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# Bottom-up effects of abiotic factors on aphid parasitoid specialization

Le Thu Ha Nguyen

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## THESE DE DOCTORAT

Présentée en vue de l'obtention du

Grade de docteur en Sciences de la Vie et de la Santé

UNIVERSITE CÔTE D'AZUR

par

**Le-Thu-Ha NGUYEN**

### **Bottom-up effects of abiotic factors on aphid parasitoid specialization**

### **Effet bottom-up du stress hydrique sur la gamme d'hôtes des parasitoïdes de pucerons**

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*Soutenue le 20 Décembre 2017 devant le jury composé de:*

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*For my parents, Tony Anh-Khôi, and Lisa Bảo-Anh*

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## Abstract

Biological control (BC - the use of natural enemies to control pests) is a sustainable, environmentally friendly and cost-effective method for potential pest management without relying on chemical pesticides. Aphid parasitoids are common natural enemies of aphids, the major worldwide pests in agriculture. The study of parasitoid host specificity contributes to (1) understanding ecological and evolutionary mechanisms underneath ecosystem functioning, and (2) evaluating the efficiency of biocontrol agents, and (3) the ecological risks for non-target species when using these biocontrol agents.

This study focuses on the parasitoids fundamental host specificity at individual level, regarding resource requirements and the context of multi-trophic interactions under environmental abiotic stress, *i.e.* water limitation. *Aphidius ervi* (Hymenoptera: Braconidae: Aphidiinae) was chosen for the present work; this aphid parasitoid is used widely as an ecological model, and is a commercial biological control agent (BCA). On a first hand, *A. ervi* host specificity index was measured on a broad range of aphid species. On a second hand, the indirect effects of water limitation in plants bearing aphid hosts were investigated on the host specificity of the parasitoid. Furthermore, water stress-induced modifications in the plant and the aphid life-history traits were measured. *A. ervi* was shown to be an intermediate specialist species who attacked all aphid species at high rates but was unable to develop well on many of them. The few that enabled parasitoid development were phylogenetically close and/or belong to the Macrosiphini tribe. Interestingly, a positive preference – performance relationship was found. Under water stress, both preference and performance of parasitoids were affected causing loss of the significant relationship. Water limitation negatively altered the plant nutritional quality resulting in low aphid performance on host plants. This in turn decreased the suitability of aphid hosts for the parasitoid. The impacts of water limitation were not similar across all plant-aphid combinations and depended on several factors, notably stress-adapted plant mechanisms and the host specialization of both aphids and parasitoids.

Keywords: host specificity, preference-performance hypothesis, tritrophic interactions, water limitation, biological control

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## **List of abbreviations**

BCA: Biological control agents

BC: Biological controls

LW: limited water supply

OW: optimal water supply

RQH: Red Queen Hypothesis

LB: lutte biologique

ALB : agent de lutte biologique

## Résumé de la thèse en français

La lutte biologique (LB) ou l'utilisation d'ennemis naturels pour lutter contre les ravageurs (espèces nuisibles pour l'intérêt humain telles que les arthropodes herbivores dans les systèmes agricoles) est une pratique agricole traditionnelle millénaire (van den Bosch *et al.*, 1982) (et ce même si le concept de lutte biologique en lui-même a été introduit en 1868 par les travaux de Riley en Californie). La pratique de la LB s'est transmise à travers les âges et continue encore aujourd'hui. Parce que les méthodes des LB sont durables, respectueuses de l'environnement et potentiellement rentables, elles sont aujourd'hui une approche systémique et post-pesticide qui permet aussi de limiter l'apparition de résistances aux pesticides dans les populations d'espèces ciblées. Les trois approches principales de LB sont la lutte classique (libération d'ennemis naturels exotiques pour contrôler les ravageurs exotiques envahissants), la lutte par augmentation (augmentation des populations d'ennemis naturels indigènes) et la lutte par conservation (aménagement des habitats pour favoriser les populations d'ennemis naturels pour réguler les ravageurs).

L'efficacité de ces approches dépend de l'efficacité de l'agent de lutte biologique (ALB) qui dépend elle-même de plusieurs facteurs dont leurs caractéristiques biologiques et leurs interactions avec l'environnement). L'utilisation des ALB nécessite donc une connaissance écologique du fonctionnement des écosystèmes *i.e.* des facteurs biotiques et abiotiques qui interagissent dans l'environnement. Les critères les plus pertinents prennent en compte la biodiversité, la spécialisation écologique (l'utilisation des ressources et les rôles des espèces dans les réseaux écologiques) ainsi que les interactions et les forces qui régulent les écosystèmes.

Les pucerons sont des parasites végétaux qui causent des pertes importantes de rendement (Valenzuela et Hoffmann 2014), soit par dommages directs en se nourrissant sur les plantes de cultures, soit indirectement via la transmission de virus (van Emden et Harrington 2007). En outre, ils résistent à plusieurs types d'insecticides (Bass 2014, Bass *et al.*, 2014). Par conséquent, l'approche LB contre les pucerons apparaît comme une méthode de lutte à fort potentiel.

Parmi les ennemis naturels des pucerons, les parasitoïdes sont couramment utilisés comme ALB aussi bien dans les serres qu'en plein champs. Les parasitoïdes sont des espèces dont les larves se développent en se nourrissant dans le corps de leur hôte, généralement des insectes. En raison de cette stratégie d'alimentation spécifique, les parasitoïdes s'adaptent à leurs hôtes et co-évoluent strictement avec eux. Grâce à leur haute spécificité, les parasitoïdes sont largement utilisés en LB en tant qu'agents contre les ravageurs des cultures. Pour choisir un ALB parasitoïde potentiel, les scientifiques doivent évaluer leur spécificité d'hôte et l'efficacité d'utilisation de leur hôte à différentes échelles. De plus, les informations sur l'écosystème où un ALB est relâché, pourraient aider à prédire ses réponses sur le terrain. L'étude de la spécificité hôte du parasitoïde contribue à (1) comprendre les mécanismes qui structurent les communautés hôtes-parasitoïdes, et (2) prédire l'efficacité et les impacts non ciblés des ALB avant leur libération.

Mon travail de thèse s'est concentré sur la spécificité d'hôtes des parasitoïdes dans un système tritrophique 'plante – puceron – parasitoïde'. L'espèce et la qualité des plantes, l'espèce et la qualité des pucerons ainsi que le comportement et la physiologie des parasitoïdes sont des facteurs susceptibles de modifier cette spécificité d'hôte. L'environnement abiotique est également susceptible de moduler cette spécificité. Cette étude propose donc tout d'abord d'évaluer cette spécificité d'hôte avec des tests comportementaux et physiologiques, puis de tester l'impact de différents facteurs biotiques et abiotiques susceptibles de la moduler.

Le chapitre I rappelle le concept de spécialisation écologique et les méthodes d'évaluation de la spécificité d'hôte. Dans notre cas, la spécialisation écologique représente la gamme d'hôte appropriée d'un parasitoïde *i.e.* le nombre d'hôtes dans lequel il peut effectuer un développement complet. Deux tendances opposées existent : les espèces spécialistes (peu d'hôtes) et les espèces généralistes (large choix d'hôte). Mais à partir de quel seuil peut-on considérer qu'une espèce est généraliste ou spécialiste ? Existe-t-il un continuum entre ces deux tendances ? Quelle serait la stratégie dominante et valorisée sur le plan évolutif ? Cette stratégie dominante dépend-elle du contexte environnemental ? La présence d'idées opposées pendant des décennies révèle la complexité de la question de la spécialisation écologique et des supports empiriques existent pour chaque hypothèse. Les principes et les

applications des méthodes de test de la gamme d'hôtes sont également rappelées dans ce chapitre. Il existe en l'occurrence de nombreuses options pour améliorer ces méthodes en précisant le degré de spécialisation au sein du continuum généraliste-spécialiste. Nous avons choisi d'utiliser deux méthodes d'évaluation pour la suite de notre étude : l'indice de spécificité d'hôte et la corrélation entre la préférence des parasitoïdes (traits comportementaux) et leur performance (traits physiologiques).

Le chapitre II rappelle le contexte écologique des effets possibles des facteurs environnementaux sur les réseaux écologiques et notamment trophiques. Un niveau trophique peut réguler d'autres niveaux trophiques par leur interaction par le biais de forces ascendantes ou descendantes. Les forces ascendantes (*bottom-up forces*) signifient que les ressources (niveau trophique inférieur ou *bottom*) influencent les consommateurs des niveaux trophiques supérieurs (ou *up*). Les forces descendantes (*top-down forces*) signifient que les consommateurs (niveaux trophiques supérieurs ou *top*) influencent les niveaux trophiques inférieurs (ou *down*). La question de la force dominante dans un écosystème (*bottom-up* ou *top-down*) fait toujours débat et des supports empiriques existent pour chaque hypothèse. La première partie du chapitre II rappelle ces différentes hypothèses, dont la démonstration dépend du contexte environnemental (comme pour le débat sur la spécialisation). Dans les deux cas, le rôle des plantes est majeur car les forces *bottom-up* et *top-down* sont le plus souvent médiées par ce niveau trophique (Power, 1992).

Dans ce contexte, on peut se demander si les forces environnementales ascendantes qui régulent les réseaux écologiques pourraient affecter le contrôle descendant, c'est-à-dire l'efficacité des parasitoïdes en modulant leur spécificité d'hôte. L'étude des effets ascendants d'un facteur abiotique, ici la limitation en eau, sur le système tritrophique 'plante-puceron-parasitoïde' pourrait aider à prédire l'efficacité d'un ACB parasitoïde sur le terrain. Cet objectif est rappelé et détaillé dans le chapitre 3.

Pour y répondre, nous avons tout d'abord appliqué les méthodes de test de la gamme d'hôtes et calculé les deux paramètres, indice de spécificité de l'hôte et corrélation préférence-performance, pour évaluer la spécificité hôte de trois parasitoïdes de pucerons (chapitre 4). Ces deux paramètres ont été testés dans l'idée de voir s'ils étaient plus pertinents et précis pour classer les parasitoïdes au sein du continuum de spécialistes - généralistes. La gamme

d'hôtes fondamentale de ces trois parasitoïdes a été déterminée par expérimentations en conditions de laboratoire permettant de calculer l'indice de spécificité de l'hôte et d'analyser la relation préférence-performance (article 1). La gamme d'hôtes fondamentale a ensuite été comparée à la gamme d'hôtes sur le terrain, rapportée dans la littérature. Enfin, l'indice de spécificité et la relation préférence-performance se sont révélés comme étant des paramètres appropriés à appliquer dans les schémas futurs de test de gamme d'hôtes, notamment dans le cadre de la LB. Dans cette étude, *Diaeretiella rapae* et *Aphelinus abdominalis* sont généralistes et peuvent se développer sur une large gamme d'hôtes. *A. ervi* est une espèce intermédiaire spécialisée dont les femelles attaquent toutes les espèces de pucerons à des taux élevés, mais était capable de se développer avec succès que sur quelques espèces de pucerons.

Dans un deuxième temps, nous avons testé les effets ascendants d'un facteur abiotique sur la spécificité d'hôte d'un parasitoïde (chapitre 5). Pour se faire, nous avons choisi d'utiliser *Aphidius ervi* (Hymenoptera: Braconidae: Aphidiinae), identifié comme spécialiste intermédiaire dans l'étude précédente. Les femelles d'*A. ervi* ont attaqué toutes les espèces de pucerons proposées à des taux élevés mais n'ont pu se développer complètement que sur quelques hôtes, tous appartenant à la tribu des Macrosiphini. Sa position médiane dans le continuum spécialiste-généraliste favorisait nos chances de voir un effet de modulation du facteur environnemental sur sa gamme d'hôte *i.e.* le parasitoïde est-il toujours capable d'évaluer la même espèce hôte, potentiellement de qualité différente dans un environnement différent ? S'il y a impact, que se passe-t-il aux niveaux trophiques inférieurs (plantes et pucerons) qui pourrait expliquer les variations de la gamme d'hôte ? Nous avons tout d'abord réalisé une étude bibliographique pour identifier les facteurs abiotiques susceptibles d'influencer la préférence et la performance des parasitoïdes par effet *bottom-up*. Cette étude nous a permis d'identifier la limitation en eau comme étant un stress abiotique pertinent pour l'étude des effets *bottom-up* sur la modulation de la gamme d'hôte.

Nous avons ainsi testé l'impact de la limitation en eau sur la préférence et la performance du parasitoïde *A. ervi* sur deux de ses meilleurs hôtes *i.e.* deux espèces de pucerons dans lequel il se développe bien (article 2). Les effets observés nous ont poussé à étudier d'autres complexes plante-puceron (six en tout) représentant des hôtes plus ou moins bons pour *A.*

*ervi* (article 3). Nous avons utilisé la même méthode que dans le chapitre 4 pour évaluer et comparer la spécificité d'hôte d'*A. ervi*. *i.e.* nous avons calculé son indice de spécificité d'hôte et analysé la corrélation préférence-performance en conditions optimales vs limitées d'apport en eau pour la plante. De plus, les modifications induites par la limitation en eau chez la plante et les pucerons ont été mesurées pour (1) confirmer l'impact de nos traitements et (2) proposer des pistes sur les mécanismes potentiels.

La corrélation positive préférence-performance ainsi que le signal phylogénétique des hôtes pucerons sur la performance des parasitoïdes ont bien été retrouvés en conditions optimales conformément aux expériences précédentes (chapitre 4). Mais dans les conditions stressées, la corrélation est perdue car la préférence et la performance des parasitoïdes ont été affectées. La limitation en eau a diminué la qualité nutritionnelle des plantes, ce qui s'est traduit par une faible performance des pucerons sur les plantes hôtes, ce qui a diminué la capacité des parasitoïdes. Ces effets de la limitation en eau sur la préférence et la performance étaient cependant espèces-dépendant.

Dans l'ensemble, cette preuve de l'effet ascendant de la limitation de l'eau du sol sur la spécificité de l'hôte parasitoïde soulève une préoccupation pour les parasitoïdes en tant que BCA. Les plantes et les pucerons peuvent tolérer une limitation modérée et à long terme de l'eau, même si leurs performances ont été négativement affectées. Les populations de pucerons pourraient être maintenues sur des plantes stressant l'eau pendant plusieurs semaines sans extinction dans cette étude. Cependant, la mortalité des parasitoïdes sur les hôtes des pucerons a augmenté de manière significative, de 60% sous un apport d'eau optimal à 94,5% en eau limitée sur les hôtes *M. persicae*. Ainsi, le niveau trophique supérieur avec un degré élevé de spécialisation alimentaire comme les parasitoïdes pourrait souffrir plus que les niveaux trophiques inférieurs. D'autres études devraient être menées pour confirmer cette affirmation, par exemple en étudiant la dynamique des populations de parasitoïdes chez les pucerons hôtes se nourrissant de plantes stressées par l'eau.

En cas d'impacts ascendants négatifs confirmés des facteurs abiotiques sur les parasitoïdes, faut-il libérer ces BCA sous contraintes abiotiques ? Cela pourrait être une perte économique. Dans l'application sur le terrain, les praticiens pourraient augmenter l'efficacité de la sélection des hôtes parasitoïdes par des méthodes telles que (1) l'apprentissage antérieur, comme les

exposer à des hôtes de faible qualité avant ou en induisant des composés végétaux volatils pour localiser les hôtes; (2) l'application d'un mélange d'ennemis naturels, par ex. spécialiste ALB sur les pucerons hôtes partagés; (3) l'utilisation d'une combinaison de plante-puceron résistante au stress abiotique pour soutenir l'ALB. Il est bien connu que les réponses des organismes sont très différentes pour chaque type de stress hydrique ou de leur intensité, durée et moment (Huberty et Denno 2004). Il pourrait être intéressant de tester toutes sortes de régimes de limitation de l'eau ou de stress abiotique combiné, par exemple, la limitation de l'eau et l'apport d'engrais sur des systèmes tri-trophiques similaires pour optimiser les régimes d'eau.

Cette étude des facteurs modulant la spécificité de l'hôte des parasitoïdes de pucerons suggère non seulement les rôles significatifs des contraintes abiotiques sur l'ACB, mais aussi contribue à une compréhension plus approfondie de la spécialisation des parasitoïdes.

**Mots-clés :** spécificité de l'hôte, hypothèse de préférence-performance, interactions tritrophiques, limitation de l'eau, lutte biologique, agents de lutte biologique

## Summary

Biological control (BC) including the use of natural enemies to control arthropod herbivore pests in agricultural systems has been a traditional agriculture practice for hundred of years (notably in China) despite being formally developed by Riley in 1868 in California (van den Bosch *et al.* 1982). As BC methods are sustainable, environmentally friendly, and cost-effective, they are nowadays a possible approach to limit the increase of pesticide resistances in targeted species (resulting from overuse of chemical pesticides). The three main BC strategies are (1) the classical method: the release of exotic natural enemies to control invasive pests; (2) the augmentative: increasing the populations of indigenous natural enemies; and (3) the conservative: enhancing natural enemy efficiency in regulating pest populations by using methods such as landscape management.

Through these approaches, the efficiency, and the ecological risks for non-target species of the biological control agent (BCA) must be assessed (Roderick *et al.* 2012). These characteristics can be influenced by several factors, including BCA traits and their interactions with the surrounding environment. BCA use needs ecological knowledge of the ecological specialization such as the diversity of resources that can be used and how the ecosystem is regulated by interactions and forces. The most unpredictable aspect is how the species specialization changes within a new or disturbed environment (Poisot *et al.* 2011).

Ecological specialization is a process whereby species adapt to their niche to survive. There are two opposite specialization tendencies (1) narrow their resource breadth becoming a specialist or (2) broaden their resource breadth becoming a generalist. Environmental constraints might increase specialization and variation in abiotic components of the environment might favor generalists. However, the effects depend on interactions between life-history and preference traits (Poisot 2011).

Predators and parasitoids are two main types of BCA to control herbivore pests. Predators are considered generalists in compare to parasitoids because they could feed on prey of different phylogenetic families (Symondson *et al.* 2002). Parasitoids are species whose larvae develop by feeding on the bodies of their host, usually insects (Godfray 1994). They adapt and co-evolve with their hosts which belong to few families. Thanks to their high specificity,

parasitoids are widely used as BCA against crop pests. The study of host specificity of parasitoids contributes to (1) understanding ecological and evolutionary mechanisms driving ecosystems and (2) evaluating the efficiency of BCA and the ecological risks for non-target species.

Aphids are pests which cause massive yield loss which could economically damage up to 500 million dollars per year (Valenzuela and Hoffmann 2014), either directly by feeding on plants, or indirectly via virus transmission (van Emden and Harrington 2007). BC strategies are essential against aphids mostly because they are resistant to several kinds of insecticides (Bass *et al.* 2014) and their control by chemical compounds may not be carried through. Among natural enemies of aphids, parasitoids are common BCA both in greenhouses and in the field. To choose a potential BCA parasitoid, scientists must evaluate host specificity and host use efficiency under laboratory conditions and on the field. Moreover, information about the ecosystem where a BCA is released, *e.g.* the abiotic and biotic environment, should be considered to predict its field efficacy.

