattern for mite performance on tomato attacked by tomato-adapted populations, that is, a lower performance on this host than on both control plant and pre-infested plant by non-adapted populations. If the host-quality varies according to the level of damage rate imposed to the plant (from few to many sucked-leave areas), we expect that the host-plant quality (and subsequently mite performance) decreases from clean plants to plants pre-infested by non-adapted populations, and from the latter to plants

infested by adapted populations. Finally, an intermediate scenario can occur if mites from adapted populations have both the ability to tolerate and to manipulate host-quality (Fig. 1e).



**Figure 1.** Five possible responses of mite performance on tomato leaves that have been exposed to (i) no previous treatment ('clean plant'), (ii) a previous infestation with mites from a population that has never evolved on tomato ('infestation by non-adapted'), and (iii) a previous infestation with mites from tomato-adapted populations ('infestation by adapted'). The grey and dark bars present the performance of females from non-adapted and adapted populations, respectively. The red double arrows present the differences in performance associated to the ability to tolerate host-plant quality. The blue dashed lines present the differences in performance associated with the ability to manipulate the host-plant quality in different ways.

## 2.2. Maintenance and experimental evolution of mite populations

In October 2000, approximately 5000 individuals of *T. urticae* mites were collected from roses in a garden near Ghent, Belgium. A population was established and maintained on potted bean plants (*Phaseolus vulgaris*, variety 'Prelude') in a climatically-controlled room at  $25 \pm 1^\circ\text{C}$ . In November 2008, approximately 800 mites (all stages and sexes confounded) were transferred to Montpellier, France, and a base population was started and maintained under the same conditions with a population size of approximately 2500 mites. From this base population, we created four independent populations by transferring for each 400 adult females of *T. urticae* in four boxes containing bean plants. The four independent populations evolving on bean plants are hereafter called bean populations. In February 2011, four independent populations were created on tomato plants (*Solanum lycopersicum*, variety Olympe HF1) by transferring 100 adult females of each bean population to each of four boxes containing tomato plants. These four independent populations evolving on tomato plants are hereafter called tomato populations. Hereafter, the populations that had evolved under the same condition (*i.e.*, on the same host-plant species) are populations with the same selection regime. The eight populations were stored in a common climatically-controlled room at  $25 \pm 2^\circ\text{C}$  with a photoperiod of 14L: 10D. Less than two years after having created the tomato populations, we compared individual life history traits on tomato of these populations with those of the bean populations. We found that individuals from the tomato populations had a higher female lifetime reproductive success than the individuals from the bean populations, suggesting adaptation of the tomato populations to this new host (Marinosci *et al.*, in prep.).

All populations were maintained in individual translucent plastic boxes (size dimensions: 505 mm length x 310 mm width x 380 mm height) containing 9 to 12 host-plants (bean or tomato plants for the bean populations and the tomato populations, respectively). For the maintenance of populations, 45 days old plants were used. Each plastic box was put on a tray containing water to prevent mite dispersal. Water was also added inside the boxes to keep host-plants alive as long as possible. Every week, rotten plants or mite-free tomato plants were removed from the boxes and replaced by a new mite-free host-plant. To facilitate mite dispersal from the old to the new plants, we put the new mite-free host-plant in contact with the oldest ones.

### **2.3. Effect of pre-infestation with mites from populations with different evolutionary histories on life history traits of conspecifics**

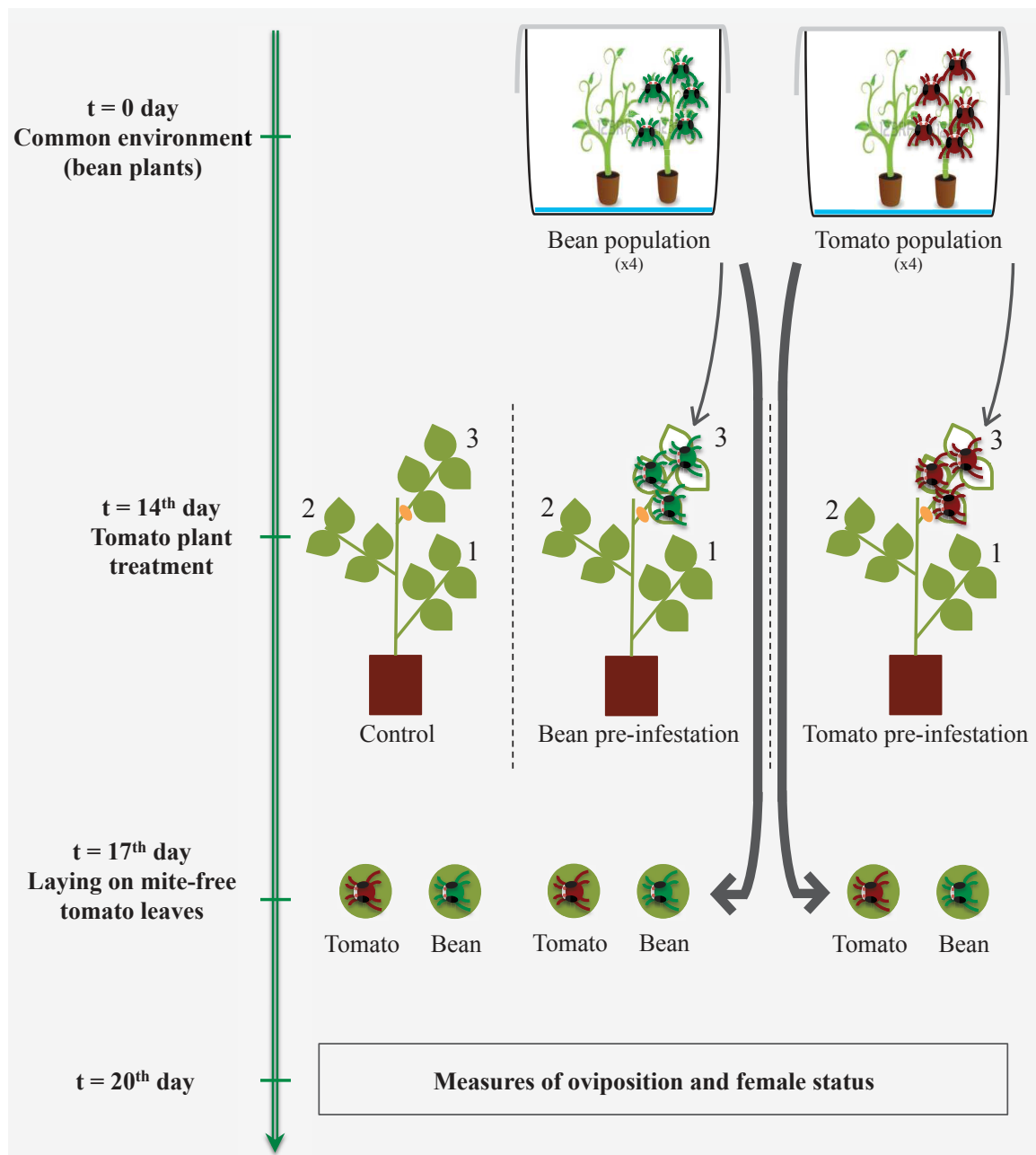
#### 2.3.1. Maternal environment

In October 2014, mature females were placed during two weeks (approximately one generation) in a common environment consisting of bean plants, to control for maternal effects and age of the females used in the experiment. Thirty mature females of each of the eight populations (thus in total 240 mature females) were transferred with a brush to four bean plants and conditioned on eight individual plastic boxes containing at least these four bean plants (one individual box per population). Bean was chosen as the common environment because it is a high-quality host for mites (Yano *et al.*, 1998), which enabled us to maximize the number of mites available after one generation (Fig. 2). Before this transfer, the tomato population had evolved on tomato plants for 44 months (approximately 88 generations) whereas the bean population had never experienced this host-plant in the lab. All plants used (for the maintenance of mite populations and for the experiment) grew in an isolated and herbivore-free room at  $23^{\circ}\text{C} \pm 2^{\circ}\text{C}$  with a photoperiod of 12L:12D.