This study focused on parasitoid host specificity in the context of the plant-aphid-parasitoid tritrophic system. Chapters 1 and 2 are respectively a literature review on host specificity and the bottom-up effect of water limitation on host specificity. In chapter 1, the ecological context of the host range testing method is provided and involves the ecological specialization concept. The presence of decade-long opposite ideas reveals the complexity of the ecological specialization issue. Therefore, the first question is: from what threshold could a specialist vs. generalist species be defined? Secondly, between specialists and generalist species, who would be dominant and/or evolutionarily favored? The dominants could be at each degree of the specialization continuum, or specialists and generalists could equally co-exist in nature. Empirical supports exist for each hypothesis and depend on the environment. Principles and applications of host range testing methods have also been presented. However, there is much room for method improvement, *e.g.* find out characteristics representing the degree of specialization or how to separate specialists/generalists. The two criteria defined and used were parasitoid host specificity index and the correlation between preference and performance, *i.e.* behavioral and physiological traits, respectively.

Chapter 2 describes the possible effects of environmental factors in an ecological network. The impacts of abiotic or biotic factors cascade up and down food chains and consist of bottom-up or top-down forces. Bottom-up forces mean resources at the bottom of trophic networks which control the upper trophic consumers. Top-down forces mean higher trophic consumers control lower trophic resources (Wollrab *et al.* 2012). Similar to the specialization issue, the debate on which forces dominate an ecosystem is still ongoing. Empirical supports exist for contrary hypotheses. Different theories of the dominant forces and the context-dependent outcomes have been presented. The primacy of the control and mediation of plants during bottom-up and top-down regulation (Power 1992) have been pointed out. In this context, our hypothesis was that bottom-up forces from environmental stress, precisely soil water limitation, could affect the top-down control, *i.e.* parasitoid efficiency, through trophic interactions. The study of bottom-up effects of abiotic factors on the tritrophic plant-aphid-parasitoid could help predict the real efficacy of a parasitoid BCA in the field conditions. Under environmental stress, especially water limitation, the whole ecosystem might be affected and could lose the ability to recover (Schwalm *et al.* 2017), and parasitoids in the field under such conditions could be altered behaviorally, physiologically, and genetically.

With this in mind, two main objectives have been defined (chap 3): The first one was to find some relevant indexes to determine the degree of parasitoid host specificity (chap 4). In the second part, the plant-mediated impact of an environmental abiotic stress (water limitation) to the whole tri-trophic system, namely bottom-up effect, has been studied (chap 5). To do so, factors from the three trophic levels that affect parasitoid host exploitation have been recorded such as plant species and quality, aphid species and quality, parasitoid behavior, and physiology under laboratory conditions. Using the data gathered, the host range testing method has been applied to evaluate parasitoid host specificity.

Chapter 4 focuses on parasitoid host specificity. The host range testing method was used to calculate the host specificity index and the preference-performance correlation to evaluate the host specificity of three aphid parasitoids on a broad range of host species. The three parasitoids *Diaeretiella rapae*, *Aphelinus abdominalis* and *Aphidius ervi* have been considered generalists in literature as they have a broad host range in both the Aphidini and Macrosiphini tribes. Their degree of host specificity has been tested using these methods; so, whether the

method is suitable to assess parasitoid host specificity and what is needed to improve future schemes of host range testing have been discussed.

In chapter 5, the bottom-up effects of water limitation on parasitoid specificity have been assessed. The same method in chapter 4 has been used to evaluate and compare parasitoid host specificity tested on aphid-plant complexes under water limitation and optimal water supply conditions. Among the three evaluated parasitoids in chap 4, the intermediate specialist *Aphidius ervi* widely used as an ecological model and a commercial BCA has been chosen to carry out these experiments. The cascade impacts of water limitation on *A. ervi* host specificity have been analyzed on six plant-aphid combinations. Furthermore, water limitation-induced modifications in plant and aphid life-history traits have also been monitored. Both preference and performance of parasitoids have been affected by water limitation. Our hypotheses were: (1) the stress will alter the quality of plants and aphids which in turn will impact the parasitoid host specificity; (2) the impacts of water limitation will differ according to plant-aphid combinations.

## **Chapter 1. Host range testing: biological control practice requiring ecological understanding**

### **1.1. Biological control of pests in the ecological context**

*Then God said, "I give you every seed-bearing plant on the face of the whole earth and every tree that has fruit with seed in it. They will be yours for food." Genesis 1:29 | NIV |*

#### **The importance of biological control**

Crop losses caused by pests challenge crop protection efforts. Pests throughout the world are destroying about 35% of all crop production (Pimentel *et al.*, 1991; Oerke 2006). Among them, insect pests cause an estimated 13% crop loss, plant pathogens 12%, and weeds 10% (Cramer, 1967). Crop protection measures could play essential roles in preventing both pre- and post-harvesting loss. Since 1942, the discovery of new chemical pesticides gave rise to their golden era where they integrate into many foods, fiber, and fuel production systems. Agricultural producers spent around 40 billion-worth for pesticides per year worldwide for estimated 2.5 x 10<sup>6</sup> tons of pesticides; these numbers increase annually (Pimentel 1991; Popp *et al.* 2012). At the first time, pesticides (in this context understood as chemical ones) were efficiency against pests as they protected up to 70% of potential crop yields (Oerke 2006). However, intensive overuse of chemical products places a heavy burden on ecology, environment, and human health in the long term and threaten the overall future of agriculture. Pesticide residues were present in surface waters, aquatic sediments, and groundwater in more than 2500 sites in 73 countries (Stehle and Schulz, 2015). They diminish soil biodiversity and spoil soil function by killing beneficial organisms, and indirectly cause soil erosion (FAO and ITPS, 2017). Residues of pesticides can also be found in a tremendous variety of everyday foods and beverages, including cooked meals, water, wine, fruit juices, refreshments, and animal feeds (Nicolopoulou-Stamati *et al.*, 2016). Adverse effects associated with chemical pesticides upon animal or human health include dermatological, gastrointestinal, neurological, carcinogenic, respiratory, reproductive, and endocrine effects (Bonner and Alavanja, 2017; Kim and Jahan, 2017). To confront these deleterious effects, the governments of the countries like USA, EU, Canada, India, China have regulated or restricted the use of several types of pesticides (United Nations, 2009). Since the publication of "Silent Spring" (Rachel Carson,

1962), the growing public concern increases the pressure on replacing chemical measures by more sustainable and “green” methods.

Most of all, pesticide application is not omnipotent, as many pest problems in agriculture root in drastic changes in the crop agroecosystem (Pimentel, 1991). Despite an apparent increase in pesticide use, crop losses have not significantly decreased during the last 40 years (Oerke 2006). In the years of '90 in the US, corn losses to rootworm pests average 12% (Pimentel, 1991) despite the application of  $14 \times 10^6$  kg insecticide per year. However, in 1945, before the invention of synthesized pesticides, corn losses to these insects averaged only 3.5% (USDA, 1954). Different mechanisms could explain the inefficiency of chemical methods. Firstly, the overuse of pesticides eliminates essential ecosystem services such as natural enemy populations, resulting in secondary pest outbreaks. Secondly, non-selective application of pesticides jeopardizes resistance among pests (R4P network, 2016; FAO, 2017), which cause the cycle of new pesticide generations - further pest resistance. Thirdly, traditional crop rotations are replaced by continuous and monocultures, resulting in the carry-over of the pest infestation from one year to the next. Fourthly, the introduction of exotic crops to a new geographic region might render plants susceptible to local pests in the absence of defensive mechanisms and cause pest outbreaks (Pimentel, 1991). Therefore, pest problems and crop protection must be approached by holistic strategies.

Under such circumstance, the concept of Integrated Pest Management (IPM) is developed and implemented at the global scale for over 20 years (FAO, 2017). IPM is a knowledge-intensive process of decision making that combines various strategies such as biological, cultural, physical, and chemical methods and regular field monitoring of the crops. IPM focuses on the reduction of pesticide use to sustainably manage dangerous pests (FAO 2017). As an ecological approach, IPM promotes biological control (BC) methods in pest prevention and suppression among other strategies (Figure 1).

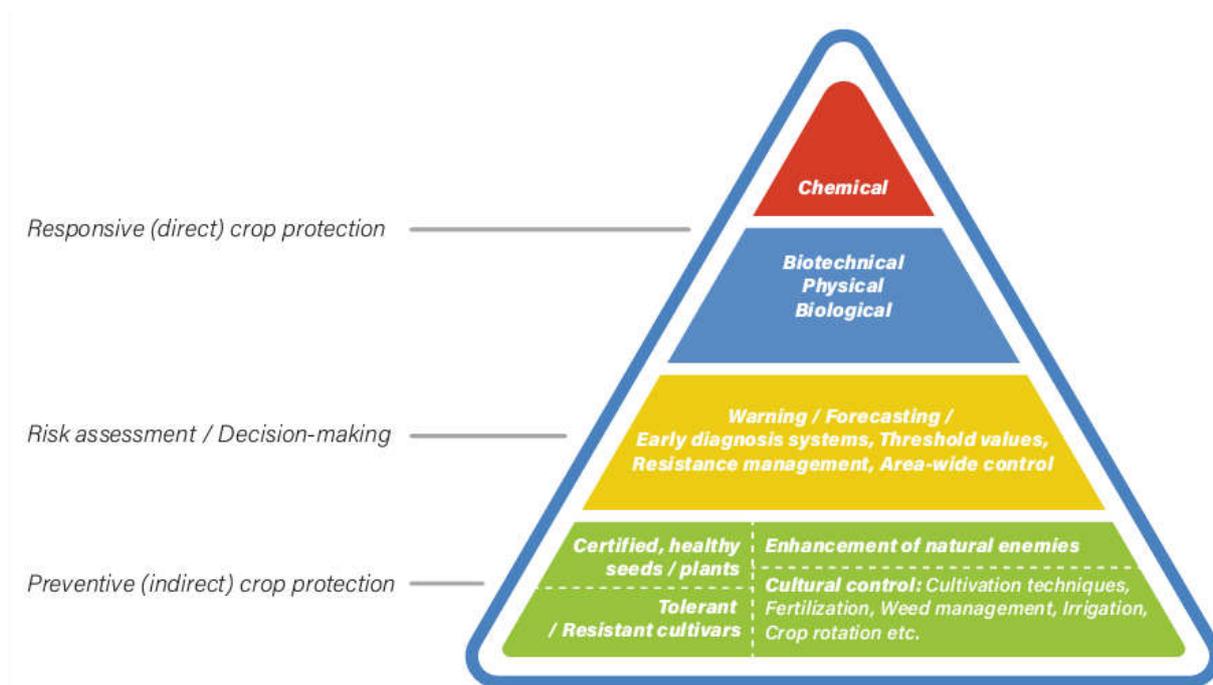
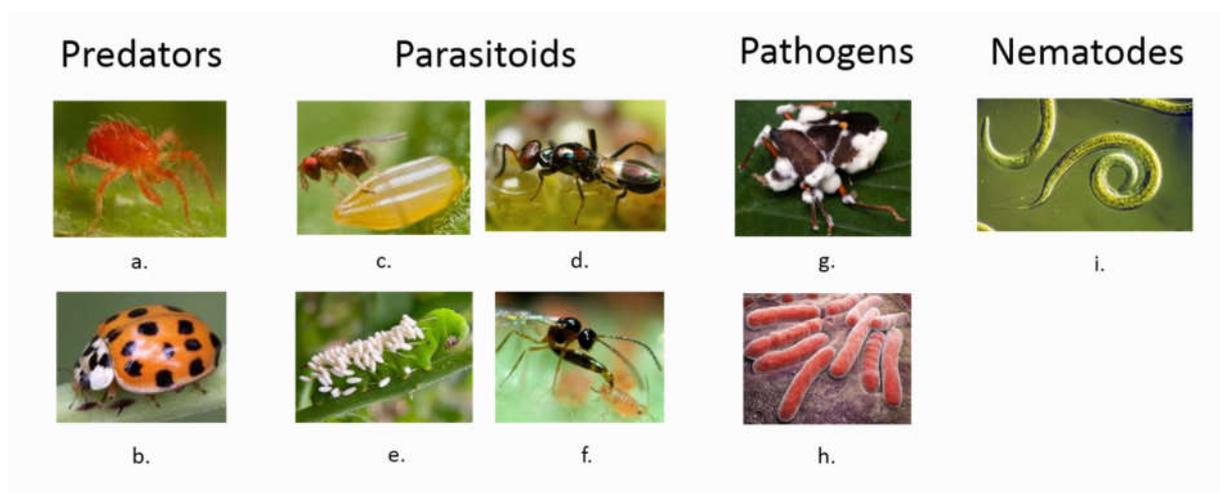


Figure 1. The concept of Integrated Pest Management

BC or the use of natural enemies to control pests has been a traditional agriculture practice up to now (van den Bosch *et al.* 1982). However, BC practices are still limited. Over 67000 pest species in the world, 300 pest species targeted to BC; among which only around 120 pest species have been controlled efficiently (Pimentel, 1991). Different types of natural enemies used as biological control agents (BCA) include predators, parasitoids (insects that lay eggs inside or on pests and eventually kill them), pathogens (such as fungi and bacterial toxins) and soil predatory nematodes (Heimpel and Mills, 2017) (Figure 2). BC has several advantages in compares to the chemical approach. Firstly, BC associate with few risks on environmental and public health (FAO, 2017). Secondly, as BCA are highly specific to few targeted pests in compare to pesticides, the efficiency of BCB are promising. Furthermore, BC could have sustainable effects as the released agents are self-powered, self-sufficient, and self-regulating and could permanently establish in the new environment. In such cases, further investments in BC are not required in contrast to the obligate annual applications of pesticides. Examples of other pest species that have been permanently controlled are numerous (Sweetman, 1958; DeBach, 1964; Huffaker, 1980). For example, the introduction of beetle predators in California (USA) has provided effective control of the cottony scale for over 100 years (Simmonds *et al.*, 1976; Pimentel, 1991). Three main strategies of BC are (1) importation or classical BC consists of the introduction of an exotic BCA to regulate a pest species. Over the past 120 years, more

than 2000 exotic BCAs were released worldwide to try to control pests in a new area (Bale *et al.* 2008). (2) Augmentative BC consists of inundative or inoculative releases of BCA and their genetical enhancement; (3) Conservation BC includes in managing the agricultural landscape to favor BCA (Debach and Rosen. 1991) (*Figure 3*). BC contribute up to US\$5.4 billion per year in the USA (Losey and Vaughan, 2006) merely for pest control, not to mention the value of controlling disease vectors. Recently, BC contributes more than US\$239 million per year in four US states in managing a single invasive pest, the soybean aphid, *Aphis glycines*, (Landis *et al.*, 2008; Schowalter, 2016). BC within the IPM practice is nowadays a post-pesticide-era approach to counteract the increase of pesticide resistance on targeted species and are a path toward sustainable agriculture.



*Figure 2. Types of biological control agents.*

*(a) predatory mites, (b) – ladybird beetles, (c, d) – egg parasitoids, (e) larval parasitoids, (f) adult parasitoids, (g) fungal entomopathogens, (h) Bacillus thuringiensis, (i) beneficial nematodes (Heimpel and Mills 2017).*

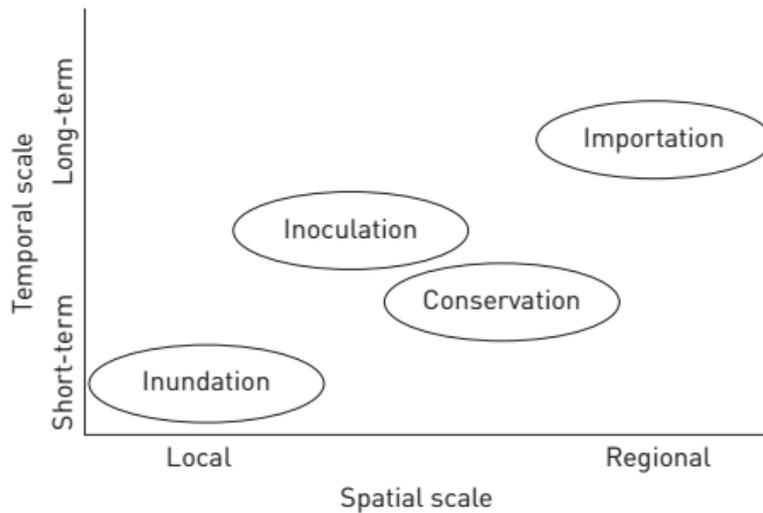


Figure 3. Spatial and temporal scales of the four main approaches of the BC process (from Klinken 1999)

### The risks of BC and requirements for BC practices

Despite all outstanding advantages, BC does not come without risks. The use of BCA also implies ecological risks, *e.g.* the extinction of non-target native species, or the unpredictable evolution of the BCA in a new environment (Kaser and Heimpel 2015; Roderick *et al.* 2012). Most of all, invasive alien species are considered among the most significant threats to global biodiversity. Exotic species once released could benefit from the lack of their natural enemies or the defensive systems of their food species and become dominant in the ecosystem through intra-guild predation (when one of two species (or both) competing for the same host or prey also consumes its competitor) (Roy and Wajnberg, 2008). As a result, the native biodiversity reduces. The rapid increase in introduced exotic species worldwide and the potential of these species to become invasive have ecological and evolutionary consequences (Olden and Poff 2004; Olden *et al.* 2006). Secondly, in many cases, the efficiency and the cost-effective of BC has been questioned. Many accidentally or intentionally introduced species fail to establish in their new range. Unlike chemical compounds, BCAs are sensible to many biotic and abiotic factors from the ecosystem and from the rearing conditions through ecological interactions. Therefore, the BCA efficiency is not thoroughly predictable. Thirdly, of those alien species that do manage to establish many have negligible effects and some species, often those introduced with agriculture and forestry, are even considered beneficial and desirable (Williamson 1999). Lastly, when the BCA are parasites or parasitoids, the

selective pressure upon pest hosts by parasite populations can cause rapid evolution in the pest hosts (Lamichhane *et al.* 2016). Therefore, BC practices require a deep understanding of the ecosystem.

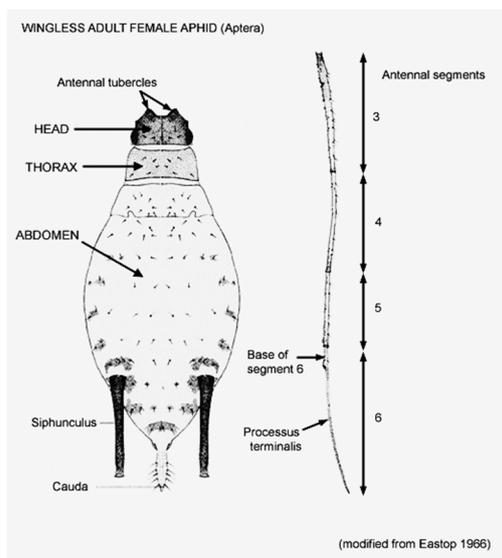
BC comes with the concept of keeping pests at an economically acceptable threshold. Often, low levels of populations of some pests are needed to keep natural enemies in the field, and IPM aims to reduce pest populations to avoid damage levels that cause yield loss. Therefore, IPM strategies, mainly BC requires understanding the crop ecosystem as a basis for right crop management decisions and are specific to each crop variety, country, region, and location (FAO, 2017). The efficiency of the BCA depends on several factors including (1) their biological traits (2) interactions with their surrounding environmental conditions, the so-called species niche, and (3) their specificity toward the ecosystem they are released in (Roderick *et al.* 2012). Also, risk assessment is an essential component in the development of any biological control strategy (Roy and Wajnberg, 2008). The prior study of a potential BCA focuses on its BC efficiency and safety. Both parameters could be predicted through the initial evaluation of the BCA host specificity.