#### 2.3.2. Pre-infestation of tomato plants

Thirteen days after having established the bean common environment, we tested the effect of tomato plant pre-infestation by mite populations adapted to bean or tomato on female oviposition rate. For that, we used 27 45-day-old tomato plants (same species and variety as above). We isolated the available youngest branch of the tomato plants (*i.e.*, the highest branch) by placing at its basis a ring of lanolin (a vegetable oil) (Fig. 2). When the youngest branch was too small to support the mites, we isolated the second youngest branch (in two plants only). To take into account the effects of plant characteristics on the oviposition rate, we recorded, for each tomato plant, the total number of branches of the tomato plant (from three to five) (for example, see Fig. 2). The next day, plants were haphazardly allocated to one of three treatments: three plants were not infected by mites, 12 plants were infected by one of the four bean populations (3 plants per population) and 12

other plants were infected by one of the four tomato populations (also 3 plants per population). Hereafter these three levels are called: (i) control, for uninfected tomato plants, (ii) bean pre-infestation, for tomato plants previously infected by one of the four bean populations, and (iii) tomato pre-infestation, for tomato plants previously infected by one of the four tomato populations (Fig. 2). For the two latter treatments (*i.e.*, bean or tomato pre-infestation), mites were collected with a mouth aspirator; 80 adult females were transferred from one of the eight populations that developed on the (bean) maternal environment. In total, 240 adult females (three tomato plants were each infested by 80 females from the same population) were haphazardly collected from their bean maternal environment and transferred to the tomato-isolated branch, in two temporal blocks of one day. During this phase, we noted the day on which female mites were transferred for the pre-infestation of tomato plant (*i.e.*, the temporal block, with two levels for the two days). The 27 tomato plants were placed in trays with water (to limit dispersal and preserve plant turgor), stored in a common climatically-controlled room at  $25 \pm 2$  °C with a photoperiod of 14L: 10D. No mite was found on mite-free branches in any tomato plant, suggesting that the lanolin and water in trays were efficient barriers preventing among-plant dispersal and hence potential contamination.



**Figure 2.** Experimental design testing the effect of pre-infestation by mites with different evolutionary histories on female performance (female survival and oviposition rate after 3 days of laying). Mites in green and red symbolize adult females from populations having evolved on bean or tomato before the experiment, respectively. The thin arrows represent the transfer of 80 adult females (laid by females from bean or tomato populations and having grown on the bean environment) used for the treatment of one tomato plant. The numbers (1, 2 and 3) indicate the position of branches for a tomato plant with three branches. Orange circles indicate the lanolin ring isolating the tomato branch that received the treatment (here the branch number 3). Only the undamaged leaves of branches without a lanolin ring (that is here the branches number 1 and 2) were used to create tomato leaf discs for the laying phase (t=17<sup>th</sup> day). The thick arrows represent adult females that were transferred and placed to lay eggs on tomato leaf discs.



After three days of treatment, we estimated the number of remaining female mites (among the 80 females initially used for the pre-infestation) on infected tomato branches, to determine the effects of mite density on the level of induced plant defences. For that purpose, we measured the approximate number of remaining females after three days of infestation and ranked this value among one of the three following density ranges [20-39], [40-59] or [60-80]. We removed all remaining mites from the 24 isolated branches infected by mites. The 27 branches isolated by a lanolin barrier were cut from the tomato plants, stored in individual Eppendorf tubes and immediately put in liquid nitrogen. Note that we also put a ring of lanolin on the youngest branch of the three control plants to control for a putative effect of this vegetable oil on tomato plants. All these samples of isolated-branches were conserved in freezer at  $-80^{\circ}\text{C}$  for potential future investigations on tomato plant compounds (defensive substances).

### 2.3.3. Life history traits of female mites on leaf discs

With the remaining mite-free branches of the tomato plants, we cut for each tomato plant 24 leaf discs (diameter  $\sim 1\text{cm}$ ). By following the same protocol as in Sarmiento *et al.* (2011), we cut leaf discs from available undamaged branches of tomato plants previously infested by *T. urticae*. To take into account potential variation in the distribution of compounds in the plant, when creating the leaf discs we noted the position of branch (numbering the position from the apex to the bottom of the plant) from which each leaf disc was extracted. The leaf discs were placed on water-saturated cotton wool in boxes to both limit mite dispersal and ensure humidity and thus persistence of leaf discs. On each leaf disc, we transferred and individually isolated one adult female that had developed on the bean environment. At least 69 females were monitored from each population (see Table 1). We counted the number of eggs produced by each female on the individual leaf disc and recorded also the female status (dead or alive) after three days of egg-laying (Fig. 2). Thus, we measured two relevant fitness components (female mortality and oviposition rate). In total, we had 608 data points for each the two previous variables (Table 1).

**Table 1.** Sample sizes for measures of oviposition rate and female mortality after 3 days of laying according to the treatment imposed to the tomato plant (Control, Bean and Tomato pre-infestation for, respectively, no previous infestation, pre-infestation by mites from the bean populations and pre-infestation by mites from the tomato populations) and to the selection regime of ovipositing females on the leaf discs (with bean laying and tomato laying corresponding to females from the bean or the tomato populations, respectively).

		Bean laying				Tomato laying				Total
		B1	B2	B3	B4	T1	T2	T3	T4	
Control	None	9	8	8	9	8	9	8	9	68
Bean pre-infestation	B1	7	9	8	9	9	8	9	9	68
	B2	6	7	9	9	9	8	8	6	62
	B3	8	7	9	9	9	9	9	9	69
	B4	8	6	9	9	9	9	9	9	68
Tomato pre-infestation	T1	9	9	9	9	9	9	9	9	72
	T2	9	7	9	9	9	8	9	8	68
	T3	7	8	8	8	9	8	9	8	65
	T4	9	8	9	9	9	9	7	8	68
<b>Total</b>		<b>72</b>	<b>69</b>	<b>78</b>	<b>80</b>	<b>80</b>	<b>77</b>	<b>77</b>	<b>75</b>	<b>608</b>

## 2.4. Statistical analysis

The analysis was carried out using the R software (R Core Team, 2013). We applied generalised linear mixed models with a binomial distribution for female mortality, and a Poisson distribution for female number of eggs during the first three days. As many females did not produce any egg after three days (327 among the 608 initially monitoring females) we applied a zero-inflated generalised linear mixed model, a model incorporating both aspects of generalised linear mixed model (here, a Poisson regression) and aspects of zero-inflated model. This last aspect allowed integrating a single constant term across the entire model estimating a zero-inflated parameter, that is the probability to have a null fecundity (that does not depend on the Poisson distribution). When analyzing the female mortality and fecundity, we kept in the model the following explanatory variables as a basis: (i) the selection regime of ovipositing females (with two levels, bean and tomato), (ii) the tomato plant treatment (with three levels: control, pre-infestation by bean populations and pre-infestation by tomato populations), and (iii) the interaction between these two factors (hereafter selection regime of ovipositing females x treatment). All these explanatory variables were included as fixed factors. Random effects initially included in the model were: plant, population of the ovipositing females used for life history assays, population used for pre-infestation treatment. Non-significant random

terms were removed from the model, using a 10% error threshold to correct for the too conservative nature of log-likelihood ratio tests LRT tests when testing random effects (see Bolker *et al.*, 2009). We included potentially confounding experimental variables as fixed effects in the model, tested their significance with LRT and removed non-significant variables from the model: these variables were the total number of branch by tomato plant (with three levels), the density of mites on the leaf during the pre-infestation (with four levels), the position of branch used to create the leaf disc on which female laid (with four levels), and temporal blocks (with two levels). When we found a significant effect of a fixed factor with more than two levels, we applied contrast tests to determine which level was significantly different from the others.

### 3. Results

#### 3.1. Effect of tomato treatment on life history traits of conspecifics

The interaction between the tomato plant treatment and the selection regime of ovipositing females had no significant effect on the female mortality or on oviposition rate (Table 2, Fig. 3a and Fig. 3b).