## 1.2. Aphid parasitoids as biological control agents

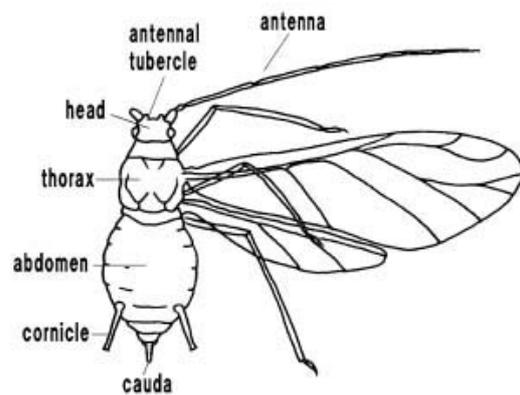
### 1.2.1. Aphids: biology, agricultural importance, and natural enemies

#### Aphid biology

Aphids (Hemiptera: Aphididae) are soft-bodied insects of less than 10 mm in length. Their body parts consist of a head, thorax, an abdomen, siphunculus, antenna, and cauda (Figure 4). They can secrete protective liquid, alarm pheromones, and honeydew. Aphids excrete honeydew, which are food resources for several insects such as ants and parasitoids to reduce the osmotic pressure of ingested phloem sap or host plant toxins (Auclair 1963). Among around 4300 aphid species, aphid pests belong mostly to the sub-family Aphidinae of two tribes: Aphidini and Macrosiphini (Kim *et al.* 2011).



A. Wingless aphids



B. Winged aphids

Figure 4. Aphid adult morphology

A: Wingless aphid with body parts as head, thorax, abdomen, siphunculus, antenna, and cauda. B: Winged aphids (from van Emden and Harrington 2007)

Aphids mainly reproduce by parthenogenetic (or asexual) to give birth to living young nymphs. Many aphid species reproduce sexually only under specific environmental conditions, such as during winter. Their parthenogenetic combined with "Russian dolls" reproduction whereby a

mother aphid carries both her daughters and their granddaughters allows populations of aphids to increase rapidly (Stern, 2008).

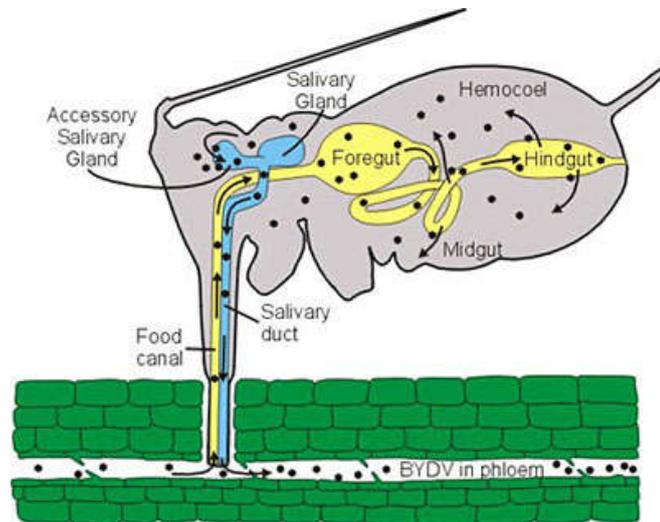


Figure 5. Aphid internal morphology

(picture of The American Phytopathological Society 2017). Salivary gland excretes saliva to plant phloem and help aphids to avoid the plant immune system. During the phloem sucking process, aphids could also transmit viruses.

Aphids feed on the phloem of plants, which an unbalanced source of nutrients, rich in sugars and low in amino acids. They rely on obligate endosymbionts, for nitrogen-deprived compounds (Pérez-Brocal *et al.* 2011). The bacterial symbiont, *Buchnera aphidicola* Munson, Baumann and Kinsey (Enterobacteriaceae) has a gram-negative cell wall and locate within the host body cavity (Baumann 2005). The *Buchnera* provides its host with essential amino acids and obtains nonessential amino acids from the host (van Hemden, 2007).

### Agricultural importance of aphids

Aphid crop damage is among the most serious of agricultural and horticultural problems. Aphids cause damage mostly by feeding and transmitting viruses. For example, effects of aphid feeding and associated virus injury on grain crops in Australia resulted in potential economic costs of \$241 and \$482 million/year, respectively (Valenzuela and Hoffmann, 2015). Aphid-feeding effects may remove plant sap to plant death, and through salivary secretion, they could manipulate the plant's physiological functions to their advantages (Figure 5). Over 200 aphid species are known to be virus vectors. Their saliva secretion is phytotoxic, causing

opportunistic plant diseases and make them powerfully prevalent vectors (van Hemden, 2007; Stern, 2008). Aphids could develop rapid resistance to pesticides (Bass *et al.*, 2014; Herron and Wilson, 2017). IPM of aphids aims to promote BCA and minimize the BCA effects on nontarget species. Strategies include cultural control methods, for example, decreasing ant populations, using ultraviolet-reflecting films to repel winged aphids, or interplanting pollen and nectar source plants among crop rows to promote natural enemies (Sorensen, 2009).

### **Natural enemies**

Natural enemies of aphids are mainly predators and parasitoids. Predators include ladybird beetles (Coccinellidae), lacewings (Neuroptera), hoverflies (Syrphidae), gall midges (Cecidomyiidae), and predatory bugs (Anthocoridae). Parasitoids include wasps of the large family Aphidiidae and several genera of Aphelinidae (van Hemden, 2007).

#### 1.2.2. Aphid parasitoids: biology and application in biological control

Insect parasitoids, their phytophagous hosts, and their host plants compose a significant proportion of the world's biodiversity (Hawkins, 1994). They represent one of the most critical and best-investigated groups because of their vital role in biocontrol as natural enemies of aphids (Zikic *et al.* 2017).

Parasitoids are parasite species whose larvae develop by feeding on the bodies of other arthropods, usually insects (its hosts) (Godfray 1994). Hymenoptera is by far the most species-rich insect order concerning the number of parasitoids (La Salle & Gauld, 1992). Among them, the subfamily Aphidiinae includes more than 400 described species worldwide, all of them parasitizing aphids (Hemiptera: Aphididae; Sanchis *et al.*, 2001; Petrović *et al.*, 2014). This group is extensively studied due to its essential role in biological control of agricultural pests, *e.g.* Hawkins & Cornell (1994); de Conti *et al.* (2008). However, their identification remains problematic as several species within genera have high morphologic plasticity or are phylogenetically close, and consequently difficult to identify (Kavallieratos *et al.*, 2001; Tomanović *et al.*, 2003, 2007; Stanković *et al.* 2015). Indeed, Derocles *et al.* (2016) suggested aphid parasitoids are cryptic complex by comparing the morphology and the genetic distances based on COI gene sequences of various generalist parasitoids.

## Parasitoid biology

The entire development of immature aphid parasitoids in the Aphidiinae and the Aphelinidae group occurs within the host aphid. Aphid parasitoids are considered in the middle of the "predator–parasite" spectrum because of their feeding mode shift during their life cycle. From egg to larvae, they adopt a parasitic mode by feeding on a live host. From larva to mummy stages, they take a predator mode by eating their host. During oviposition, the female lay eggs inside the aphid. The egg then hatches and get through three larval instars (O'Donnell 1987). During the second instar, the larva spins its silk cocoon and turns into a pupa; during that period the cuticle of the aphid hardens and dried and leaves an exoskeleton called mummy (Quicke 1997). The parasitoid only kills the aphid host during its last larval instar by consuming all tissue inside the aphid. The emerging parasitoid adult cut a hole to escape from the mummy.

Upon emergence, the female parasitoid mates and starts to search for aphid hosts. They may attack aphids on the same patch or the same plant where they were emerged (Weisser and Völkl 1997). If host density is low, she may disperse in search of a new aphid colony. In most species, the females search for hosts within a few meters (Weisser and Völkl 1997; Langhof *et al.* 2005). However, some species may disperse over 100 km in a year (Cameron *et al.* 1981).

Aphid parasitoids locate potential hosts in responding to signals from host and host plants (Royer and Boivin 1999). These cues for host finding could be visual, sensory or volatiles. Visual and volatile signals from plants induced by aphid feeding serve as long-range cues to locate aphid patches. Once an aphid colony has been located, the female aphid parasitoids adjust their level of exploitation based on several short-range cues associated with aphids such as sensory cues, color, or kairomones (Powell *et al.* 1998). Aphid parasitoids show clear preferences towards specific aphid species and aphid instars, which is based on host quality (Barrette *et al.* 2009). Patch residence time depends on aphid colony quality such as the size (Pierre *et al.* 2003), the distance between potential resources (Tentelier *et al.* 2006) and the presence of competitors (Le Lann *et al.* 2011, Wajnberg 2006).

### *Life-cycle of juvenile parasitoids inside aphid hosts*

The parasitoid wasp (in our example is *Aphidius ervi*) lay the egg in the haemocoel of the host aphids (

A.

B.

Figure 6). During their development, immature parasitoid produces an embryo structure with a thick wall to protect eggs. The structure is thought to adapt to the deficient nutrient reserves of *A. ervi* eggs which are fluid-filled, yolkless, and contain only few lipid globules. Under nutrient constraint, early egg development depends on how fast the embryo uptake resources from its host and defend against the immune systems. The embryo complexity of *A. ervi* different from other taxa-closed parasitoids and shared-host parasitoids, i.e. *Praon pequodorum* (Martinez *et al.* 2016, Sabri *et al.* 2011).

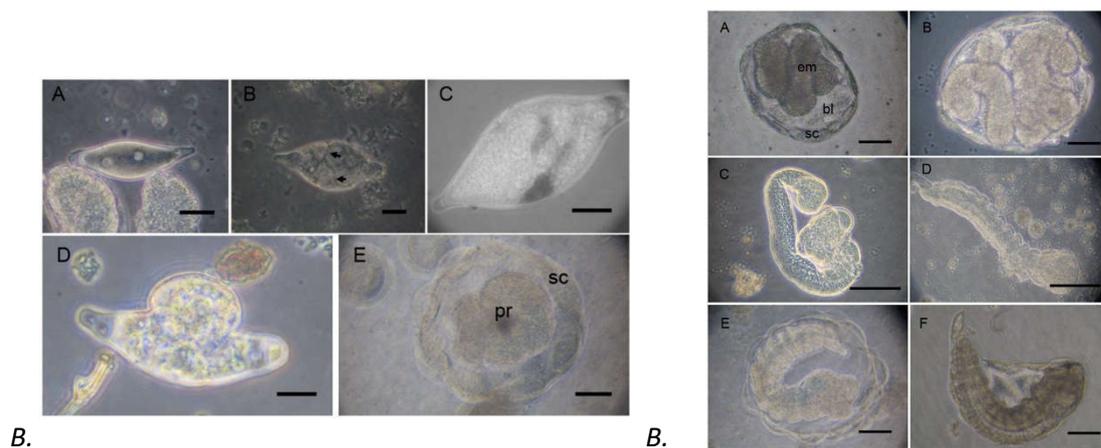


Figure 6. Egg development from oviposition to first hatching

A: Stage 1 - egg oviposition and hatch

B: Stage 2 - from egg hatching to larval development (from Sabri *et al.* 2011).

The larval midgut of the hymenopteran parasitoid *Aphidius ervi* transport nutrients from aphid organ to the haemocoel, provide most of the organic molecules necessary for rapid insect development, especially L-amino acids in general, and leucine (Fiandra *et al.* 2010).

### 1.2.3. Co-evolution of parasitoids and aphid hosts

The *Red Queen hypothesis* (RQH) (Van Valen 1973) indicating that antagonist species would co-evolve in an arms race between consumer attack and prey defenses as counter-responses, was proved by several studies (Agrawal *et al.* 2012). For instance, plant-aphid – parasitoid coevolve through their defense/virulence traits and specialize their strategies: plant against pest and aphid against parasitoids (Martinez *et al.* 2016). The alternative RQH (Lapchin and Guillemaud 2005; Ibanez *et al.* 2012) state that the co-evolution is unequal within a pair of consumer – prey; the prey's defenses often cost expensive and require compromise, so the higher trophic species likely win the race. This characteristic, called asymmetric are also observed on the host-parasite (Dybdahl and Lively 1998) and plant – pathogen pairs (Clay and Kover 1996).

Parasitoid suffers strong selection pressures from the resistance of aphid hosts. They strictly co-evolve with their hosts as they must face the full host immune response (). The host-parasitoid model hence provides the insight of species interactions at both molecular, ecological, and evolutionary levels.

### 1.2.4. The significance of parasitoid host specificity in biological control

The roles of parasitoids in biological control are well stated in the literature (Boivin *et al.* 2012; Nega 2014; van Emden and Harrington 2007). They are essential ecosystem service providers and mainly help to regulate pest populations (Godfray 1994; Godfray & Shimada, 1999). Parasitoids are used widely in the BC because they could target specific host species (Bass *et al.* 2014). However, the release of exotic parasitoids could increase the extinction risk for indigenous species (Jervis 2005). As a result, both efficiency and risk of a potential BCA must be assessed before being released. These characteristics depend on host specificity of parasitoids. For example, specialist parasitoid agents are anticipated to be efficient in host use pattern, to be safe for the environment and to establish well in the context they are

released following classical BC approach (Gagic *et al.* 2016; Klinken 1999) (see more chapter 1.1.9).

Table 1. Specialists vs generalists: pros and cons in biological control

<b>Trade-off hypothesis</b>	<b>Specialist</b>	<b>Generalist</b>
Ecological safety	+++	-
Pest control efficiency	++	+
Establishment success	++	+
Adaptability	-	++

*Annex 1. Physiological defense mechanisms of aphids and parasitoid counter-defenses (adapted from Vinson 1990, (Basu et al. 2016), Züst and Agrawal 2016, Poirie and Coustau 2011, Gerardo et al. 2010)*

Plant defenses	Aphid offenses/counter defenses	Aphid defenses: resistance	Parasitoid counter defenses: resistance
<p><b>1. Avoidance</b></p> <p>a. Escape in time plasticity in allocation patterns and developmental rates</p> <p>b. Escape in space</p> <p>c. Chemical escape repellent production, no attractant</p> <p style="padding-left: 40px;">a. Morphological escape</p> <p style="padding-left: 40px;">b.</p> <p>2. Resistance</p> <p>a. Morphological resistance hairs, spines, hook sticky glands, immobilizing insects or puncturing their body wall</p> <p>b. Mechanical resistance squirt-gun</p> <p>3. Host recognition From wounding, feeding or mechanical damages</p> <p>a. Herbivore-associated</p>	<p><b>1. Behavioral avoidance</b> feeding/oviposition choosiness</p> <p>2. Behavioral counter defenses/offense</p> <p>- Vein cutting, trenching, leaf rolling, mining</p> <p>- Gardening</p> <p>- Gregarious feeding</p> <p>3. Biochemical counter defenses</p> <p>- Actively manipulate host plant nutrition &amp; defense</p>	<p><b>1. External, behavioral</b></p> <p>- avoidance</p> <p>- escape</p> <p>- mimicry</p> <p>- repellency</p> <p>2. External, physiological</p> <p>- gut pH</p> <p>- Cuticular barrier</p> <p>- Deterrents and anti-microbial agents</p> <p>3. Internal-external</p> <p>- Reflex bleeding</p> <p>- Cuticular encystment</p> <p>4. Host recognition signal production from 4 pathways</p> <p>- Toll, immunodeficiency (IMD)</p> <p>- c-Jun N-terminal kinase (JNK),</p> <p>- Janus kinase/Signal transducers</p> <p>- activators of transcription (JAK/STAT)</p>	<p><b>1. Resistance due to a protective coating</b></p> <p>a. Coating an egg</p> <p>b. Coating larvae</p> <p>2. Resistance by host attrition</p> <p>a. Rapid development and feeding by host</p> <p>b. By teratocytes</p> <p>3. Resistance to organ occupation</p> <p>c. By pseudogerms</p> <p>d. By gregarious habit</p> <p>4. Resistance by an enveloping membrane</p> <p>a. Parasitoid embryonic membrane</p> <p>b. Host-derived membrane</p> <p>5. Resistance due to the stage of host attacked</p> <p>a. Insect eggs</p> <p>b. Young larvae</p> <p>6. Resistance to the activity of parasitoid</p> <p>a. By a parasitoid secretion</p> <p>b. By physical</p>

<p>molecular patterns (HAMPs)– Chemicals, e.g. fatty acid-amino acid conjugate (FAC), benzyl cyanide – Enzymes: Glucose oxidase, <math>\beta</math>-glucosidase – Proteolytic fragments of plant protein or enzymes from plant chloroplastic - ATP synthase b. Talking tree: volatiles emitted from infested plants</p>			<p>repulsion of defense reaction</p>
<p>4. <i>Various toxic compounds</i> a. Chronic (quantitative) defense: Large/complex molecules reduce digestibility / nutrition (tannins, lignins, cellulose, silica, etc). b. Acute (qualitative) defense: Small/simple molecules target specific insect system. -Toxic amino acids -Toxic proteins - Proteinase inhibitors (=PIs) - Allelochemicals</p>	<p>Detoxification of toxins: cytochrome P450 monooxygenase (P450), esterase, glutathione-S-transferase (GST) • Target site insensitivity • Rapid excretion • Sequestration of toxins</p>	<p>5. Internal to the immune system a. Coagulation b. Humoral (body fluids) - Inducible factors + antibacterial proteins + lysozymes - constitutive factors + lectins (agglutinins) + phenyloxidases - cellular + phagocytosis + nodule formation + encapsulation 6. External by bacterial symbionts - primary symbionts - secondary symbionts</p>	<p>Handling the insect immune system 1. Avoidance - hide eggs in an organ that is inaccessible for aphid's hemocytes -adhere eggs to the host fat body - avoidance of host immune system by mimicking host tissue in the protective egg layers 2. Evasion a. Molecular mimicry b. Cloaking (Stealth) c. Rapid development in host d. Target proliferation 3. Destruction</p>

<p>(=secondary compounds)  + cyanide,  glycosides, alkaloids,  terpenoids,  flavonoids  + saponins,  furanocoumarins,  indoles,  phytoecdysteroids  - Signaling  hormones  + JA (jasmonic acid), Ethylene (ET),  SA (salicylic acid)  + abscisic acid (ABA), auxin,  gibberellic acid (GA),  cytokinin (CK),  brassinosteroids (BR)</p>		<p>- bacterial phages (toxins)  7. Arm-race  - Sequestration and use of plant toxins to kill larval parasitoids.</p>	<p>a. Blockage of the immune system  b. Attrition  c. Destruction of responding cells  4. Suppression  a. Interfere with recognition  b. Interfere with response  5. Subversion  a. Develop despite host response  b. Development aided by the host response</p>
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### 1.3. Ecology of host specificity

The study of host specificity in model host-parasitoid models is important considering the ecological services provided by parasitoids as BCA (see chapter 1.1). Understanding of the ecological specialization of parasitoids provides a solid background for the design of BCA risk and efficiency assessments, and the prediction of impacts of the potential BCA on an ecosystems. In return, the study of host specificity plays a key role within the theme of ecological specialization, which is one of the fundamental concepts of evolutionary ecology and the most studied question in the XX<sup>th</sup> century (Sutherland *et al.* 2013). Aphid parasitoids co-evolve with their hosts, which in turn co-evolve with host plants because aphids themselves are plant parasites (see chapter 1.2.3, Boivin 2012). The model plant-aphid-parasitoid could shed light on how organisms interact and evolve, as well as the impacts of these interactions, *e.g.* bottom-up and top-down forces on ecosystems, which is also a fundamental question in ecology (Sutherland *et al.* 2013, see chapter 2.3).