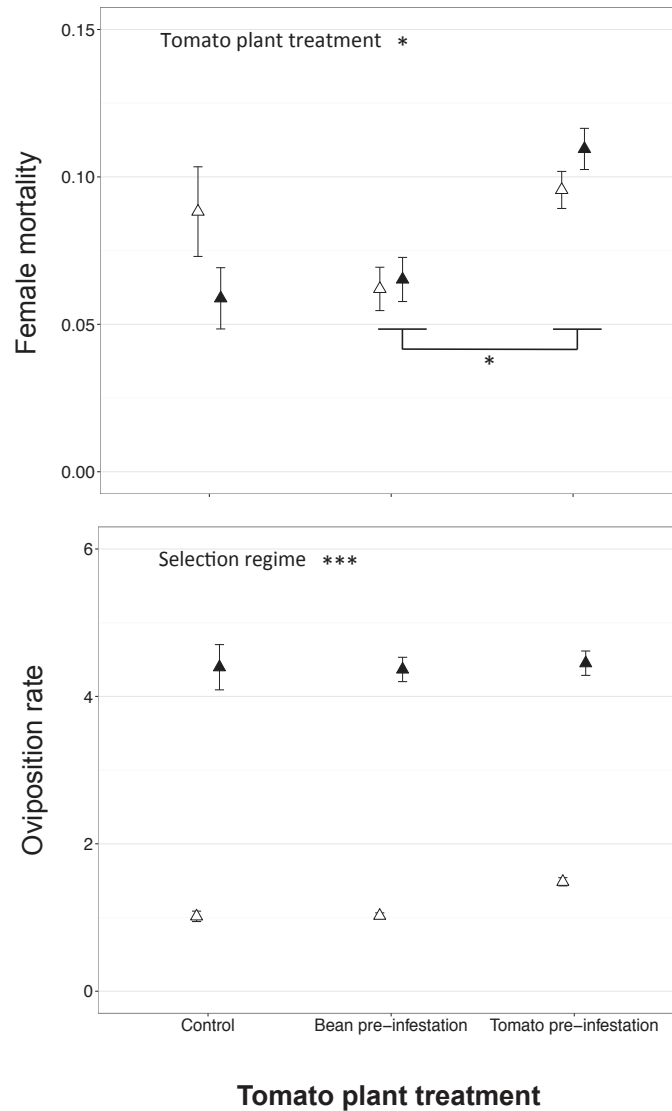
**Table 2. Results of the statistical analysis of female mortality and oviposition rate on tomato leaf discs.**

	Treatment	Selection regime	T X SR	Leaf disc	Block	Laying population	Plants
Female mortality	$\chi^2 = 6.81$	$\chi^2 = 0.04$	$\chi^2 = 0.33$	$\chi^2 = 9.65$	$\chi^2 = 5.57$	-	-
	<b>P = 0.03</b>	P = 0.84	P = 0.85	<b>P = 0.02</b>	<b>P = 0.02</b>	-	-
Oviposition	$\chi^2 = 0.58$	$\chi^2 = 11.52$	$\chi^2 = 4.32$	$\chi^2 = 44.56$	-	$\chi^2 = 34.04$	$\chi^2 = 56.6$
	P = 0.75	<b>P = 0.0007</b>	P = 0.12	<b>P &lt; 0.0001</b>	-	<b>P &lt; 0.0001</b>	$\sigma^2 = 0.10$ <b>P &lt; 0.0001</b>

The ‘-’ indicates that the variable was not included in the model for the corresponding trait. T x SR indicates the interaction between the tomato plant treatment (T) and the selection regime of ovipositing females (SR). The P-values (hereafter P) are in bold when the significance level of the explanatory variables is less than 0.05.

Female mortality was only affected by the treatment imposed to the tomato plant (Table 2, Fig. 3a) whereas the oviposition rate only differed according to the selection regime of ovipositing mites (Table 2, Fig 3b). In particular, female mortality was higher on tomato plants previously infested by

mites from populations evolving on tomato (from raw data:  $0.10 \pm 0.04$  (for mean  $\pm$  CI)) than on tomato plants previously infested by mites from populations evolving on bean ( $0.06 \pm 0.03$ ;  $P=0.04$ ). However, none of these treatments differed from control plants without infestation (see Figure 3). Furthermore, females from the tomato population had oviposition rates the first the three days nearly four times higher ( $2.99 \pm 0.42$ ) than females from the bean population ( $0.75 \pm 0.18$ , Table 2), irrespective of the treatment that the plants received. For this last trait, we found a significant variance associated to the plant used in the experiment and also to the precise population from which the females originated (Table 2).



**Figure 3.** Graphs of (a) the proportion of dead females (female mortality), and (b) the number of eggs produced the first three days (oviposition rate) for females placed on tomato leaf discs from plants exposed to different treatments. ‘Control’ corresponds to tomato plants without infestation by mites before the laying phase, (ii) ‘Bean pre-infestation’ corresponds to tomato plants previously infested by mites from a population that did not experience the tomato plant in the lab, and (iii) ‘Tomato pre-infestation’ corresponds to tomato plants previously infested by mites from a population adapted to the tomato host-plant. White and dark triangles present the average of predicted values ( $\pm$ CI) of females from the bean and the tomato selection regimes, respectively. The symbols ‘\*’ and ‘\*\*\*’ indicate the significance effects. For the female mortality, only significantly different contrasts are presented (that is bean pre-infestation vs tomato pre-infestation).

### 3.2. Other variables affecting life history traits

The position of the leaf disc on the plant had a significant effect on both female mortality and fecundity. Indeed, the proportion of dead females was higher on leaf discs from the second branch

than on those from the first, youngest, one ( $0.11 \pm 0.04$  vs  $0.04 \pm 0.03$  for female mortality on leaf disc from the second branch vs the first branch, respectively; contrast test with  $z$ -value=2.72,  $P=0.03$ ). Mites had also a higher fecundity on leaf discs from the second branch ( $1.62 \pm 0.38$ ) than on those from the first, youngest, branch ( $1.47 \pm 0.37$ ; contrast tests with  $z$ -value=2.64,  $P=0.03$ ). Moreover, the fecundity of females was significantly higher on leaf discs created from the third oldest branch ( $2.58 \pm 0.52$ ) than that on leaf disc from the second branch ( $1.62 \pm 0.38$ ; contrast tests with  $z$ -value=2.59,  $P=0.04$  for fecundity on leaf disc from the third branch vs the second branch). Finally, we found a higher female mortality in the first temporal block ( $0.11 \pm 0.06$ ; Table 2) than in the second temporal block ( $0.08 \pm 0.02$ ).

#### 4. Discussion

In this study, we set out to test whether performance (survival of females and fecundity during the first three days) of mites on tomato can be affected by previous exploitation of conspecifics from populations with different evolutionary histories. As life history traits measures were collected on tomato leaves that were not previously infested and that pre-infestation was realised on another tomato branch, this experiment allowed detecting the effects of tomato systemic defences on mite life history traits. These defences are tomato defences released within the plant in response to the damages caused by herbivore attacks, which may affect host-plant quality. We found that females from the tomato-adapted populations had a higher fecundity on tomato leaf discs than females from the bean populations, consistent with previous findings on this same set of populations. This suggests that mites have adapted to tomato (but see Marinosci *et al.*, in prep., for more details). The evolutionary history of spider mites pre-infesting tomato did not modify the fecundity of their conspecifics placed on those plants, suggesting that tomato plant pre-infestation did not change the host-plant quality for this trait response in mites. However, we found that females survived better on leaf discs from plants infested by bean populations than on leaf discs from plants previously

infested by tomato-adapted populations, which conversely suggests that the pre-infestation by adapted mites decreased the host-plant quality. Female mortality was however not affected by the evolutionary history of populations (populations evolved on bean plants *versus* tomato plants) as found previously for those same populations (see Marinosci *et al.*, in prep.).

#### **4.1. Is tolerance the only mechanism underlying host-plant exploitation in generalist species?**

We never found that host-plant quality improved after infestation by mites, and infestation by adapted mites either had no effect on fecundity or decreased survival of subsequent colonizers of the plant, which is not expected if adapted mites downregulated plant defences as found by Wybouw *et al.* (2015). In Godinho *et al.* (2016), the authors used three mite species with different ranges of diet specialization to the tomato plant and measured the effect of mite infestation on the production of proteinase inhibitors, which is the end-product of the jasmonate defence cascade, and the consequences on mite oviposition rate on this host. They found that a specialist of Solanaceous plants (*T. evansi*) downregulated the level of these proteinases and that *T. ludeni* (a less generalist herbivore than *T. urticae*) also reduced the level of this proteinase (but to a lesser extent than *T. evansi*) and finally that *T. urticae* upregulated the production of this defensive compound. This pattern potentially described a continuum of manipulation abilities in mites. It could be that, according to their host-plant ranges, herbivores developed different abilities from manipulation (for specialists) to tolerance (in generalists) to face plant defences. In *T. urticae*, most studies did not show downregulation of induced-tomato plant defences (see Kant *et al.*, 2004; Ament *et al.*, 2004; Kant *et al.*, 2008; Sarmiento *et al.*, 2011; de Oliveira *et al.*, 2016 and Godinho *et al.*, 2016). This could result from a cost associated to the ability to equally perform on more than one thousand host-plants (Grbić *et al.*, 2011) according to the concept of 'Jack of all trades, master of none' (Chevin *et al.*, 2010; Ali and Agrawal, 2012). In particular, if the ability to manipulate plant defences entails a cost, we could expect that this capacity has been acquired by specialized mites only.

In the context of host-plant co-exploitation, the upregulation of plant defences may be also a strategy (to some degree) to reduce competition in nature by decreasing the survival of other mites. By decreasing their environment quality, herbivores can decrease the occurrence of other exploiters (as argued in de Oliveira *et al.*, 2016 and Godinho *et al.*, 2016), in particular if tomato-adapted populations tolerate the defences of their host-plant better than non-adapted populations. This suggests that upregulation could confer a selective advantage to spider mites adapted to novel host plants. However, we here found that all populations (adapted to tomato or not) suffered from the increased mortality after exploitation of the plant by adapted mites, so the advantage is unclear.

Possibly, the defences of tomato plants are triggered to a higher level of toxic compounds following exploitation by tomato-adapted populations because these populations caused stronger damages on this host than non-adapted populations. We could expect that mites from tomato-adapted populations feed more on this host by, for example sucking more the cell content or alternatively by piercing more different leaf areas of this host-plant whatever the number of mites remaining on tomato after three days of pre-infestation, than mites from non-adapted populations. Indeed, one study reported that the concentration of volatile compounds released by a plant may be positively correlated to the infestation rate (Takabayashi *et al.*, 2000). However, other studies with different herbivores species showed no such correlation (Shiojiri *et al.*, 2010). Infestation rate was controlled for in our experiment but adapted mites may cause more damages to the plant.

Note that we found no evidence that pre-infestation by non-adapted populations induces higher levels of plant defences compared to clean plants, contrary to the frequent finding that attack by *T. urticae* elicits such defences (Li *et al.*, 2002; Kant *et al.*, 2004). Our assessment of performance on clean plants was however based on a reduced number of plants and higher levels of replication would be necessary to confirm this result. Our control populations maintained on bean may belong to those few strains that do not induce higher levels of defence upon infestation, as found by Kant *et al.* (2008) for some strains of *T. urticae*. Alternatively, the density of mites infesting the plant may have been too low to induce a strong response. Preliminary experiments



testing higher density of mites (up to 200 on a single leaf) however found no consistent effect of pre-infestation whatever the density used when using (results not shown).

#### 4. 2. A contradictory story depending on life history responses

In previous studies, oviposition rate on tomato plants was lower when tomato defences were upregulated (Li *et al.*, 2002; Kant *et al.*, 2004) relative to clean plants, and higher when defences were downregulated (Sarmiento *et al.*, 2011; de Oliveira *et al.*, 2016, Godinho *et al.*, 2016). In line with this, the adult survival in *T. evansi* was higher on tomato plants with lower concentrations of defensive compounds than on clean plants and on plants with higher induced defences (Sarmiento *et al.*, 2011). In other words, globally negative correlation between mite performance, whether measured by survival or fecundity, and the level of defensive compounds was found. However, in the present study we found contradictory responses for these two last life history traits (female survival and oviposition) in response to same tomato plant treatments. If the tomato plant releases more defensive compounds leading to a higher mortality rate in females, we can wonder why this does not affect their fecundity as reported in literature.

A possible explanation is that defensive compounds differentially affected life history traits in our mite populations. In our study, plants may induce other toxic compounds than those referred in literature and these could affect female mortality only. Other studies also found effects of defensive compounds on herbivore longevity (Kaloshian *et al.*, 1997; Musser *et al.*, 2002). The different responses of mortality and fecundity are even more intriguing given that female lifespan should have affected their fecundity, those dying early leaving fewer eggs. Further analyses should attempt to analyse both traits together and model their dependency, for instance using aster analysis as in Marinosci *et al.* (in prep.). Previous life history assays in those populations showed that different life history traits followed different evolutionary trajectories during adaptation on a new host (Marinosci *et al.*, in prep.). In particular, we previously found that fecundity improved in tomato-adapted populations compared to control populations, but not female lifespan, consistently

with the present findings comparing the performance of mites evolving on bean vs tomato on tomato plants receiving different treatments. Fecundity and survival may be negatively correlated, for instance because of resource allocation issues. This would be consistent with results about the effect of leaf discs; leaf discs with the significant highest rate of female mortality were those with the highest number of eggs produced by females. This apparent spatial heterogeneity in host-plant quality between leaves of the same plant can be explained by the vascular architecture in tomato (Orians *et al.*, 2000) that distributes defensive compounds within the plant in different concentrations. The contrasted responses of life history traits between leaves from a same plant may reflect differences in levels of tomato plant defences and the different sensitivity of fecundity and survival to these defences. However, we cannot conclude without further additional analyses on plant chemical composition.

### 4.3. Conclusion and perspectives

This study suggests that in a generalist herbivore, the main mechanism allowing exploitation a host-plant able to induce defences after damages is tolerance to host defences. However, we also suggest that evolutionary history (*i.e.*, previous evolution on the host-plant) may induce changes in the ability to manipulate the host-plant, by modifying levels of defensive compounds. A recent study has shown that the release of *T. evansi* salivary compounds in *Nicotiana benthamiana* plants blocks its defensive signalling pathways (Villarroel *et al.*, 2016). In our study, we did not measure proteinase inhibitor activity as in previous experiments (Li *et al.*, 2002; Kant *et al.*, 2008; Sarmiento *et al.*, 2011; de Oliveira *et al.*, 2016; Godinho *et al.*, 2016) or gene expression involved in plant induced defences (Sarmiento *et al.*, 2011; Wybouw *et al.*, 2015). We suggest to investigate in future works the responses to attack at the plant scale to decipher explicitly how host exploitation by mites can facilitate a new colonization event of this environment.