#### 1.3.1. Ecological specialization concept

Ecological niches are a set of biotic and abiotic conditions in which a species can persist and maintain stable population sizes (Futuyma and Moreno 1988, Devictor 2009). Ecological specialization means the pattern of one species adaptation or resource utilization in its niche. Ecological specialization holistically describes the 'niche breadth' (or 'niche width') of one species. This concept disentangles the roles of one species in interactions with its surrounding, answers questions like why and how one species fit its environment, what happens next in case of perturbation. Understanding of ecological specialization shed light on mechanisms by which communities shaped from collections of species assemble (Mouillot *et al.* 2007); to predict outcomes of organism responses threaten by environmental fluctuation (Wiens 2016); the direction of community shift and impacts of community shift on the ecosystem (Devictor *et al.* 2010a, Nock *et al.* 2016).

The ***fundamental niche***, as known as "potential specificity," represents the total multi-dimensional ecological space in which a species could persist (Futuyma & Moreno 1988). Potential specificity is determined by interactions between species genotype and environment (Poisot *et al.* 2012). The ***realized niche***, as known as "realized specificity," is the ecological space in which a species persists (Futuyma & Moreno 1988). The realized specificity

reflects the impact of ecology, chance events and history on potential specificity (Bolnick *et al.* 2003; Devictor *et al.* 2010; Poisot *et al.* 2012). These concepts in host specificity assessment correspond to different scales of these tests where laboratory tests give information of fundamental host range and field tests give information of realized host range (see chapter 1.4.4).

### 1.3.2. Shades of ecological specialization: specialist vs. generalist species

The degree of specialization of one species, (as known as the specificity) is evaluated by its niche breadth, as known as or spectrum of resources they can use (Futuyma and Moreno 1988) and niche relatedness (phylogenetical or geographical clusters) (Jorge *et al.* 2014). A specialist occupies a narrow niche, and a generalist fills a large niche. As ecological niches are multidimensional, *i.e.* consisting of habitat, diet breadth, etc; the degree of specialization one species could be different at each dimension. For example, one parasitoid could be habitat specialist and host generalist (Vet and Dicke 1992). However, the concept of specialist and generalist is also relative and context-dependent. Comparing host specificity of a predator and a parasitoid as BCA, a predator is relatively generalist because it could feed on prey from different families, but a parasitoid attacks hosts from only one family (Jervis 2005). Among predators, omnivores are considered more generalist than carnivores. Among parasitoids, the one attacks over 20 host species is a generalist in compare to the one attack only one host species (Zikic *et al.* 2017). Therefore, the term host specialist/generalist in this study is applied in a pairwise comparison among species share same food items: (relative) specialists and (relative) generalists. Specificity also depends on the measured dimensions such as habitat and patch. The habitat is the location of plant hosts on which suitable aphid hosts occur. Similar to the definition of host specialist or generalist, habitat specialists exploit few habitats when generalists can detect and forage several (Stilmant *et al.* 2008). The patch is the location of aphid hosts on plant hosts. A patch generalist shows the same fitness in one patch or another, while a patch specialist shows similar fitness in its specific patch compare to others (Rosenzweig 1981). The specificity of each dimension could be different, *e.g.* one parasitoid could be: (1) host and habitat specialist, (2) host specialist but habitat generalist, (3) host generalist but habitat specialist and (4) host and habitat generalist (Vet and Dicke 1992).

Specialization can also be viewed at different levels of biological organization, *e.g.* among species in a community or individuals within populations. As such, the processes of specialization can involve the diversity of populations in different environments or the variety of genotypes within a population on same environment types (*Figure 7* *Erreur ! Source du renvoi introuvable.*, Poisot *et al.* 2012).

The debate about specialist/generalist raises the need for re-defining these terms. Also, the measurement of ecological specialization should be clarified in specific contexts, *e.g.* individual- or population-level. Given the multidimensional and context-dependent characteristics, the definition, analyses, and evaluation of species specialization are hence indispensable and are indeed central stones of various studies (Devictor *et al.* 2010a; Dennis *et al.* 2011; Loxdale *et al.* 2016; Krasnov *et al.* 2011; Straub *et al.* 2011). The relation between different degrees of multidimensional specificity of parasitoids is still unknown and could be interesting to study.

### 1.3.3. The continuum of specialization patterns: specialist - generalist

*“The one who eats everything must not treat with contempt the one who does not, and the one who does not eat everything must not judge the one who does, for God has accepted them.”* Romans 14:3 | NIV |

In any network, both hypotheses of dominant generalists and dominant specialists exist and are supported by empirical evidence. Among those hypotheses, one could prevail over others depending on the ecological networks, and new evidence found. Moreover, the criteria of “specialist” or “generalists” is not clear due to three reasons. Firstly, the concepts of specialist or generalist are context-dependent and multidimensional (Loxdale, 2010). Secondly, in each dimension, there is indeed a continuous spectrum of the degree of specialization without clear cut between specialist/generalist (Krauskopf and Fabricant, 2014). Thirdly, ecological specialization is not static but dynamic. Species could evolve through two directions under environmental pressures, specialism to become more specialists, and generalism to be more generalists. The situation raises the importance of host specificity study and the necessity of having clear, quantifiable criteria for being specialist or generalist and possible evolutionary tendency of specialism/generalism.

## Efficiency vs. plasticity, specialist vs. generalist

To survive and adapt to a specific niche, one organism must possess the ability of exploit specific resources, which is called **efficiency**; and the flexibility to change according to the environment, called **plasticity**. There are different paradigms which predict how the two competencies evolve in specialists and generalists. Debate histories and evidence for specialization hypotheses are listed as following.

In the host-parasitoid network, the popular paradigm of "the jack-of-all-trades is master of none" assumes one species faces a trade-off between its ability to exploit a broad range of resources and its efficiency to use a specific resource (May and MacArthur 1972). In other terms, the 'trade-off' model forecasts generalists are less efficient but more flexible than specialists. The 'resource-breadth' paradigms assume the ability to exploit a broad range of resources supports the efficiency to use a specific resource (Brown 1984). The 'resource breadth' model predicts generalists are both more efficient and flexible than specialists. As a result, generalists are more competent and abundant because they have more choice of food in both quantity and species diversity. (Krasnov *et al.* 2004; Williams *et al.* 2006; Rader *et al.* 2017; Hawro *et al.* 2017). Finally, the alternative hypothesis states evolution not necessarily involves trade-off (Morand and Guegan 2000) or "trade-off," and "resource-breadth" are context-dependent (Fry *et al.* 1996; Forister *et al.* 2012; Pinheiro *et al.* 2016).

In the predator-prey network, "the rich get richer" paradigm suggest generalist predators are more abundant than specialists as they can optimize nutrient intake in reducing accumulation of toxic compounds (Freeland and Janzen 1974; Pulliam 1975; Karban and Agrawal 2002; Stohlgren *et al.* 2003; Weise *et al.* 2010). The "body size" principle argues generalist consumers are at the lower abundance and rarer in the community because they are at higher trophic levels and eat hosts/preys of a broader range of body size (Cohen *et al.* 2005).

In the mutualistic networks, *e.g.* pollinators-plants, the "trade-off" between pollinator effectiveness and resource breadth prevail. Specialist pollinators are believed to be more efficient in their duty but more sensitive to environmental perturbation than generalist flower visitors (Larsson 2005). However, Ashworth *et al.* (2004) found evidence against this prediction that under habitat fragmentation, both generalists and specialist are similarly

susceptible. Among pollinators, plant generalist pollinators have been believed to be more abundant (Raguso 2008). Recently in a review, Krakos and Fabricant (2014) found a continuum of specialists and generalists among flower visitors in 26 *Oenothera* taxa.

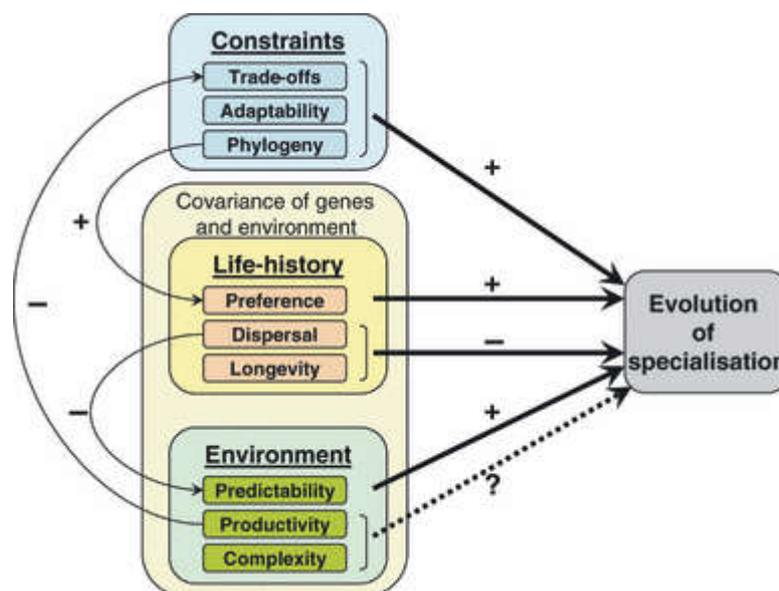
### **Who would win in nature and evolutionary races, specialists or generalists?**

Overall, in the host-parasitoid network, the trade-off paradigm is more popular and widely accepted (Straub *et al.* 2011). The trade-off model based on arguments that specialist organisms physically and behaviorally adapt to few hosts, so they must be more efficient than generalists. The trade-off also means that specialist species can only tolerate a limited range of environmental conditions. Consequently, due to disturbance caused by climate change and human activities, specialists face a higher risk of extinction under environmental perturbation as they fail to switch hosts (MacKinney 1997; Devictor *et al.* 2008, 2010; Colles 2009; Christian *et al.* 2009; Chacón and Heimpel 2010) and could be highly constrained by a heterogeneous habitat (Gagic *et al.* 2016). Under the weight of evidence of the evolutionary dead-end of specialists, specialist abundance has nowadays considered an indicator of sustainability (Fanelli and Battisti 2015). In the classical BC, generalist species are thought to have several advantages over specialists such as establishing better in a new landscape, surviving in low-abundant resources, tolerating environmental stresses and thriving in a large number of habitats (Raymond *et al.* 2015). However, a recent meta-analysis proved that specialists establish in their native hosts more successfully than generalists even in a new environment (Rossinelli and Bacher 2015). The results could be explained by the fact that even though generalists could exploit a more extensive range of resources, their adaptation to homogeneous habitats, such as monocultures, is not so easy (Kassen 2002; Duffy 2007). Interestingly, there is a hypothesis both specialists/extreme generalists could survive in turbulence whereas intermediate specialists/generalists extinct (Poisot *et al.* 2012). The issue leads to further questions of species in the middle of the continuum specialists/generalists, called intermediate specialist/generalist, of their efficiency and plasticity. In some studies, they are thought to be not efficient, *e.g.* they could not discriminate their resources (Jorge *et al.* 2014), or not having good adaptation strategy (van Velzen and Etienne 2013). Intermediate specialist or generalist parasitoids could be potential subjects given the fact that the majority of parasitoid species, *i.e.* Aphidiinae subfamily is in the middle of the spectrum extreme

specialist – generalist (Zikic *et al.* 2017). The cut among specialist/intermediate specialist/generalist and the context should be emphasized at the first place in such studies

#### 1.3.4. Evolutionary mechanisms of ecological specialization

The evolutionary tendency of specialism/generalism under current global changes is actively debated throughout literature, which relates to mechanisms underlying those processes. Specialism is claimed to be an evolutionary dead-end, or more positively their extinction gives rise to generalists (Colles *et al.* 2009; Day *et al.* 2016). On the contrary, Loxdale *et al.* (2011) claim that generalism does not even exist because species must morphologically, behaviorally and genetically tolerate their niches under natural selection pressure; generalism is not favored in nature, or some generalist species are indeed cryptic or sequential specialists (Derocles *et al.* 2016; Desneux *et al.* 2009b; Joppa *et al.* 2009; Kaartinen *et al.* 2010; Mitrovski—Bogdanović *et al.* 2013). Combined those ideas, Dennis *et al.* (2011) argued specialism be driven by environmental fragmentation and generalism by heterogeneity. Pandit *et al.* (2009) suggest different mechanisms governing each group of habitat specialization that habitat specialists respond to species abundance and diversity or environmental factors and habitat generalists respond to dispersal processes. In other arguments, the authors considered the transition of narrowing (specialization) or broadening (generalization) one species resources is bi-directional and balance in nature (Nosil and Mooers 2005; Angosta *et al.* 2010).



*Figure 7. A conceptual model for the evolution of ecological specialization.*

*The two main forces affecting specialization are fundamental biological constraints and the covariance between genes and environment (from Poisot et al. 2011).*

Generalization may also occur at various levels. Bolnick *et al.* (2003) have emphasized that many apparent generalist species are in fact composed of a range of ecologically variable, individual specialists which are specialized on different resource or habitat types. Likewise, the population of individual specialists could get both advantages of being specialist/generalist, such as they are efficient at resource use, and the whole species could shift between different resources if necessary (Colles *et al.* 2009).

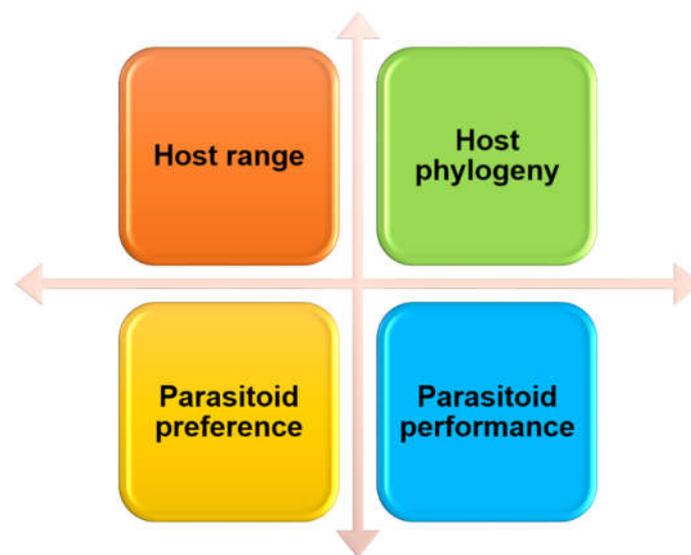
Overall, phylogenetic data prove that theory based on pure genetic trade-offs in host use not enough to explain the evolutionary picture. Multitrophic interactions are the necessary framework for understanding specialization that reveals the bidirectionality in transitions between generalist and specialist lineages (Forister *et al.* 2012).

#### 1.4. How to evaluate the host specificity of aphid parasitoids?

Here we present terms related to host specialization of one parasitoid by Klinken (2000)

- Host: suitable aphid for the reproduction of a parasitoid
- Host range: the sum of all hosts
- Host range breadth: host range, counting on taxonomy diversity among those hosts
- Host specificity: = host range breadth x host relative acceptability (and/or) suitability

Host specificity could be evaluated under different dimensions (*Figure 8*), first of all, is evaluated by the number of aphids one parasitoid can attack and develop on (Stary 1981). For example, the Aphidiinae subfamily comprises numerous specialist species parasitizing few aphid hosts, but some generalists can parasitize dozens of aphid species (Kavallieratos *et al.*, 2004; Starý 2006; Tomanović *et al.*, 2009; Benelli *et al.*, 2014).



*Figure 8. Multi-dimensions of the host specificity*

The definition of host specificity is broadened to consider the phylogenetical distance between aphid hosts, as the phylogenetically broader host ranges ( ) (Poulin and Mouillot 2005). Moreover, the field host ranges are also reflected parasitoid behavioral and physiological traits. Parasitoid behavioral traits (preference) are subsequent actions leading to host acceptance or rejection and measured by parameters such as the oviposition rate or preference index (Cock, 1978). Physiological host range (performance) are the number and taxonomy diversity of species that the agent could complete development on if attacked.

Parasitoids are proved to show a preference for some hosts, regardless of host availability or their performance on these hosts. The performance on aphid hosts, *e.g.* survival rate, parasitism rate, emergent rate, sex ratio, offspring size (Jervis 2005) could reflect the host quality for parasitoid development. Both these behavioral and physiological traits could determine parasitoid population on a specific host species and therefore their specificity toward hosts ( ) (Klinken 2000).

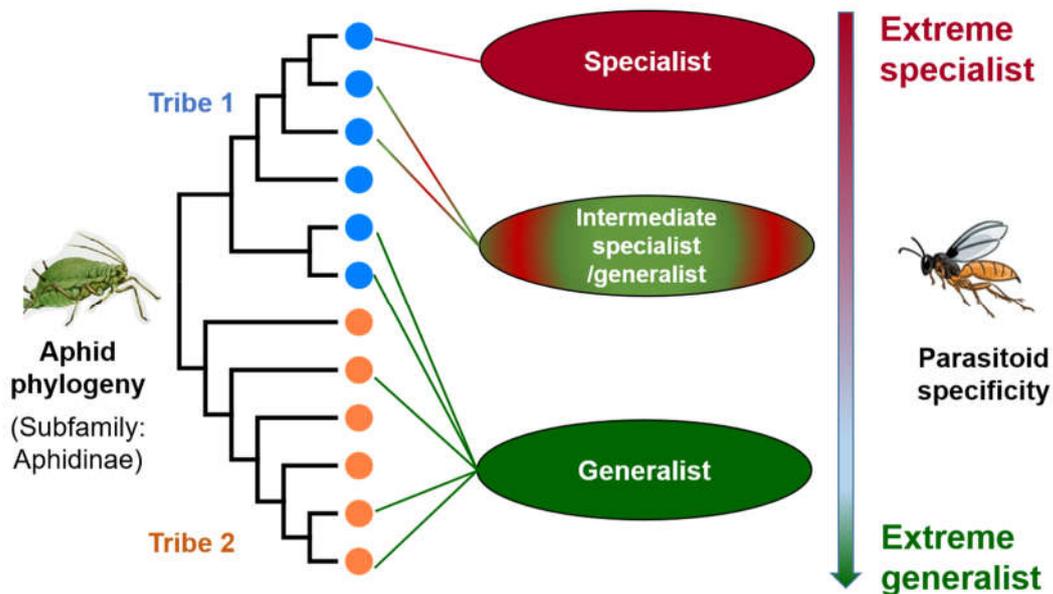


Figure 9. A gradation model of host specificity from specialist to generalist based on the number of host species and host phylogeny

(Adapted from Gagic 2016, Poulin 2003; Helmus 2007; Desneux 2012).

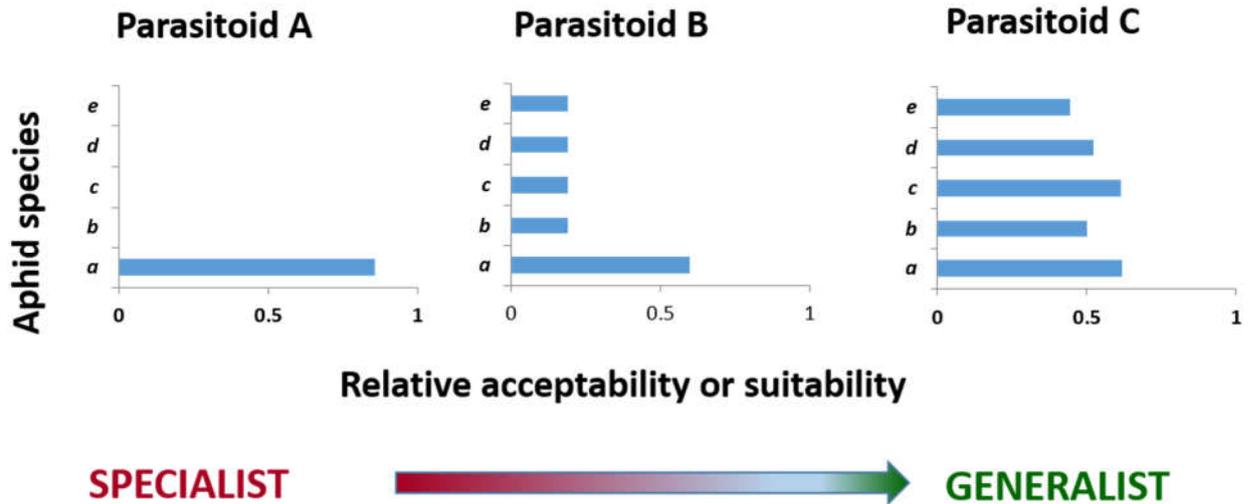


Figure 10. A hypothetical gradation of host specificity from specialist to generalist based on relative host suitability/preference (Adapted from Klinken 2000, Poulin et Mouillot 2005, Godfray 1994). (A): specialists accept or develop well on only one host species, (B): intermediate specialist/generalist accept/develop on several host species but prefer/perform well on only few host species, (C): generalists which accept and develop relatively well on several host species.

#### 1.4.1. Host specificity index

##### **Host specificity index for parasite-host interaction**

In a review of host specificity indexes, Skoracka and Kuczyński (2012) identified two host specificity indices as valuable to evaluate the fundamental host specialization, which is the taxonomic index of specificity (Poulin and Mouillot 2005) and the Rohde index (Rohde and Rohde 2008) as listed below.

**Taxonomic index of specificity** (Poulin & Mouillot 2005):

$$S_{TD^*s} = \frac{\sum_{i=1}^h \sum_{j=1}^h \omega_{ij} P_{si} P_{sj} [i < j]}{\sum_{i=1}^h \sum_{j=1}^h P_{si} P_{sj} [i < j]}$$

where:  $S_{TD^*s}$ – taxonomic index of specificity of species s,  $\omega_{ij}$ – taxonomic distinctness between host species i and j (the number of taxonomic steps required to reach a node common to both),  $P_{si}$ ,  $P_{sj}$  – prevalence (the frequency of hosts that are parasitized) of species s on host species i and j, respectively.

This index measures the average taxonomic distinctness of all host species used by a given parasitoid species. The value of this index is inversely proportional to specificity: the greater the taxonomic distinctness between host species, the higher the values of the index.

**Rohde index of specificity** (Rohde & Rohde 2008):

$$S_s = \frac{\sum_{i=1}^h P_{si}/r_{si}}{\sum_{i=1}^h P_{si}}$$

where:  $S_s$  – Rohde index of specificity of species  $s$ ,  $h$  – number of all examined host species,  $P_{si}$  – mean prevalence of species  $s$  on  $i^{\text{th}}$  host,  $r_{si}$  – rank of host species  $i$  (the species with the highest prevalence has rank 1).

This index considers the uneven distribution of parasites across different hosts. In the numerator of this index, prevalence is weighted by the inverse rank (hosts which are less used contribute less to the sum). Thus, the value of the index is more stable and less affected by accidental or ephemeral occurrences of parasite species. The higher the value of this index, the higher the host specificity. The Rohde index allows evaluating relative host prevalence and compares the specialization level between parasitic species encountering different host ranges, either by experiments, and either by geographical observations. (Rohde and Rohde 2008).

The two indices reflect different dimensions of the specificity concept. The taxonomy index of specificity for one parasite species is calculated primarily by the **taxonomic distinctness** among hosts in considering the **prevalence** of the parasite in these different hosts (Poulin and Mouillot 2005). It thus accords to the most widely accepted definition of the “host specificity” concept (Skoracka and Kuczyński, 2012). The Rhode index is measured by the **prevalence** of the parasites but not the phylogenetic difference among hosts (Rohde and Rohde 2008). It could be a complement to the taxonomy index in case the tested hosts are phylogenetically close, *e.g.* aphid hosts on the same subfamily have the same taxonomic distinctness values so the taxonomic index could be similar.

#### 1.4.2. Host specificity specter of Aphidiinae parasitoids

Zikic *et al.* (2017) develop from the classification of Aphidiidae host specificity groups (Starý, 1981a) to a spectrum of host specificity of Aphidiinae parasitoids, which mostly relies on aphid phylogeny and phylogenetic relations among aphid hosts (, 3). The spectre is: 1) monophagous: a single host species, (2) narrow oligophagous: two or more species of the same aphid genus, (3) moderate oligophagous: species of two or more genera of the same aphid subfamily, (4) broad oligophagous: species of two or more genera of two or more subfamilies of the same aphid family, (5) polyphagous: species of several genera of two or more aphid families.

Table 2. Host specificity of five *a priori* defined categories displayed over host range. A—monophagous, B—narrow oligophagous, C—moderate oligophagous, D—broad oligophagous, E—polyphagous (from Zikic *et al.* 2017).

Host specificity group	Species host range	Generic host range	Subfamily host range	Average host range (species-genus-subfamily)
A	1	1	1	1–1–1
B	1–12	1–2	1	4–1–1
C	2–11	1–4	1–2	3–2–1
D	5–29	2–11	1–4	9–5–1
E	12–168	4–58	1–7	50–19–2

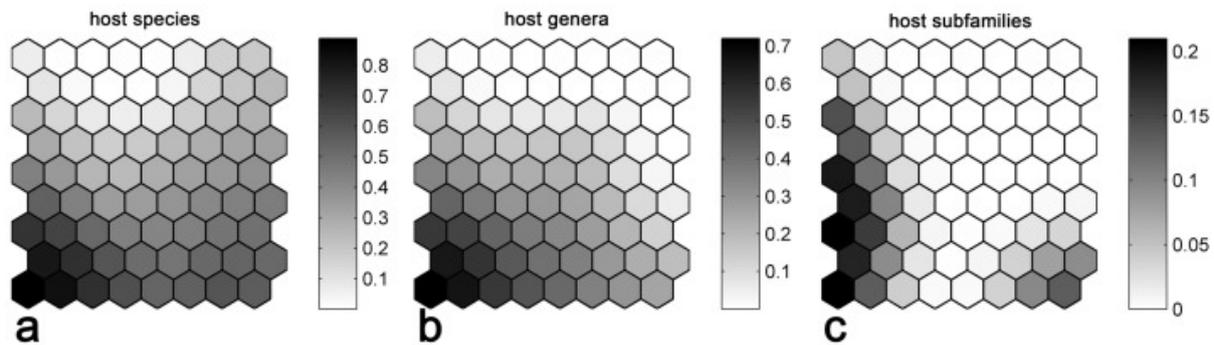


Figure 11. Visualization of aphid host diversity parameters in grey scale with the presented range of variability for parameters: (a) aphid host species, (b) aphid host genus and (c) aphid host subfamily. Bars for each map represent transformed values of the number of analyzed members. The shade of black for each parameter is highly correlated with its maximum value in the study. A lighter shade of grey indicates a decline of these parameters. The majority of the group Aphidiinae are intermediate specialists within the group besides a few species are extreme specialists and generalists" (from Zikic et al. 2017).

The study of Zikic *et al.* (2017) provides criteria to classify aphid parasitoids by their host ranges, which now remains challenging due to high specificity of parasitoids.

#### 1.4.3. The optimal foraging behavior: correlation preference-performance.

The parasitism process includes several steps from host finding until successful adult emergence (Desneux *et al.* 2009a, 2009b). Regarding behavior traits that are relevant in parasitism, the first step is **host detection** which involves: habitat location (plants), patch location (plant parts where hosts locate) and host location (individual aphids). Parasitoids locate patch and hosts based on physical, visual or chemical cues. They rely on both plant and aphid cues. Aphid host original cues are highly reliable but low detectable. Plant-original odors are less reliable but easy to detect. Host-induced plant volatiles is both detectable and dependable (Rehman and Powell 2010). Host specialist parasitoids show specificity to chemical cues from plants and aphids (Vet and Dicke 1992). The second step is **host evaluation**, when the female encounters the potential host, evaluates it with antennae and ovipositor probing. The cues for host evaluation could be host color, shape, and texture, chemical and sensory signals (Rehman and Powell 2010). If an aphid is accepted as a host, the female parasitoid will decide to oviposit and deposit an egg at the third step of **host acceptance**. In the case of Aphelinidae family, the parasitoid will determine to feed or oviposit

on hosts. Sometimes aphid movements or defense could trigger the attack of parasitoid (Desneux *et al.* 2009a, 2009b, figure 12).



Figure 12. Host selection process

from host detection – acceptance – successful sting (adapted from Desneux *et al.* 2009)

After parasitoids successfully deposit an egg inside aphid hosts, the suitability of its offspring depends on the capacity of host manipulation (to defend the host immune system) and regulation (the parasitoid development may affect its host development, behavior, physiology, and biochemistry). Female parasitoids inject venoms and particles into aphid hosts during oviposition to increase the host suitability for their eggs and larvae ().

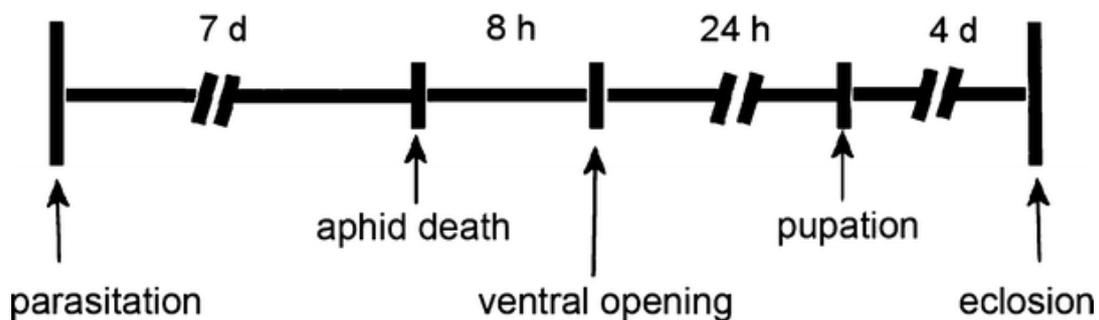


Figure 13. Immature *Aphidius ervi* pass through different stages inside aphid hosts from eggs – 1<sup>st</sup> instar – 2<sup>nd</sup> instar (aphid death) – 3<sup>rd</sup> instar (pupation, mummy forming) – 4<sup>th</sup> instar (eclosion) (from Gutierrez-Ibanez *et al.* 2007)

The success in the control of a pest is dependent upon parasitoid behavior of host selection and their host suitability. Overall, the 'optimal foraging strategy' stands as a central paradigm of host selection pattern (Jaenike 1978). This hypothesis states that "mothers know best" - females try making best choices for the sake of their offspring - and is applied to multi-dimensions of specialization. The optimal foraging pattern is determined by the correlation between parasitoid preference and performance (Desneux *et al.* 2009a). The correlation preference-performance could be a criterion of effective BCA because it proves that parasitoids have a good host selection capacity, which is essential in BCA assessment. For example, in classical BC, parasitoids with the optimal foraging will tend to have the preference on targeted aphids (which are high in density) will lead to higher suppression of the pest and success in biological control. However, on augmentative BC, parasitoid host choice of hosts to maximize offspring fitness will lead to the refusal of small size aphids and the patch leave before the pest has been suppressed to the desired level (Mills and Wajnberg 2008).

The pattern of the correlation of preference (adult oviposition) - performance (of offsprings) is not universal in all parasitic species such as aphids or parasitoids which means that other factors than mere host quality could drive parasitoid behaviors. There are examples of no correlation (Chesnais *et al.* 2015; Rivero and West 2005) or positive one (*e.g.* Singer *et al.* 1988; Ode *et al.* 2005; Desneux *et al.* 2009a; Moiroux *et al.* 2015) or both in one study (Mayhew 1997). This non-conclusive correlation is shaped by behavioral strategies of specialists/generalists, as specialists are behaviorally more selective than generalists (Gripenberg *et al.* 2010; Thompson 1988a; b). This non-correlation could also be determined by food quality, *i.e.* when food quality is low, the female might be less choosiness (Karban and Agrawal 2002; Price 1990). Another reason for the non-correlation is the capacity of host selecting, as specialists are more efficient in evaluating hosts than generalists (Straub 2011).

#### 1.4.4. The host specificity testing process in biological control

The host specificity testing scheme of a BCA () is now mandatory in BC industry and regulatory schemes. The assessment occurs at various scales (1) small area no-choice laboratory test (one parasitoid - one test species at a time; naïve females); (2) large arena choice test (one female - two or more species at a time, simultaneously or sequentially); (3) field test (release natural enemies in a non-target habitat with non-target species) (van Lenteren *et al.* 2006; Sands 1998). The BCA host specificity must be tested at the laboratory, greenhouse and field scales on both preference and performance on a wide range of aphid hosts including non-target and indigenous aphids. Only when the non-target impacts of the BCA are low, or the benefice outweighs the damage on non-targeted species that the BCA is recommended. The no-choice assays in step 1 provide information on the parasitoid fundamental host range as well as its behaviors when encountering aphid hosts. On the choice assays in step 2, the info shows learning mechanisms of parasitoids. In complementary by the understanding of a specific environment of applying the agent, the test results help to predict post-release outcomes such as the realized host range, the preference, the non-targeted hosts, and the ability of host switching (van Lenteren 2010, figure 14).

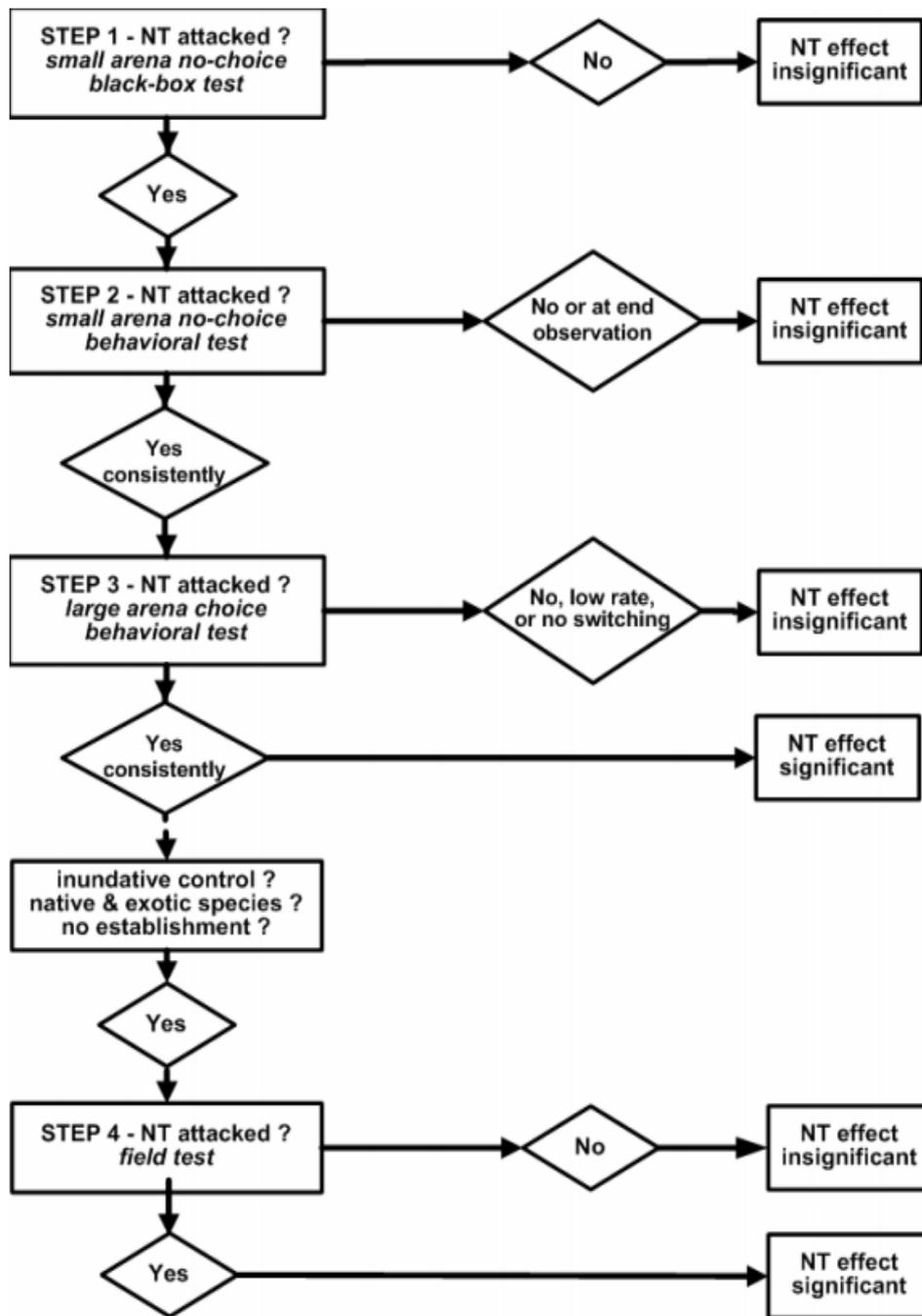


Figure 14. Testing schemas to approve one biological control agent - BCA as ecologically safe and get permitted to use this BCA in the field (van Lenteren 2010). NT stands for non-targeted species

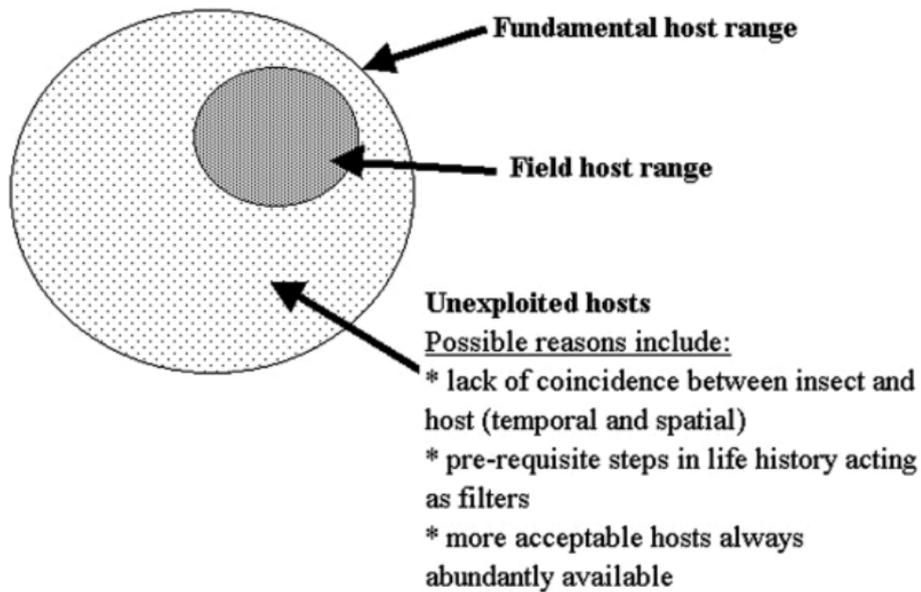


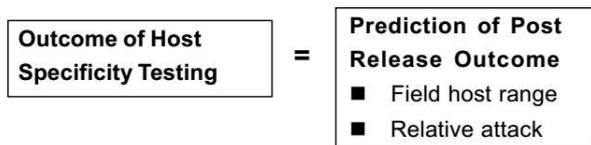
Figure 15. The comparison between fundamental host range tested in the laboratory and the realized host range in the field (Klinken 1999).