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## Résumé principal

Les travaux de cette thèse apportent des éléments nouveaux sur la capacité d'un généraliste à persister suite à un changement d'hôte. L'étude des réponses évolutives de traits d'histoire de vie chez *Tetranychus urticae*, un redoutable ravageur de cultures, nous suggère qu'une diversité de mécanismes et de processus peut intervenir dans le maintien de populations suite à la colonisation d'une même plante hôte (la tomate). Chez cet herbivore généraliste, j'ai montré notamment que la plasticité phénotypique (*via* des effets maternels) peut jouer un rôle clef dans l'exploitation de cette plante hôte. Parallèlement à ce mécanisme, l'évolution génétique des populations exposées à un nouvel hôte participe fortement au processus d'adaptation à la plante (voir Tableau 1). Si la sélection sur le nouvel hôte peut conduire à une augmentation de la valeur sélective, d'autres forces évolutives (comme la dérive) liées à l'histoire démographique durant la colonisation peuvent compromettre l'adaptation, ce qui peut conduire à l'extinction des populations. Au cours de mes travaux, j'ai aussi montré que la tolérance aux défenses de la plante hôte jouait un rôle important dans l'adaptation à la plante hôte. De plus, il apparaît dans ces travaux que l'infestation par des populations d'acariens adaptées à la plante hôte a une incidence sur la survie de femelles congénères sur la même plante. Une plus forte mortalité des femelles pourrait être induite par une dégradation plus forte de la qualité de la plante par des acariens de populations adaptées relativement à des plantes témoins et à des plantes exploitées préalablement par des populations non adaptées. Pour finir, cette thèse montre de manière répétée que les effets de l'environnement ou de l'histoire évolutive des populations diffèrent fortement entre différents traits d'histoire de vie à différents stades (juvénile et adulte) mais aussi au sein d'un même stade (survie adulte et reproduction). Ces résultats renforcent l'idée qu'il est nécessaire d'intégrer l'étude indépendante des traits d'histoire dans une analyse conjointe afin d'établir les conséquences de l'évolution d'un changement d'hôte sur la valeur sélective des individus. Au cours de cette dernière partie, je rappellerai pour chaque partie les principaux résultats de mon étude afin de les replacer dans un contexte plus général permettant de souligner des potentiels axes à investir.

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**Tableau 1.** Récapitulatif des cinq régimes de sélection (concombre, tomate (dérivé de concombre), haricot, tomate 19 et tomate 39 (ces deux derniers dérivés de haricot)) utilisés au cours des trois chapitres de cette thèse pour tester l'adaptation de populations de *T. urticae* à la plante hôte de tomate.

Chapitre de thèse	Concombre	Tomate	Haricot	Tomate 19	Tomate 39
	1	1	2 et 3	2 et 3	2
Nombre de générations sur l'hôte témoin	594 générations	570 générations	286 générations	248 générations	204 générations
Nombre de générations sur l'hôte de tomate	0 génération	24 générations	0 génération	38 générations (chapitre 2), 88 générations (chapitre 3)	78 générations
Réponse évolutive à la plante de tomate	Témoin	Sexe ratio	Témoin	Survie juvénile, succès reproducteur femelle (chapitre 2), fécondité (chapitre 3)	Survie juvénile
Nombre de générations sur la plante de tomate avant extinction	-	60 générations	-	-	128 générations

L'hôte « témoin » correspond à l'hôte d'origine sur lequel ont évolué les réplicats des régimes de sélection transférés sur des plantes de tomate (*i.e.*, hôte témoin concombre pour le régime de sélection tomate et hôte témoin haricot pour les régimes de sélection tomate 19 et tomate 39). L'histoire évolutive sur la plante hôte de tomate au moment des mesures d'adaptation est indiquée par le nombre de générations passées sur cet hôte ainsi que la réponse à cette plante. Les réponses évolutives indiquent les traits pour lesquels nous avons détecté un signal adaptatif en réponse à l'évolution sur la plante (par comparaison au témoin respectif). Les nombres de générations passés sur la plante hôte de tomate avant extinction des populations des régimes de sélection tomate et tomate 39 sont également présentés.

### 1. Adaptation à la plante hôte : règle ou exception chez un généraliste ?

#### 1.1. La colonisation d'un nouvel hôte peut se solder par une absence d'adaptation

Au cours des différents chapitres de cette thèse, j'ai montré que l'adaptation à un nouvel hôte n'était pas une règle chez l'acarien généraliste *T. urticae* (cf. tableau 1). En effet, dans Marinosci *et al.* (2015 ; chapitre 1 de cette thèse) nous avons notamment trouvé qu'après plus de 24 générations d'évolution sur des plantes hôtes de tomate, les traits d'histoire de vie mesurés (hormis le sexe-ratio) n'avaient pas évolué des valeurs différentes de celles des populations témoins non exposées à la tomate. Par contre, la plupart des traits étaient modifiés par l'environnement maternel. Dans le chapitre 2, cette expérience d'évolution sur un nouvel hôte a été répétée à partir de populations témoins différentes (maintenues sur haricot). Nous avons cette fois détecté un clair signal

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d'adaptation avec un succès de reproduction des femelles sur tomate plus élevé dans des populations exposées à la tomate depuis 38 générations (cf. « Tomate 19 » dans le tableau 1) que dans les populations témoins. Néanmoins, d'autres populations ayant évolué sur des plantes de tomate depuis un plus grand nombre de générations, environ 78 générations (cf. « Tomate 39 » dans le tableau 1) ne présentaient pas, elles non plus, de signal clair d'adaptation en termes de valeur sélective des femelles. Pourtant, en analysant indépendamment les traits d'histoire de vie individuels de ces populations, plus de 85% des traits répondaient similairement à ceux de populations s'étant adaptées à la tomate après environ 38 générations (« Tomate 19 » dans le tableau 1) d'évolution sur cet hôte.

### **1.2. Dérive génétique et plasticité, un frein à l'adaptation ?**

#### 1.2.1. Même les ravageurs subissent le changement

L'analyse de la diversité génétique des populations ayant évolué sur des plantes de tomate pendant le plus grand nombre de générations (78 générations au moment des mesures visant à tester l'adaptation à la plante, cf. Tableau 1) nous apprend qu'il y a eu une plus forte différenciation génétique entre ces populations depuis leur divergence, comparée à la différenciation entre populations ayant évolué sur la tomate pendant 38 générations, elle-même plus grande que celle entre populations témoins sur haricot, malgré des temps de divergence similaires. Ces résultats, ainsi que les observations de réduction de la taille des populations suite à la colonisation, suggèrent que l'adaptation à cette plante hôte a vraisemblablement été compromise par de sévères goulots d'étranglement. La taille efficace d'une population est un paramètre clef qui détermine la force de la dérive et les conséquences génétiques qui y sont associées. En effet, des populations de petite taille peuvent se voir contraintes par des événements de dépression de consanguinité, d'accumulation de mutations délétères ou encore de perte de la diversité génétique (Weber et Diggins, 1990) qui limitent l'action de la sélection naturelle. Cela peut, à terme, conduire à l'extinction des populations.

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Peu d'études se sont attachées à étudier les conséquences des goulots d'étranglement sur l'évolution des populations de parasites. Pourtant, la réduction de taille chez de tels organismes semble être un scénario fortement envisageable dans la nature, en particulier dans le cadre d'un processus de colonisation de différentes plantes hôtes aux caractéristiques plus ou moins stressantes. Il a déjà été établi que de petite tailles de populations peuvent contrecarrer les processus adaptatifs (Weber et Diggins, 1990) ou encore que l'adaptation à un nouvel environnement est moins répétable (Willi *et al.*, 2006; Lachapelle *et al.*, 2015). Parallèlement à cela, il est surprenant de constater que malgré la détection de forts signaux de goulots d'étranglement, ces populations ont pu se maintenir sur la nouvelle plante hôte pendant plus de 120 générations. De même, les populations non adaptées au bout de 24 générations d'évolution ont été maintenues pendant au moins 60 générations sur la plante hôte. A partir de ces résultats, nous pouvons nous demander si la plasticité n'a pas pu compenser l'absence d'adaptation à la plante hôte.

### 1.2.2. La plasticité, un atout pour l'exploitation ou une limite à l'adaptation ?

La plasticité phénotypique d'un trait permet aux organismes de répondre suite à un changement perceptible de leur environnement (Bradshaw, 1965 ; Stearns, 1989). Il a été suggéré que la plasticité phénotypique peut permettre d'élargir la gamme écologique d'un organisme par le fait que ce mécanisme peut lui permettre de survivre suite à un changement de son habitat (Chevin *et al.*, 2010). Ainsi, les effets maternels améliorant le taux d'éclosion des œufs ou encore la survie juvénile (chapitre 1) après exposition des mères à la tomate présentent un avantage conséquent pour les populations sur la plante hôte de tomate. En effet, il a été montré que la plante de tomate peut exercer de très fortes pressions de sélection sur les jeunes stades, induisant parfois des taux de mortalité supérieur à 70% pour des populations ne s'étant jamais confrontées à la tomate (Fry, 1990 ; Agrawal *et al.*, 2002 ; Magalhães *et al.*, 2007). Cette réponse plastique adaptative peut permettre ainsi d'étendre la gamme d'exploitation de la plante hôte chez *T. urticae* en limitant des effets négatifs abrupts sur la démographie des populations. Lorsque de tels mécanismes interviennent suite à la colonisation d'un nouvel hôte, cela peut aider au processus d'adaptation

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notamment en limitant la forte réduction de taille des populations et les conséquences qui peuvent y être associées (comme énoncé précédemment).

Cependant, même si les effets maternels peuvent aider à l'exploitation d'une nouvelle plante, il apparaît également qu'ils puissent avoir limité l'adaptation à la plante hôte. En particulier au cours du chapitre 1, il a été trouvé que les effets maternels entraînent sur les descendants de mères exposées à la tomate à la fois une survie plus forte aux jeunes stades mais aussi une plus faible fécondité (pour les femelles) et une acceptation de la plante hôte plus faible. Il est assez délicat de déterminer les conséquences de telles réponses contradictoires sur la valeur sélective d'un individu en réponse à la plante hôte sans les avoir analysées conjointement au sein d'une analyse intégratrice. En effet, sans une analyse de ce type il aurait été moins évident d'établir que les populations ayant évolué depuis un plus grand nombre de générations sur la tomate (tomate 39 dans le tableau 1 du chapitre 2) ne présentaient pas de signal adaptatif clair sachant que plus de 87 % des traits d'histoire de vie des individus de ces populations ont répondu similairement à ceux des populations adaptées (tomate 19 dans le tableau 1). Dans le chapitre 1, il est possible que la plus faible fécondité des filles dont les mères ont été exposées à la tomate, comparées à celles des mères exposées au concombre, ait exacerbé des problèmes démographiques au cours de l'évolution des populations sur la plante hôte notamment ceux liées à des populations de petite taille. Cet effet maternel est opposé à celui détecté dans le chapitre 2 où les mères exposées à la tomate font des filles avec une plus grande fécondité sur tomate que les mères exposées au haricot. Cet effet maternel a potentiellement aidé au maintien des populations sur les plantes de tomate pendant un plus grand nombre de générations (*i.e.*, 128 générations sur plantes de tomates pour les populations du chapitre 2 (qui ont fini par s'éteindre) contre 60 générations pour les populations du chapitre 1 avant extinction).

## 2. Mécanismes de l'adaptation

Il a été établi dans le chapitre 2 que le seul trait d'histoire de vie qui a répondu différemment entre populations tomate 19 et tomate 39, contribuant à expliquer les différences de valeur sélective entre ces populations, et donc la réussite ou l'échec de l'adaptation à un nouvel hôte, est la fécondité

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journalière. Dans la littérature, il a déjà été reporté qu'une adaptation à la plante hôte peut être associée à une augmentation de la fécondité chez des populations de *T. urticae* (comme par exemple détectée chez Fry, 1990 ; Magalhães *et al.*, 2007). Parallèlement à cela, de nombreux travaux ont porté sur l'effet des défenses induites de la plante de tomate, libérées ou non en fonction du type d'organisme exploitant la plante, sur la fécondité de ravageurs (Kant *et al.*, 2008; Sarmiento *et al.*, 2011; Godinho *et al.*, 2016; de Oliveira *et al.*, 2016). Notamment, lorsque des organismes étaient capables de réprimer la production de toxines défensives de la plante hôte de tomate (comme par exemple *T. evansi*, un spécialiste de la tomate), les herbivores présentaient une meilleure fécondité sur cette plante que ceux présents sur une plante non-infestée. De plus, certaines souches de *T. urticae* n'induisent pas les défenses des plantes, au contraire de la plupart des populations de cette espèce (Kant *et al.*, 2008 ; Wybouw *et al.*, 2015). Je me suis donc attachée à déterminer si l'amélioration de la fécondité était liée, au cours de l'évolution des populations de *T. urticae* sur des plantes de tomate, à l'évolution d'une capacité à tolérer les défenses (constitutives et induites) de la plante ou encore à une capacité de réprimer les défenses de la plante induisant une meilleure qualité de la plante hôte pour son exploitation ultérieure.

Nous avons examiné deux traits d'histoire de vie, la mortalité et la fécondité des femelles adultes, ces deux traits montrant des réponses différentes lors de l'adaptation à la plante hôte (chapitre 2). Les conclusions du chapitre 3 suggèrent que, suite à l'adaptation à la plante de tomate, (i) l'acarien généraliste *T. urticae* semble être capable de diminuer la qualité de sa plante hôte, comme trouvé pour certaines souches de *T. urticae* (voir Li *et al.*, 2002 ; Kant *et al.*, 2004), induisant ainsi une plus forte mortalité de ses congénères adultes femelles sans que cela n'affecte néanmoins leur fécondité (contrairement aux résultats obtenus dans les études précédemment citées), mais aussi (ii) qu'il est capable de tolérer les défenses de la plante de tomate au vu de sa fécondité meilleure quelle que soit la pré-infestation de la plante, sans que la mortalité des femelles ne diffère de celles des populations témoins

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Dans un contexte d'exploitation d'un hôte, il peut être avantageux pour un génotype donné de diminuer la qualité de son hôte afin de limiter la colonisation par d'autres organismes et ainsi la compétition interspécifique à la ressource. Cela ne peut toutefois être vrai que dans le cas où le génotype diminuant la qualité de l'hôte souffre moins des conditions de son hôte que d'autres génotypes. Si la capacité à diminuer les défenses de la plante relève d'une spécialisation coûteuse et longue à la plante hôte, il est vraisemblable que ce généraliste ait été sélectionné pour tolérer les défenses de ses hôtes au lieu de les éteindre.

### 3. Perspectives

Nous avons montré que, chez une espèce généraliste, le succès d'adaptation à une plante hôte nouvelle était fortement affecté (i) par des effets maternels, (ii) par la démographie des populations suite au changement de plante hôte, (iii) qu'il reposait sur des réponses variées entre traits d'histoire de vie au cours du cycle de vie dans une même population, ou pour un même trait entre populations, et (iv) était associé à l'évolution d'une plus grande tolérance aux défenses de la plante hôte. Cependant, ces résultats soulèvent de nouvelles questions dans le cadre de l'évolution d'une espèce généraliste en réponse à ses plantes hôtes. Nous définissons ici de futurs axes à investir afin d'aller plus loin dans ce contexte d'étude.

#### **3.1. Evolution de la plasticité chez un généraliste**

Les travaux de cette thèse suggèrent que la plasticité, *via* des effets maternels, tient un rôle clef au cours de la colonisation d'une nouvelle plante hôte, la tomate. Je me demande comment évolue cette plasticité chez une espèce généraliste exploitant pendant plusieurs générations une même plante hôte en milieu naturel (par exemple par contrainte géographique) et quelles sont les conséquences de cette évolution (s'il y a évolution) sur la capacité des généralistes à persister sur un hôte.

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Il serait intéressant de mesurer l'évolution de cette plasticité dans différents régimes de sélection où l'environnement maternel est plus ou moins prédictif de l'environnement des descendants, en alternant des périodes plus ou moins longues sur différents hôtes. On pourrait alors espérer obtenir des populations variant dans leur plasticité et mesurer leur succès de colonisation sur un nouvel hôte.

De même, il serait intéressant d'explorer les conséquences des réponses plastiques contrastées entre différents traits au cours du cycle de vie chez ce généraliste (cf. chapitre 1 sur les réponses des traits d'histoire de vie aux stades juvénile et adulte) sur le succès reproducteur des femelles lorsqu'on analyse de manière conjointe l'expression de ces traits via une analyse aster par exemple comme nous l'avons fait dans le chapitre 2. Ces études complémentaires permettraient d'apporter d'affiner nos conclusions sur le rôle de la plasticité au cours de la colonisation et l'exploitation d'un nouvel hôte.