Among those steps, laboratory host specificity testing, which estimates the physiological host range of a BCA (5) provides perhaps the most crucial evidence used to predict post-release host range, *i.e.* the ecological host range within the region of importation. However, given the physiological host range can include species that are not preferred but are suitable to complete development for the agent; the laboratory test can overestimate the agent's field host range and misinterpret its arranged risk/benefit. (Gilbert and Webb, 2007; Pemberton, 2000; Van Driesche and Reardon 2004; van Lenteren *et al.*, 2006, Haye *et al.* 2005). The host distribution, the lack of experience or the host preference and host density could also result in the difference between realized host range and the fundamental host range (Klinken 1999).

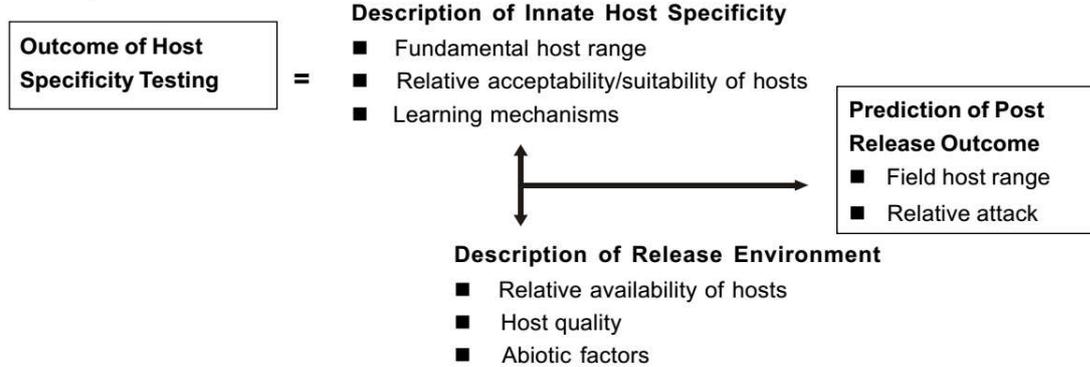
The host specificity testing outcomes occupy both description and assay roles. In one hand, the outcomes describe the parasitoid intrinsic host specificity, particularly the fundamental host range, the host preference ranking, the relative host preference/performance and their learning ability. In the other hand, parasitoid field efficiency, *i.e.* their field host range and behaviors could be predicted from the testing outcomes given information of the ecosystem such as plant and host density, plant and host quality, and abiotic factors (Klinken 1999, 6).

Figure 16. The implication of host specificity testing in biological control (Klinken 1999).

**A. Assay Role**



**B. Description Role**



## Chapter 2. Bottom-up and top-down forces in ecological network

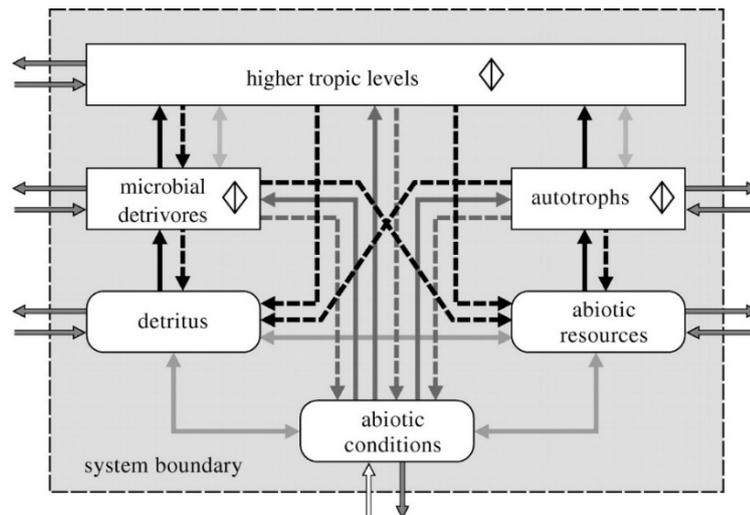
### 2.1. Ecological networks and interactions

Ecological networks are composed of the nexus of interactions among organisms. Ecological networks can be subdivided into three broad types: 'traditional' food webs, mutualistic networks and host-parasitoid networks (Ings *et al.* 2009, Hagen *et al.* 2012). Traditional food webs consist of trophic interactions (who eat who, *i.e.* predator-prey and primary consumer-basal resource relationship) and are backbones of an ecosystem (Hall & Raffaelli 1993). Host-parasitoid networks also contain trophic interactions. However, they concentrate on the particular types of feeding relationships between parasitoids and their hosts. Parasitoids are insects that lay eggs on or in the body of other insects, their hosts (Godfray and Shimada 1999). When the egg hatch, the larva consumes its hosts either immediately or after a delay during which the hosts are still alive. In the early stage, larva parasitoid has a close relationship to its host, similarly to parasitism. Finally, they always kill their hosts by feeding equally to predation. Mutualistic networks are non-consume networks. Three mutualistic networks receiving particular attention are (1) *pollination* between plants-pollinators, (2) *frugivore networks* between plants-seed dispensers, (3) *ants-plants* (Ings *et al.* 2009). Besides trophic interactions, non-trophic interactions also play significant roles in the composition and stability of an ecological network (Muller and Godfray 1999; Charles and Godfray 2004; van Veen *et al.* 2006; Sanders and van Veen 2012; Terborgh 2015; Frost *et al.* 2016; Mougi 2016). Interactions are the interplay of organisms with these biotic and abiotic factors. Olf *et al.* (2009) classify six main types of interactions in ecosystems. They are:

- (1) consumer-resource interactions,
- (2) interactions between organisms and abiotic (non-resource) conditions,
- (3) spatial interactions (inputs and outputs of energy, nutrients, organisms),
- (4) non-trophic direct interactions among organisms,
- (5) physical and chemical interactions among factors/compartments,
- (6) external forcing of abiotic conditions.

These six types of interactions potentially operate among three biotic and three primary abiotic compartments (Figure 17). The abiotic compartments are (1) abiotic resources, such as light, nitrate, ammonium, phosphate, consumed by autotrophs, (2) non-consumed abiotic

conditions, such as salinity, soil texture, sediment aeration, soil and water pH, temperature and (3) detritus, *i.e.* non-living organic material. The main three biotic compartments are (1) autotrophs that can harvest their energy, either from light or chemical sources, (2) microbial detrivores that break down detritus into mineral components, thus producing resources for autotrophs and (3) higher trophic levels that consume autotrophs, microbial detrivores and/or each other, and mineralize nutrients for autotrophs.



- 1) Consumer–resource interactions**  
 —→ effect of resources on consumers    - - -> effect of consumers on resources (depletion, production)
  - 2) Interactions of organisms with abiotic environmental conditions**  
 —→ response of organisms to abiotic environmental conditions    - - -> effect organisms on conditions
  - 3) Spatial interactions**  
 —→ energy, material, organisms and propagule inputs, outputs (including colonisation, dispersal)
  - 4) Non-trophic direct interactions (e.g., induced defence, behavioural modification, direct interference, pollination, toxicity etc.)**  
 - - ->
  - 5) Physical and chemical interactions**  
 <—>
  - 6) External forcing of abiotic conditions**  
 ==>
- ◇ unresolved networks of tropic and non-tropic interactions

Figure 17. An ecosystem consists of six types of interactions among three biotic and three abiotic compartments. Three abiotic compartments are (1) abiotic resources, (2) abiotic conditions, and (3) detritus. Three biotic compartments are (1) autotrophs (2) microbial detrivores and (3) consumers at higher trophic levels (from Olff et al. 2009).

Ecological interactions may be characterized according to parameters such as consume or non-consume, positive or negative/antagonistic effects on other organisms, reciprocal or unilateral, direct or indirect, obligatory or facultative, intraspecific or interspecific (Table 4).

Annex 1. A summary of direct and indirect interactions (adapted from Olff *et al.* 2009, Han Peng Ph.D. thesis 2014).

Sub-types of interaction	Effects on other organisms	Examples	References
<b>Consume-resource</b> <b>Herbivory</b> <b>Predation</b> <b>Parasitism</b>	- antagonistic (against each other) - direct - reciprocal	plants – herbivores preys – predators hosts - parasitoids	Polis <i>et al.</i> 1989 Olff <i>et al.</i> 2009
<b>Direct competition (intraspecies)</b> <b>Competition</b> - Apparent (two preys/host species share one predator /parasitoid) - Exploitative (two predators/parasitoids share one prey/host species)	- antagonistic - indirect - reciprocal	<i>intra-guild</i> , <i>inter-guild</i>	Holt 1977 Elias <i>et al.</i> 2013, Montoya <i>et al.</i> 2006
<b>Facilitation</b> <b>Mutualistic</b> <b>Facultative</b> <b>Obligate</b>	- benefits for both partners - indirect or direct - reciprocal	flowers – pollinators bacterial symbiosis - aphids	Callaway 2007 Oksanen 1988; Vandermeer 1980; Ulanowicz 1997
<b>Commensalism</b> One species obtain benefits such as food, shelter, or locomotion from another species without causing adverse effects	- positive - direct - unilateral	clownfish and corals	Olff <i>et al.</i> 2009 Mougi 2016
<b>Amensalism</b> One organism harm another organism without receiving any costs or benefits	- negative - direct - unilateral	Penicillium kills certain bacteria by producing penicillin	Olff <i>et al.</i> 2009
<b>Trophic cascades (higher trophic consumers suppress the abundance or alter the behavior of their prey, thereby releasing the next lower trophic level from their consumers)</b>	- positive - indirect - unilateral		Carpenter <i>et al.</i> 2008

In an ecosystem, forces are factors that have the power to affect the interactions and characteristics, *e.g.* population, the behavior of other species. Depending on their influences, forces could be driven, organizational or structural. Bottom-up forces are the influence of organisms at the lower trophic level, *e.g.* soil conditions or resources, to higher trophic forms (consumers). Top-down forces are the influence of higher trophic forms to lower trophic forms. For example, the predation has the force to control or suppress herbivore's population and imply cascade impact on plants, as they create a "free enemy space" for plants. Ecological interactions are also characterized by the direction of the forces.

One of the critical issues of a network study is to measure the strength of forces and interactions controlling network's structure, which are essential in applying such as BC or conservation (Agrawal *et al.* 2007; Evans 2016). Among six types of interaction, the external forcing of abiotic factors has not yet fully mentioned in the study of ecological networks (Olf *et al.* 2009). However, changing environment could disrupt an ecological network through interactions, *e.g.* mediated by plants (Power 1992). In reverse, ecological interactions could alleviate or aggravate the forces. The context such as species density and distribution, intra- and inter- competition, *e.g.* sharing hosts/prey, superparasitism or indirect interactions influence or even reverse the outcomes of forces. For instance, mutualism, *i.e.* rhizobacteria and plants could buffer impacts of environmental stresses across multi-trophic levels (Lescano *et al.* 2012; Marquis *et al.* 2014) and drive the outcomes of trophic cascades (Morales *et al.* 2008). Antagonism could evolve to mutualism under tolerance strategy of the lower trophic level, if the antagonistic risk is weak and the cost of tolerance is acceptable (for example the ant-aphid interactions (Oliver *et al.* 2009). The reverse of mutualism becoming antagonism also happens, *e.g.* among aphids and their facultative bacterial symbionts (Zytynska and Weisser 2016).

Ecologists measure interaction strengths by different parameters of (1) an individual link, *e.g.* specific maximum feeding rates, biomass flow along on a link, or (2) the impact of a change in the properties of one link or of a set of links, *e.g.* all links to and from a given species, on the dynamics of other species or on the functioning of the whole system (Olf *et al.* 2009). On the host-parasitoid networks, one parameter measures the strength of parasitism is the frequency of hosts that are parasitized called parasite prevalence (Berlow *et al.* 2004).

## 2.2. Bottom-up versus top-down forces

Among the dominant forces which influence the structure of an ecological network, bottom-up and top-down process are two primary control forces. In a bottom-up process, resources provide energy flow for the ecosystem against trophic levels. In a top-down process, consumers determine the distribution of energy flow at each trophic level (Montoya *et al.* 2006; Bukovinszky *et al.* 2008). Like the debate specialist/generalist, the debate of which forces control an ecological network, the bottom-up or top-down ones also endure in ecology. Substantial evidence supports both hypotheses, and no model entirely fit observation. The 'bottom-up' hypothesis states resources are primary control from bottom-up because resources are limited (Lindeman 1991; Mcqueen *et al.* 1986; Montoya *et al.* 2010). Plants have apparent primacy in food webs; their primary productivity is a fundamental control of higher trophic levels. Other plant attributes, such as architecture (*e.g.* Bernays and Graham 1988; Kareiva and Sahakian 1990) or chemical constituents (*e.g.* Price *et al.* 1980; Price and Clancy 1986) also have substantial effects on the performances and interactions of higher trophic levels. These other attributes, however, are often molded or constrained by plant growth rates, in either physiological or evolutionary time (Bloom *et al.* 1985; Coley *et al.* 1985; Oksanen 1990; Power 1992). 'Top-down' hypothesis states consumers at the top of trophic levels dominantly shape the network structure through regulation of plant consumers (Hairston *et al.* 1960; Menge and Sutherland 1976; Sanders *et al.* 2013). Invasive species could also control a new ecosystem through top-down forcing. Exotic species are favored by the absence of their traditional enemies as stated the '*enemy release hypothesis*' (Keane and Crawley, 2002) and/or their novice defensive chemistry - the '*novel weapons hypothesis*' (Callaway and Ridenour, 2004). Once successfully integrating into the network, they could shift their host range and the community structure (Harvey *et al.* 2010). The "exploitation ecosystems" hypothesis emphasizes on context-dependence of the bottom-up and top-down processes as control forces (Oksanen and Oksanen 2000), *e.g.* the resource availability. Bottom-up forces prevail in the ecosystem if resource deficiency is important. Given adequate resources, top-down predators control herbivore populations thus indirectly support plant productivity (Hunter and Price 1992). The strength of forces will weaken along food chains or when resources are opulent (Mcqueen *et al.* 1986; Terborgh 2015). The dominant forces also

depend on the community, *i.e.* above- or underground networks. In a forest ecosystem, Schuldt *et al.* (2017) found a significant top-down effect of the below-ground community (pathogens, symbionts, decomposers), which, in their turn, imply a strong bottom-up effect on aboveground species (herbivores, predators, parasites), the all mediated by the plant. On the contrary, abiotic factors had a strong plant-mediated bottom-effects on the aboveground community but not on the belowground one. Overall, these theories seem to complement mutually but not exclusive (Hunter *et al.* 1997). Further meta-analysis in the subject could be realized to compare between ecosystems and give hints about the control forces.

### **2.3. Bottom-up forces of abiotic factors on a tritrophic plant-aphid-parasitoid system**

#### 2.3.1. How could plant traits mediate bottom-up and top-down forces?

Plant traits that determine the tri-trophic interaction include species, nutritional quality, defenses against herbivores, mutualism with soil bacteria and fungi (van Veen 2015). The adaptation of each trophic level to the system are multilateral: plants tolerate or defense against herbivory. Aphids develop top-down offense or counter-defenses against plants, and they defend against parasitism from bottom-up. Parasitoids evolve offense or counter-defenses against aphids and by that indirectly protect plants from their herbivores. In reverse, plants reward their mutualist parasitoid by emitting semiochemicals locating plant hosts or producing nectar as food. However, plants might indirectly harm parasitoids through aphid "arm-race" strategy, as plant toxins sequestering in the aphid host body is lethal to larval parasitoids. The whole system is impacted by surrounding abiotic factors like temperatures, soil conditions, water. Through those interactions, plant quality influenced by abiotic factors might ladder up to the top levels of natural enemies and notably reduce their performance. Parasitoid adapt to the plant hosts of their aphid hosts, *e.g.* parasitoids on the same plants have the same enzyme families (Ryalls *et al.* 2017). Parasitoid performance, or more specifically parasitism rate change when aphid hosts feed on different plants (Jervis 2005). Moreover, plants could change parasitoid behaviors as their volatiles and color served as cues for host location (Kaplan 2012, Ortiz-Martinez *et al.* 2013). Plant toxins could indirectly harm to parasitoids if they are sequestered by aphids (Ibanez *et al.* 2012). The presence of plant mutualists, *e.g.* soil arbuscular mycorrhizal fungi, combined with aphid mutualists, can have

subtle - but significant - effects on plant fitness and insect success. The evidence is the counteract of two mutualist systems - soil fungi and aphid endosymbiont in a tri-trophic plant *Solanum* – aphid *Macrosiphum euphorbiae* – parasitoid *Aphidius ervi* could both benefit and harm to parasitoids (Bennett *et al.* 2016; Martinez *et al.* 2014; McLean and Godfray 2017; Sanders *et al.* 2016).

### **Plant defensive strategies and possible mechanisms**

Under constraint conditions, each species can resist, tolerate or avoid stress. While resistance refers to traits that reduce the amount of damage, tolerance refers to traits that reduce the impact of damage to species fitness. Several paradigms are proposed to explain and predict the plant “choice” of defensive strategies under specific circumstances. The "biochemical coevolution theory" of Ehrlich and Raven (1964) states one plant family acquire a complex of defenses that exclude all but specialist herbivores. The “plant apparency theory” (Feeny 1976) hypothesizes that when the risk of herbivory is high, *i.e.* plants are apparent to herbivores), plants invest on quantitative defenses such as expensive constitutive toxins that are effective against all generalist as specialist herbivores. Unapparent plants should invest in less-costly toxins (qualitative, induced) that are effective to most herbivores except specialists (20). Regarding the trade-off plant nutritional quality vs. defense, the “resource availability theory” (Coley 1985) predicts that fast growing plants on abundant nutrient soils should invest less in defenses because the damage costs of herbivory are low and plant loss is less important. The "growth-defense trade-off" states that high resource investment in defenses means lower resource availability for growth and higher herbivory resistance. The ‘slow-growth-high-mortality’ SG-HM hypothesizes that plants repulsive shields, *e.g.* tannins, fiber, and toughness, which only delay the development but do not kill herbivores, are useful only when plants interact with the third trophic level. Indeed, the slower growth of herbivores exposes them more to natural enemies, which increase their probability to be parasitized or eaten (Benrey and Denno 1997). Plant tolerance strategies include exible rates of photosynthesis and nutrient uptake, and plasticity in allocation patterns and developmental rates (Nunez-Farfan 2007).

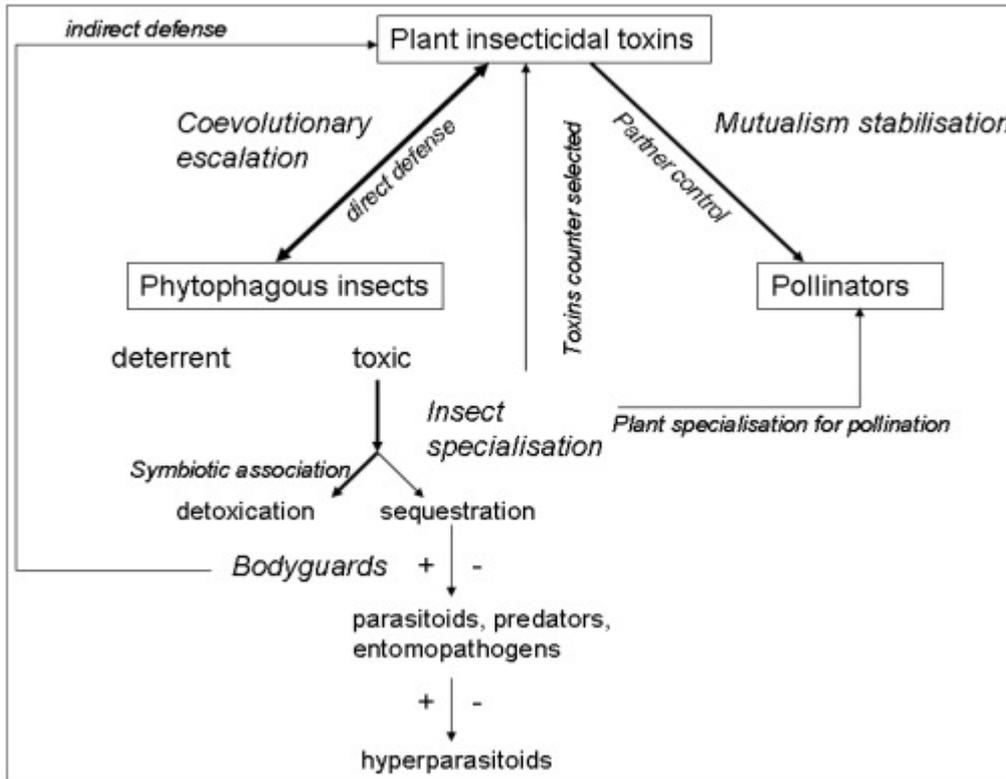


Figure 18. Bottom-up impact of plant insecticidal on the community.

Arrow size: the probable strength of the effect; the double-headed arrows: the co-evolution. + or - signs: positive or negative effects of plant toxins on higher trophic levels, respectively" (From Ibanez et al. 2012).

### 2.3.2. How could aphid traits mediate bottom-up and top-down forces?

Effects of multiple aphid traits on parasitoid specialization were demonstrated in the review of Gagic *et al.* (2016). Firstly, parasitoids rely on cues from aphid hosts to locate them (Rehman and Powell 2010). Those cues could be aphid odors like alarm signaling pheromones or kairomones (Outreman *et al.* 2010). In one study, *Aphidius ervi* refused wet aphid hosts, which could result from the parasitoids being unable to detect the host kairomones (Weinbrenner and Volk 2002). Female *A. ervi* were found to show active oviposition attempts to object with the color similar to those reflected by its primary host, the aphid *Acyrtosiphon pisum* (Battaglia *et al.* 2000). Aphid texture, shape and aphid body liquid are evaluated by parasitoid antennal and ovipositor probing (Rehman and Powell 2010). Secondly, aphids are both food resource and developmental environment of parasitoids. The host nutritional quality could be constraints for parasitoid survival. Female's diet might impact the fitness of

their juvenile offspring (Martinez-Ramirez *et al.* 2016). *A. ervi* offspring performance depends on host nutritional quality (Sequeira and Mackauer 1992). Host body size (Cohen *et al.* 2005) and host ages (Trotta *et al.* 2014) correlates with parasitoid body size, as parasitoid larval development is restricted by limited developmental volumes of aphid hosts, so do their adult sizes.

**Aphid defense/counterdefenses** - In the tri-trophic system, aphids must multilaterally defend against parasitism and counter-defend against plant immune system for their feeding. The vital defense mechanisms are aphid immune system (innate defenses) (Poirie and Coustau 2011, 2), symbionts-dependent defenses (acquired defenses) (Vorburger 2014) and 'arms-race' defenses (by sequestering plant toxins against natural enemies) (Züst and Agrawal 2016).

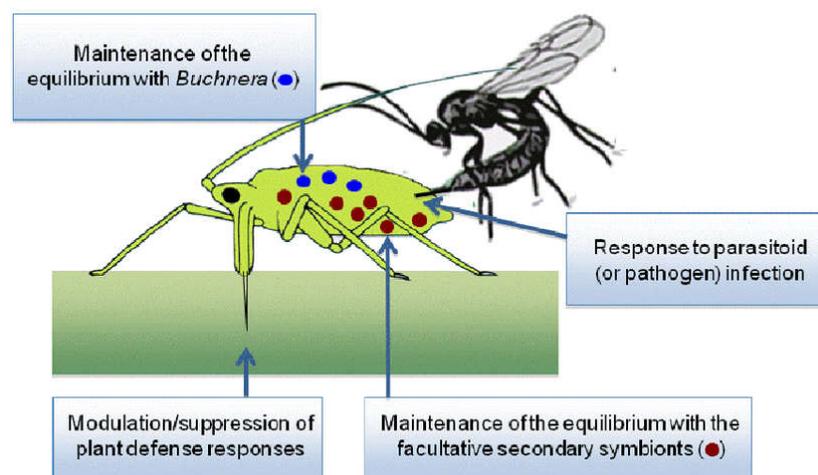


Figure 19. Aphid immunity interactions

Aphid immunity interaction with the host plant, the primary and secondary symbionts, as well as the pathogens or parasitoids (Poirie and Coustau 2011).

### 2.3.3. How abiotic stresses level-up to parasitoids through the tri-trophic interaction?

In the field, plants simultaneously face several stressors such as combined abiotic stresses (e.g. drought and heat, drought and cold), combined biotic stresses (e.g. leaf-chewing and sap-feeding insects), or combined abiotic and biotic stresses (e.g. drought and herbivores). The response of plants to stress combinations is unique and cannot be directly estimated from the impacts of each stress (Suzuki *et al.* 2014). Overall, when facing combined stresses plants

could have one of three strategies: (1) well-developed tolerance and poor defense, (2) well-developed defense and poor tolerance, or (3) something between these two extremes (van der Meijden *et al.* 1988; Cipollini *et al.* 2014).

The responses of plants to combined stresses depend on what came first and the severity of each stress. Ramegowda and Senthil-Kumar (2015) proposed four scenarios of combined stresses on plants (1). In the scenario 1, plants undergo combined stresses; water stress happens before pathogen infection. In the second scenario, plants sequentially expose to water stress then pathogen infection. In the third one, water stress and pathogens simultaneously happen. In the fourth one, plants undergo combines stress but being pathogen infested first. All scenarios could lead to two possible outcomes: plants increase stress resistance or stress susceptibility due to the same mechanisms.

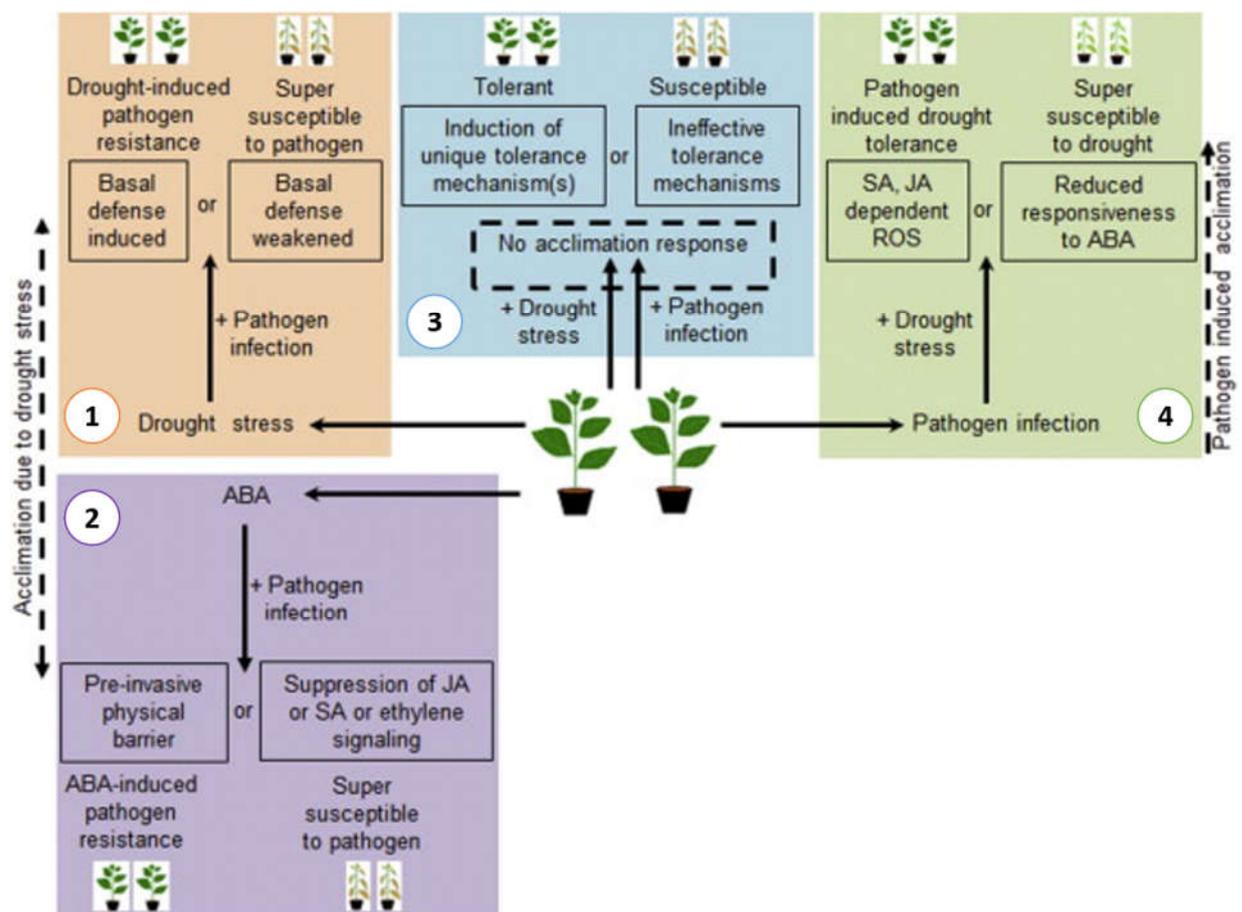


Figure 20. The potential phenotypic response of plants exposed to a combination of water stress and pathogen infection.

(1) Drought could induce or weaken basal defenses on plants which protect plants from pathogen infection. (2) The increase of ABA level could increase or decrease the stress-

induced gene expression. (3) Plants undergoing simultaneous stresses could develop tolerance to both or fail resistance to both due to exceeded damage. (4) Pathogen infection could increase SA, JA signaling in plants and prepare plants for the early stage of water stress or reduce resistant gene expression. Plant basal defenses are early and non-specific responses against pathogens (From Ramegowda and Senthil-Kumar 2015).

However, under stress combinations, plants apply complex mechanisms to cope with stresses resulting in contrast effects on other trophic species. Those mechanisms could be an adaptation at the physiological level, *e.g.* stomatal close, reallocate resources, or change volatiles emissions or toxin production. Those changes lead to plant food quality changes, as well as their interactions with parasitoids or mutualisms with under-ground bacteria and fungi. Regarding plant nutritional quality, herbivores might benefit from nutrient leakage of plants as the result of hastening senescence under mild and/or intermittent drought, as stated the "plant stress hypothesis." Under severe and/or continuous drought conditions, plants nutrient resources reduce as a trade-off for stress tolerance which diminishes herbivore fitness (Price 1991, Huberty and Denno 2004). At the same time, the hardened structure of plants, the stomatal closure or the increase of plant trichomes under stress may cause difficulty for herbivores in foraging (Couture et al. 2015). In term of plant immune system, the exposure to mild drought could activate the plant induced defenses such as trehalose and abscisic acid (ABA). Both regulators can increase the pathogen resistance of plants (Ramegowda and Senthil-Kumar 2015). Nevertheless, the trade-off between drought-tolerance and defense in the mustard lead to a decrease in levels of glucosinolate toxins function in defense against generalist herbivores (Alsdurf et al. 2013) and potentially reduce the mortality rate of natural enemies feeding those herbivores. Overall, one external force of abiotic stresses could change the interactions and the efficiency of each organism. The strength and result of abiotic bottom-up forces could be different to each plant-aphid-parasitoid complex.

As a conclusion, organism traits that influence interactions and might be influence by bottom-up forces in a tritrophic plant-aphid-parasitoid system are:

- Plant traits include species, nutritional quality, defenses against herbivores, mutualism with soil bacteria or fungi.

- Aphid traits include species, nutritional quality, defenses against parasitoids and counter-defenses against plants, mutualism with bacterial symbionts.
- Parasitoid traits include species, states (egg load and age), food resources, and counter-defenses against aphids (figure 23).

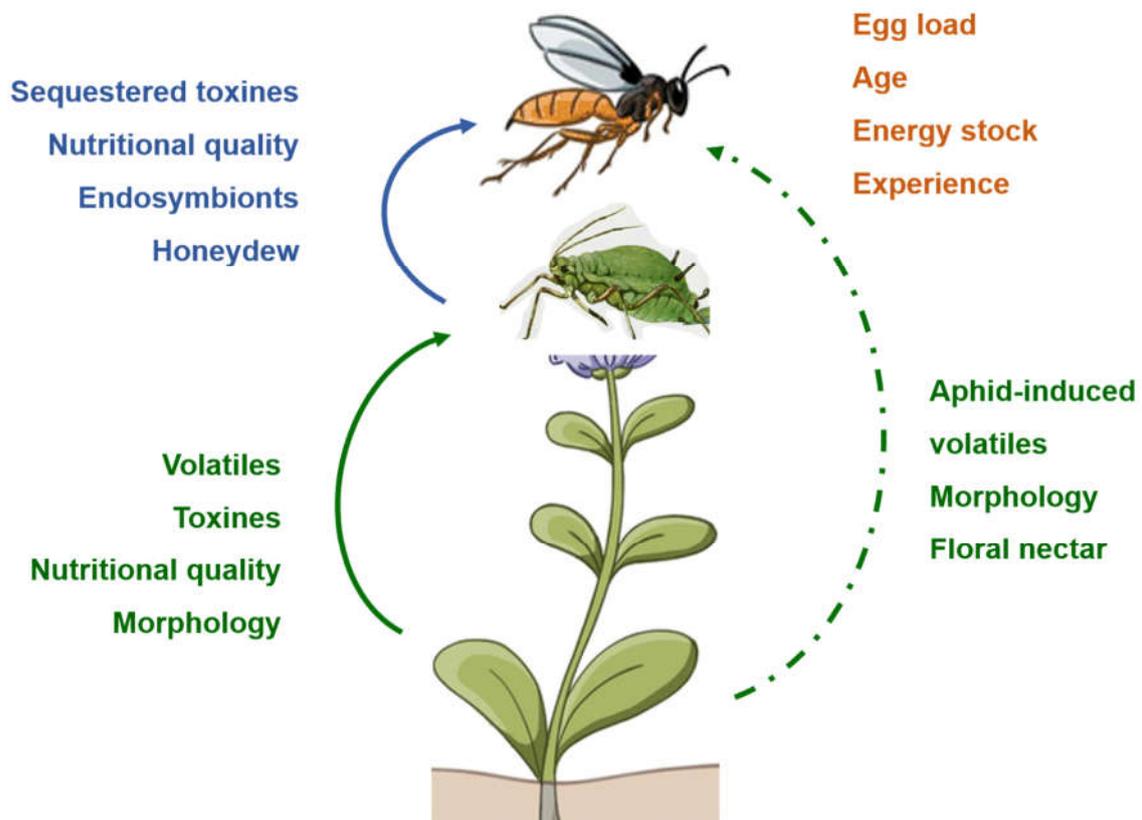


Figure 21. Impacts of plant, aphid and parasitoid traits on parasitoid host specificity. The green arrow and texts mean plant traits. The blue arrow and texts mean aphid traits. The orange texts mean parasitoid traits. The continued line means direct effects. The dashed line means indirect effects.

#### 2.3.4. Bottom-up and top-down forces in biocontrol context

In the BC, the use of natural enemies represents top-down forces to regulate lower trophic level, herbivore pests. The efficiency of BCA to suppress pest populations depend on the presence of other biotic factors and interactions of the ecological networks (Prado *et al.* 2015, figure 18, 19), *e.g.* the presence of aggressive predators or resource abundance (Denno and Finke 2006). The BCA effectiveness could also depend on abiotic factors affecting the network. Previous studies showed that continuous water and/or nitrogen limitation adversely

impact both herbivorous insect and omnivore predator (Han *et al.* 2014a) as well as parasitoid BCA (Romo and Tylianakis 2013). On the contrary, intermittent drought might benefit pest and cause aphid outbreaks in the field (Banfield-Zanin and Leather 2015).