### **3.2. Freins de l'adaptation à la plante hôte chez un ravageur de cultures**

Les réponses des traits d'histoire de vie chez *T. urticae* nous ont permis de montrer que l'adaptation à la plante hôte n'est pas toujours possible suite à la colonisation d'un hôte nouveau (chapitre 2). Ces résultats d'échec adaptatif peuvent potentiellement être liés aux conséquences démographiques (goulots d'étranglement) intervenant suite à un événement de colonisation.

Je me demande en quelle mesure le processus d'adaptation chez un ravageur de culture est limité par les conséquences démographiques (par exemple une limitation de la taille efficace des populations, une contribution hétérogène des familles dans la fondation des populations, de la consanguinité) occasionnées par un changement d'hôte. Plus largement, d'un point de vue du contrôle des populations de ravageurs, comment ces paramètres affectent-ils leur capacité à coloniser une plante hôte et à échapper à l'extinction? Nous pourrions répondre à ces questions en établissant de nouvelles populations à partir de différents nombres de femelles fondatrices (puisque les femelles sont les principaux individus dispersants chez cette espèce) et suivre l'évolution démographique des populations sur une même plante hôte sur la base de cette variabilité initiale d'individus colonisant l'hôte en question. Par ailleurs, est-ce que le succès de colonisation de la



plante (avec différents nombres de femelles fondatrices) peut être affecté par la présence de congénères sur la plante et son exploitation (cf. chapitre 3) ?

### **3.3. Des traits d'histoire de vie qui n'en font qu'à leur tête, contraintes ou stratégie pour des généralistes ?**

Nous avons pu montrer que l'évolution des traits d'histoire de vie de cet acarien en réponse à un changement d'hôte était très variable selon les traits comparés. Par ailleurs, certains traits montrent des patrons d'évolution comparables entre différentes expériences de changement d'hôte, alors que certaines réponses semblent au contraire très idiosyncratiques. On peut se demander si la variabilité des réponses entre traits résulte de compromis évolutifs. Pour répondre à cette dernière question, il conviendrait de mener des mesures de génétique quantitative afin de révéler de potentielles corrélations génétiques ou phénotypiques entre traits au cours du cycle de vie chez *T. urticae* (voir Magalhães *et al.*, 2007). Il conviendrait aussi d'établir si ces traits d'histoire de vie ont une plus grande variabilité génétique que d'autres ou encore que les différents régimes de sélection exercent de plus fortes pressions de sélection sur certains traits.

Parallèlement, il serait intéressant d'investir plus en détail les conséquences de la variation de certains traits d'histoire de vie que nous n'avons pas intégrés dans notre mesure de succès de reproduction, tels que la durée de vie des mâles adultes, sur l'adaptation à la plante hôte. De même, il reste encore à explorer d'autres réponses de traits d'histoire de vie sur l'adaptation à un nouvel hôte tels que le succès reproducteur des mâles ou encore la fécondité de femelles fertilisées (plutôt que la fécondité de femelles vierges qui ne pondent que des œufs mâles), ou encore l'effet des interactions entre individus sur la démographie d'une espèce généraliste (plutôt que les traits de vie d'individus isolés).

### **3.4. Sélection de la tolérance chez une espèce polyphage : quelles conséquences sur la démographie des populations ?**

Pour finir, nous avons montré que la tolérance aux défenses de la plante était potentiellement un trait important pour le processus d'adaptation à la plante hôte. Il a également été proposé que la pré-

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infestation de la plante hôte par des populations aux histoires évolutives différentes puisse affecter variablement la qualité de la plante (en se basant sur la réponse de la survie des femelles). Cependant, sans analyse complémentaire sur l'expression des molécules impliquées dans la défense à l'échelle de la plante, il est difficile d'inférer les mécanismes responsables des modifications occasionnées à la plante par ces populations. Dans cette optique, il est nécessaire de réaliser des analyses sur la composition chimique de la plante ou encore l'expression de gènes impliquées dans son système de défense face à l'herbivorie.

Il conviendrait également d'explorer plus en détail la réponse de la fécondité des femelles encore vivantes après 3 jours de mise en ponte sur la plante de tomate afin d'établir si nous détectons un effet du traitement de la plante sur la fécondité totale des femelles après avoir contrôlé pour la période de ponte des femelles. En effet, nous ne pouvons pas déterminer pendant combien de temps les femelles trouvées mortes (lors de la mesure de fécondité) ont pondu. Il serait également intéressant de mieux intégrer et analyser les effets conjoints sur la survie et la fécondité de nos traitements expérimentaux, afin d'en examiner les conséquences sur une mesure de performance globale. Une analyse complémentaire de type aster pourrait permettre de nous renseigner en partie sur ces derniers points.

Finalement, compte tenu de la forte variance de la fécondité associée aux plantes utilisées dans les expériences et le faible nombre de plantes utilisées dans notre traitement témoin sans infestation, il serait pertinent de réitérer cette expérience avec un plus grand nombre de plantes, et de mieux contrôler les effets liés au disque de feuille utilisé, afin de détecter plus finement les effets du traitement de la plante. A cette occasion il pourrait aussi être intéressant d'examiner l'effet de la pré-infestation et de l'origine des populations en ponte non plus sur des traits de vie mesurés sur des disques de feuille mais sur la démographie des populations à l'échelle de la plante. En effet, nos mesures de traits d'histoire de vie, collectée à partir de fragments de la plante hôte, peuvent se trouver limiter par une dégradation des composés toxiques au sein de ces environnements tests artificiels (relativement à ce que l'on peut trouver à l'échelle de la plante).

### Conclusion générale

Au cours de cette thèse, j'ai montré que la colonisation d'un nouvel hôte n'était pas nécessairement associée à un processus d'adaptation à la plante hôte mais plutôt qu'il existe un continuum de réponses évolutives chez un polyphage, incluant l'absence de détection d'adaptation, conduisant à l'extinction des populations, la présence de réponses plastiques adaptatives, jusqu'au processus d'adaptation génétique à la plante hôte. Cet organisme généraliste peut persister sur une plante stressante, la tomate, à l'aide de différents mécanismes pouvant compenser son manque d'adaptation initial à cette plante hôte. La persistance sur un plus ou moins grand nombre de générations peut notamment s'établir sur la base d'effets maternels. Lorsque l'on étudie finement les traits biologiques de cet acarien en réponse à la plante hôte, il est parfois difficile d'interpréter leurs réponses à la nouvelle plante hôte ceci à cause des fortes variations (contradictoires) dans l'expression de ces traits tout au long du cycle de vie. Au cours de mes travaux, il est apparu que la plante hôte de tomate pouvait être un environnement stressant au cours de l'évolution des populations. Une réponse rapide de la fécondité chez cette espèce généraliste est apparue comme un facteur clef permettant l'adaptation à l'hôte et sa persistance à long terme. Finalement, il a été montré que l'évolution de cette composante de la valeur sélective était dépendante de l'acquisition d'une aptitude à tolérer les défenses de l'hôte.

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# *Annexes*





## Chapitre 2 – La taille d’une population peut compromettre l’adaptation

**Appendix S1.** Expected heterozygosity (mean  $\pm$  sd) of the four replicate populations having independently evolved in each of the three selection regimes *i.e.*, the bean SR, the tomato 19 SR and the tomato 39 SR.

Replicate population	Selection regime		
	Bean	Tomato 19	Tomato 39
1	0.53 $\pm$ 0.23	0.41 $\pm$ 0.23	0.34 $\pm$ 0.23
2	0.53 $\pm$ 0.15	0.49 $\pm$ 0.20	0.48 $\pm$ 0.15
3	0.50 $\pm$ 0.18	0.48 $\pm$ 0.14	0.41 $\pm$ 0.18
4	0.50 $\pm$ 0.19	0.49 $\pm$ 0.18	0.39 $\pm$ 0.23

**Appendix S2.** Pairwise  $F_{st}$  values for populations from the (a) bean, (b) tomato 19 and (c) tomato 39 selection regime (SR). The numbers (1, 2, 3 and 4) discriminate the four replicate populations within each SR. The numbers enclosed in parenthesis are the confidence intervals.

(a)

Replicate population	Bean		
	2	3	4
1	0,05 (0.03 - 0.08)	0,03 (0.00 - 0.06)	0,05 (0.00 - 0.13)
2	-	0,004 (-0.01 - 0.02)	0,003 (-0.01 - 0.02)
3	-	-	0,005 (-0.01 - 0.04)

(b)

Replicate population	Tomato 19		
	2	3	4
1	0,2 (0.14 - 0.26)	0,16 (0.05 - 0.27)	0,21 (0.10 - 0.34)
2	-	0,11 (0.05 - 0.18)	0,18 (0.10 - 0.26)
3	-	-	0,19 (0.08 - 0.32)

(c)

Replicate population	Tomato 39		
	2	3	4
1	0,26 (0.14 - 0.38)	0,38 (0.24 - 0.49)	0,41 (0.25 - 0.56)
2	-	0,14 (0.05 - 0.23)	0,25 (0.17 - 0.32)
3	-	-	0,32 (0.22 - 0.48)

## **Sélection, plasticité et dérive façonnent les traits d'histoire de vie chez l'acarien ravageur de cultures *Tetranychus urticae* suite à un changement de plante hôte.**

Les herbivores polyphages sont des généralistes capables d'exploiter une large gamme de plantes hôtes. Au cours des travaux de cette thèse en évolution expérimentale, nous étudions l'évolution de traits d'histoire de vie de différentes populations d'une espèce de ravageur de culture, l'acarien *Tetranychus urticae*, suite à la colonisation d'un même nouvel hôte, la tomate. Au cours des deux premiers chapitres, des mesures de traits d'histoire de vie ont été collectées depuis le stade œuf jusqu'à la mort des individus permettant de décrire finement le cycle de vie de cet acarien en réponse à l'exploitation de la tomate. Dans le chapitre 1, j'ai montré que la survie au stade juvénile était étroitement liée à des effets maternels. Notamment, les mères s'étant préalablement développées sur la plante de tomate conféraient à leurs descendants une meilleure survie juvénile sur cet hôte. Cependant, ces juvéniles quittaient davantage la plante une fois adulte et avaient une fécondité (pour les femelles) réduite. De plus, l'histoire évolutive des populations affectait la proportion de femelles produites par les mères améliorant potentiellement la démographie des populations. Dans le second chapitre, j'ai montré que plusieurs traits d'histoire de vie (survie juvénile, survie adulte mâle et fécondité) avaient évolué dans les populations exposées à la tomate depuis plusieurs générations à comparer des populations témoins ayant évolué sur haricot. Néanmoins, l'étude du succès reproducteur total des femelles intégrant l'effet de plusieurs traits de vie montre paradoxalement un signal clair d'adaptation au nouvel hôte seulement pour des populations ayant évolué sur cet hôte pendant environ 38 générations et non pour des populations ayant évolué sur cette plante hôte pendant environ 78 générations. L'étude de la diversité génétique, sur la base de marqueurs microsatellites, suggère que ces dernières populations ont souffert de goulets d'étranglement, ce qui pourrait avoir compromis leur adaptation. Pour finir, dans le chapitre 3, je teste si les populations nouvellement adaptées à la tomate sont plus tolérantes aux défenses de la plante, induites par l'attaque d'herbivores, ou bien si ces populations induisent différents niveaux de défense chez les plantes attaquées, affectant la performance des acariens qui les colonisent ultérieurement. Pour cela, des acariens ont été mis en ponte sur des plantes de tomates non pré-infestées, pré-infestées par des acariens adaptés à la tomate ou pré-infestées par des acariens non adaptés à cet hôte. Les populations adaptées à la tomate ont une fécondité plus forte sur cette plante, quel que soit le traitement de la plante, tandis que toutes les populations d'acariens voient leur mortalité augmenter sur les plantes pré-infestées par des acariens adaptés à la tomate. Mes résultats semblent indiquer que l'évolution sur tomate se manifeste par une plus grande capacité à tolérer les défenses de cette plante et une plus grande induction de ces défenses.

Ainsi, mon étude décrit un continuum de réponses évolutives chez un polyphage allant de l'absence de détection d'adaptation, conduisant à l'extinction des populations, à la présence de réponses plastiques adaptatives, jusqu'au processus d'adaptation à la plante hôte *via* possiblement l'acquisition de la capacité à tolérer les défenses de la plante hôte. Ces travaux soulignent l'importance d'intégrer l'effet des variations contrastées de différents traits d'histoire de vie dans une mesure de valeur sélective afin de décrire l'adaptation à une nouvelle plante hôte. Des investigations futures en ce sens permettraient d'enrichir la littérature sur la persistance des herbivores suite à la colonisation de nouvelles plantes hôtes mais aussi d'affiner nos compétences en terme de contrôle d'espèces de ravageurs.

**Mots clefs :** Changement de plante hôte, histoire évolutive, sélection, adaptation, effets maternels (plasticité adaptative), dérive, réponses des traits d'histoire de vie, *Tetranychus urticae*

## **Selection, plasticity and drift shape the life history traits in the crop pest *Tetranychus urticae* after a host-plant shift.**

Polyphagous herbivores are generalists able to exploit a large range of host-plants. In this thesis, using experimental evolution, I study the evolution of life history traits in different populations of a crop pest, the spider mite *Tetranychus urticae*, after colonization of a new host, the tomato plant. In the first two chapters, measures of life history traits were collected from the egg stage to the death of individuals allowing the precise description of the life cycle of mites in response to the exploitation of tomato plants. As described chapter 1, I found that juvenile survival on the new host was influenced by maternal effects. In particular, mothers having developed on tomato had offspring surviving better on this host as juvenile. However, these juveniles left more often the plant as adults and had a reduced fecundity (for females). Moreover, the evolutionary history of populations affected the proportion of females produced by mothers, potentially enhancing demography of populations having previously evolved on this host. In chapter 2, I show that several life history traits (juvenile survival, male adult lifespan and fecundity) had evolved in all populations exposed to tomato for several generations relative to control populations evolving on bean. Nevertheless, the study of female lifetime reproductive success integrating the effect of several successive traits only showed, paradoxically, an adaptive signal for populations having evolved on this host for approximately 38 generations and not for populations having evolved on tomato for approximately 78 generations. The study of genetic diversity with microsatellite markers suggests that these latter populations may have suffered from bottlenecks, which could have compromised their adaptation. Finally, as shown chapter 3, I test whether populations newly adapted to tomato are more tolerant to the host-plant defenses, induced by herbivore attacks, and/or whether these populations differentially trigger the defences of damaged plants, affecting the performance of mites that subsequently colonize this host. For that purpose, I recorded the fecundity and mortality of female adult mites put on clean tomato plants, or on tomato plant pre-infested by tomato-adapted mites or by mites not adapted to this host. Populations adapted to tomato had a higher fecundity on this host irrespective of the plant treatment, while mortality increased for all populations on plants pre-infested with tomato-adapted mites. My results thus suggest that evolution on tomato leads to an increased capacity to tolerate host-plant defences and also to a higher induction of such defences.

My studies describe a continuum of evolutionary responses in a polyphagous species from failure of adaptation, leading to the eventual extinction of populations, to the presence of adaptive plastic responses and finally to host-plant adaptation *via* the possible acquisition of higher tolerance to host-plant defenses. My work also underlines the relevance of integrating the effects of different life history traits with contrasted variations within a same fitness measure to describe host-plant adaptation. Further investigations in this direction should enrich our understanding of mechanisms of herbivore persistence on a new host-plant but also allow developing better crop pest management strategies.

**Key words:** Host-plant shift, evolutionary history, selection, adaptation, maternal effects (adaptive plasticity), drift, life history trait responses, *Tetranychus urticae*