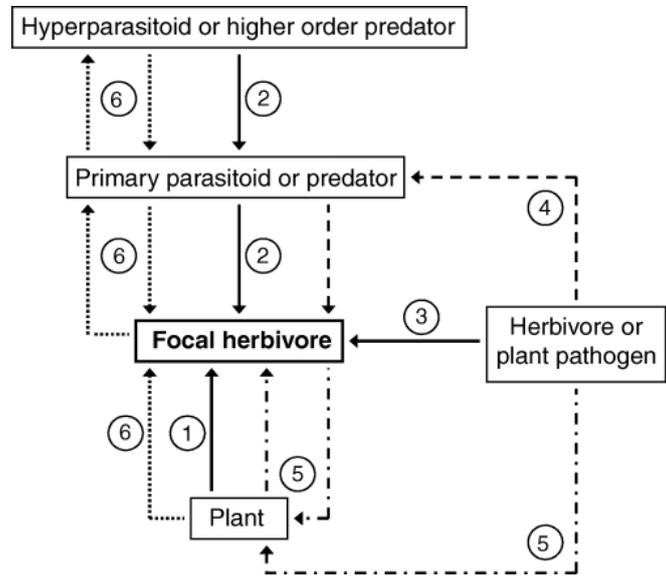


Figure 22. *Multitrophic level interactions might affect herbivorous insects 1. direct bottom-up effects, 2. direct top-down effects, 3. direct competition, 4. apparent competition, 5. induced defenses, 6. host-plant quality affecting natural enemies (from Gripenberg et al. 2007).*

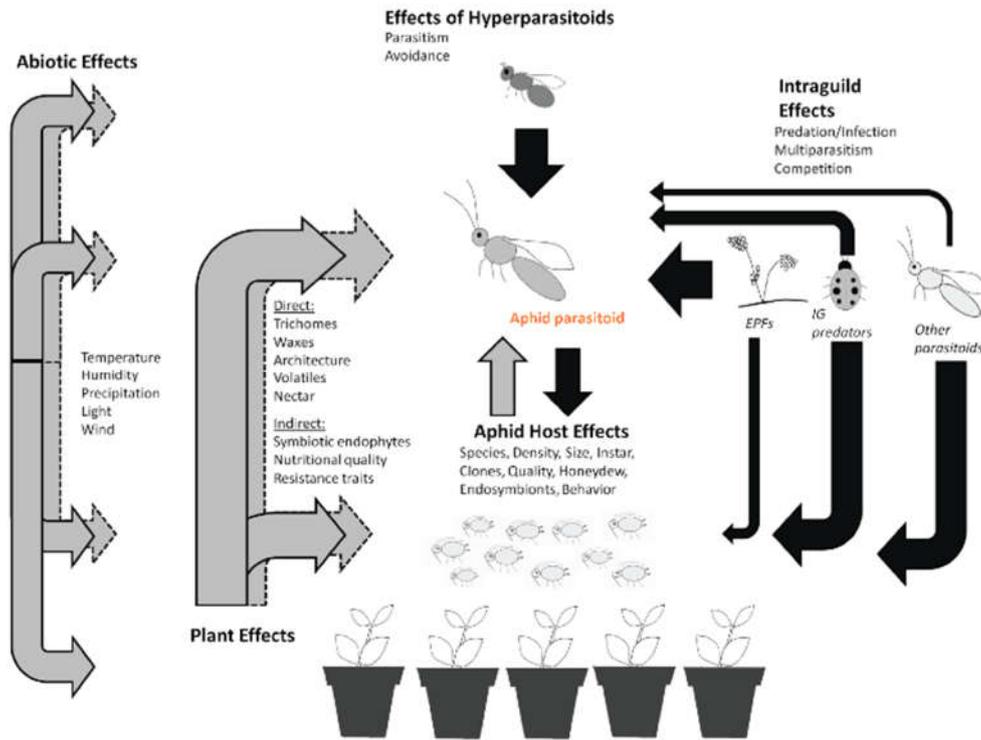


Figure 23. Ecological interactions impact the efficacy of aphid parasitoids in greenhouse conditions. The effects are on either the wasp or the pest. Full black arrows: direct negative effects, full grey arrows: direct positive or negative effects; dashed grey arrows: indirect positive or negative effects; the size of arrows approximately corresponds to the size of the effect; EPF: entomopathogenic fungi (from Prado et al. 2015).

## Chapter 3. Objectives

In this study, we investigated factors modulating the host specificity of aphid parasitoids. The principal question, illustrated in figure 24, is:

***Could abiotic environmental stresses imply bottom-up effects on parasitoid host specificity?***

**Objective 1. Find a parasitoid where we could detect both negative and positive effects of bottom-up forces on parasitoid host specificity: an intermediate specialist/generalist (chapter 4)**

- Task 1: Assess the fundamental host ranges of three aphid parasitoids, *Aphidius ervi*, *Diaeretiella rapae* and *Aphelinus abdominalis* by the host range testing method.
- Task 2: Classify these three parasitoids and other three parasitoids with known host range in a spectrum of host specialist/generalist through the preference-performance correlation and the host specificity index

**Objective 2. Evaluate the bottom-up effects of key abiotic stress on parasitoid host specificity and underneath mechanisms (chapter 5)**

- Task 3. Review the impact of abiotic factors on the plant-aphid-parasitoid tritrophic system in the literature.
- Task 4. Evaluate *A. ervi* host specificity under water limitation in comparison to optimal water supply:
  - Task 4a. Testing preference and performance of *A. ervi* on good quality aphid hosts under the bottom-up effect of water limitation
  - Task 4b. Comparing bottom-up effects of water limitation on the host specificity of *A. ervi* on various plant-aphid complexes

**Our hypotheses are:**

(1) In host generalist parasitoids, there is no correlation between their preference for and performance on aphid hosts. The correlation and host specificity index could be combined to find a cut between specialist and generalist parasitoids.

- (2) The preference and performance of parasitoids could be impacted both negatively and positively by bottom-up effects of abiotic factors, depending on the plant-aphid complexes.
- (3) Host specificity could modify in both direction: parasitoids could become either more generalist or more specialist.

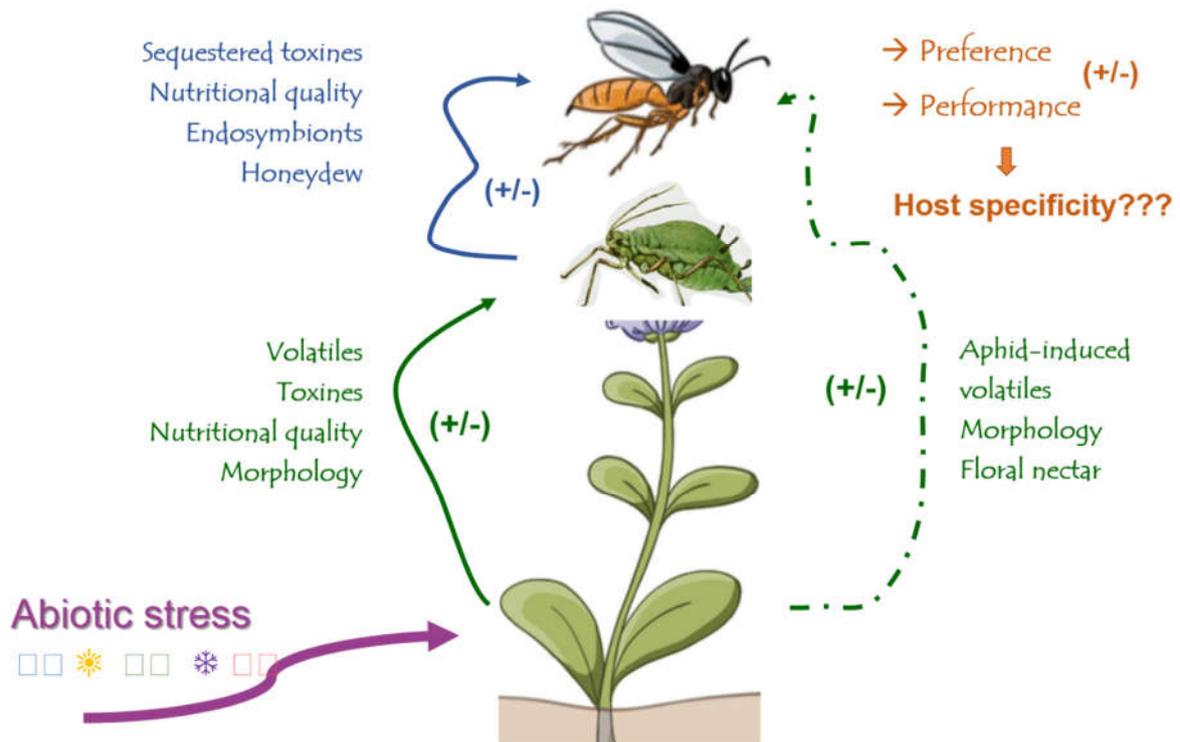


Figure 24. Could abiotic environmental stresses imply bottom-up effects on parasitoid host specificity?

The green arrow and texts mean plant traits. The blue arrow and texts mean aphid traits.

The orange texts mean parasitoid traits. The continued line means direct effects. The dashed line means indirect effects. The plus (+) symbols mean positive effects; the minus (-) symbols mean negative effects.

## Chapter 4. Aphid-parasitoid host specificity

The choice of one or an assemblage of BCA against pests based on their host range is crucial as it determines the BCA's efficiency. In classical and augmentative BC strategies, host specialist BCA is preferred as they attack and achieve high performance on targeted pests; they promise to be more efficient and do not attack non-targeted species comparing to shared-host generalists. The thriving questions are where the cut is being specialist or generalist and how to evaluate the host range of a BCA.

Two approaches are available to evaluate the host range of a potential BCA and complete each other: the laboratory host range testing and the observations from the field (Van Driesche and Reardon, 2004). The laboratory approach describes the 'fundamental host range' of each parasitoid genotype/phenotype at small scales, which often overestimate the real host range or 'field host range' observed in the field (). The field host range reflects the realized host range under particular environmental conditions at significant scale. However, field host ranges could be the sum of host ranges of different biotypes of one species due to the misidentification of both parasitoids and their associated hosts. The reasons could be (1) parasitoids have high plasticity; they can adapt their performance, morphology and behavior to their niche (Zepeda-Paulo *et al.* 2013) and (2) parasitoid populations could be composed of cryptic or sub-species species (Derocles *et al.* 2016). The field host range could also miss some host species due to technical problems, *i.e.* sample collections (Van Driesche and Reardon, 2004).

Furthermore, to approach the reality, the information of the classical parasitoid host range (the number of aphid hosts) should be accompanied by information such as the host taxa closeness, the parasitoid behavioral decision during host selection process (including search and oviposition on host) and the performance of parasitoids (the suitability of aphid hosts for parasitoid larval development). All these characteristics shape parasitoid host specificity. These parameters might be estimated through the calculation of the host specificity index and the analysis of the preference-performance relationship.

We calculated two specificity indexes: the taxonomic specificity index ( $S_{TD}^*$ ) (Poulin and Mouillot 2005) and the Rhode indexes of specificity ( $S_S$ ) (Rhode and Rhode, 2008) (see chapter 1.1.1) to compare the value. As  $S_{TD}^*$  are more sensible to the taxonomic distance among hosts and  $S_S$  are more sensible to parasitism rates, the two indexes could provide a hint of where and when should an index be applied and the pros/cons of each index.

The behavior of parasitoids (so-called preference, *i.e.* deciding for host oviposition) determines the successful implementation of a BCA (Mills and Wajnberg 2008). The host suitability for larval parasitoid (so-called performance) also plays a crucial role. The optimal foraging hypothesis (Jaenike 1978) states that parasitoids tend to oviposit on most suitable hosts for their offspring. Indeed, Desneux *et al.* (2009a) proved that parasitoid preference positively correlates with its performance on one host in the case of a specialist parasitoid. Our question is whether such correlation exists for host generalist parasitoids. Does the strategy of being physiologically adapt to a wide range of hosts relate to the less choosiness behavior (as known as the generalist behavior)? Do the change in preference/performance could result in the change of host specificity. In other terms, do parasitoids become more specialist or generalist under field conditions?

The primary goal of this chapter was finding an intermediate specialist/generalist parasitoid to detect their adaptation, as they could be flexible toward both directions of specificity spectrum. Our objectives are (1) to assess the fundamental host range in laboratory conditions for three parasitoids(2) calculating the host specificity index and analyze the preference-performance of six parasitoids based on the set of data generated in our laboratory (article 1), and (3) to compare the fundamental host range, the field host range reported from the literature and the correlation preference-performance pattern to propose specific and quantifiable criteria to classify host specialist/generalist parasitoids. The three parasitoids *A. ervi*, *D. rapae* and *A. abdominalis* are good models to test our question because they are BCA, are considered host generalists and represent two different families of parasitoids with different life-history traits. Our study could provide information on the host switching ability and ecological risks on non-target species of specific biotype parasitoids that are legally mandatory.

### **Biological materials - parasitoids**

Aphidiinae parasitoids comprise numerous specialist species, but some generalists can parasitize dozens of aphid species (Kavallieratos *et al.*, 2004; Starý, 2006; Tomanović *et al.*, 2009; Benelli *et al.*, 2014). We used three Eurasian generalist parasitoids ( ) including *Aphelinus abdominalis* (Aphelinidae: Aphelininae), *Aphidius ervi* (Braconidae: Aphidiinae) and *Diaeretiella rapae* (McIntosh) (Braconidae: Aphidiinae). They have broad field host ranges, *i.e.* more than ten host species as described previously for host generalist parasitoids (Dassonville *et al.* 2013, Kavallieratos *et al.* 2004, Zikic *et al.* 2017). In contrast, the fundamental host ranges of these three parasitoids have not been yet reported.



***Diaeretiella rapae***

***Aphidius ervi***

***Aphelinus abdominalis***

Figure 25. Morphology of the three parasitoids: *Diaeretiella rapae*, *Aphidius ervi* and *Aphelinus abdominalis* (From Bernard Chaubet, INRA)

The field host range was found in the literature by searching on Web of Science<sup>®</sup> with the keywords '*Aphidius ervi*', '*Aphelinus abdominalis*,' '*Diaeretiella rapae*.' In case of no or few sources on one species, we reported the host range of phylogeny-related parasitoid species.

***Aphidius ervi*** - The host range of *A. ervi* on both crops and non-crops aphids was reported on the field in Southeastern Europe (Kavallieratos *et al.* 2004a,b; Kavallieratos *et al.* 2005; Tomanovic *et al.* 2009) on 14 species in total. Crops aphid hosts include *Acyrtosiphon pisum*, *Aulacorthum solani* (foxglove aphid), *Hyperomyzus lactucae*, *Macrosiphum euphorbiae* (potato aphid), *Metopolophium dirhodum*, *Myzus persicae* (green peach aphid), *Rhopalosiphum padi*, *Schizaphis graminum*, *Sitobion avenae*, *S. fragariae*, *Diuraphis noxia*. On non-crop aphid hosts, *A. ervi* were found in *Macrosiphum cholodkovskyi*, *M. carnosum*.

***Aphelinus abdominalis*** - is considered as polyphagous (Honek *et al.* 1998). However, there was no publication of their full field host ranges. *A. abdominalis* primarily parasitized big aphids, *A. solani*, *M. euphorbiae*, and *Myzus* species. In the laboratory and semi-field

conditions, *A. abdominalis* parasitizes efficiently ten aphid species: *Aphis craccivora*, *A. fabae*, *Aphis gossypii* (melon/cotton aphid), *Aulacorthum solani*, *Chaetosiphon fragaefolii*, *Macrosiphum euphorbiae*, *Macrosiphum rosae*, *Myzus ascalonicus*, *Myzus persicae*, *Rhodobium porosum* (Dassonville *et al.* 2013).

***Diaeretiella rapae*** - is the only species in the genus *Diaeretiella* and morphologically very similar to the genus *Aphidius* (Stary *et al.* 1960, ). On the field, *D. rapae* is reported worldwide as a polyphagous parasitoid for several aphid species on different crop and non-crop plants. It can parasitize about 98 species of the aphids infesting more than 180 plant species both cultivated and wild (Kavallieratos *et al.* Singh, R. and G. Singh, 2015). Among them, the significant hosts consist of *Brevicoryne brassicae*, *Myzus persicae*, *Lipaphis erysimi* (on *Brassicaceae* family plants) and *Diuraphis noxia* (on wheat). Other host aphids include *Aphis craccivora*, *A. fabae*, *A. gossypii*, *A. nasturtii*, *A. pomi*, *A. rumicis*, *Brachycolus asparagi*, *Brachycaudus helichrysi*, *B. rumexicolens*, *Capitophonis*, *Dactynotus sp.*, *Hayhurstia atriplicis*, *Hyadaphis foeniculi*, *Macrosiphum euphorbiae*, *Myzus certus*, *M. persicae*, *Protaphis sp.*, *Rhopalosiphum fitchii*, *R. maidis*, *R. padi* and *Schizaphis graminum*. (Singh, R. and G. Singh, 2015; Kavallieratos *et al.* 2004, 2005, 2013).

Furthermore, these three generalist parasitoids are popular BCA. Since the years of 1970, *A. ervi* were released to control *A. pisum* and blue-green aphid, *A. kondoi* Shinji in New Zealand (Cameron *et al.* 2013), *A. gossypii*, *M. persicae*, *M. euphorbiae* and *A. solani* in Japan (Takada 2002). *D. rapae* was reported as the most effective natural enemy against the cabbage aphid, *B. brassicae* (Tatsumi *et al.* 2005) and Russian wheat aphid, *D. noxia* (Zhang and Hassan 2003). *D. rapae* was imported in USA, Iran, and China from regions throughout the world to control the Russia wheat aphid *D. noxia* (Gonzalez *et al.* 1992a, b). There is no report of *A. abdominalis* release as BCA at the national level as the other two parasitoids. However, *A. abdominalis* and *A. ervi* are popular, commercialized products, whereas *D. rapae* have not been yet commercialized.

The three species show different egg loads (the number of eggs available for oviposition). *A. ervi* and *D. rapae* are pro-ovigenic with high egg load and short lifespan. The egg load of *D. rapae* is 50-70 eggs per female per days (Kant *et al.* 2012) and 200-300 eggs/female/days for *A. ervi* (Sequeira and Mackauer 1994). They rely on honeydew to floral nectars for energy

(Gazmer *et al.* 2015; Tena *et al.* 2016). *A. abdominalis* is synovigenic (low egg load, high longevity). They can lay 5-10 eggs/day and can directly feed on early-stage aphids. They have a relatively long life (several weeks) and are more robust than *Aphidius* species (Shrestha *et al.* 2015). Both the physiological trait of egg load and the behavioral trait of host feeding affect host selection, *i.e.* time-constraint females tend to accept low-quality hosts (Deas and Hunter 2014; Hopper *et al.* 2013, Jervis *et al.* 2001).

### **Biological materials – aphid host species and their plant host**

Based on our estimation of field host ranges of *A. ervi*, *D. rapae*, and *A. abdominalis*, we chose 12 species of aphids belonging to the tribes of Aphidini and Macrosiphini (family Aphididae, subfamily Aphidinae) feeding on seven plant hosts in the study. These aphids are major pests on crops worldwide (van Emden and Harrington, 2007) and different on taxa (among Aphidinae species). The list of aphid-plant host association is detailed below and illustrated in 6. They are: *Aphis fabae*, *A. craccivora* and *A. pisum* on spring bean (*Vicia faba*, *Fabaceae*); *M. dirhodum*, *R. padi*, *S. graminum* and *S. avenae* on wheat (*Triticum sativa*, *Poaceae*); *B. brassicae* and *M. persicae* on cabbage (*Brassica oleracea*, *Brassicaceae*); *Aphis nerii* on swamp milkweed (*Asclepias incarnate*, *Apocynaceae*); *A. gossypii* on squash (*Cucurbita moschata*, *Cucurbitaceae*); *M. euphorbiae* on potato (*Solanum tuberosum*, *Solanaceae*) and on tomato (*Lycopersicon esculentum*, *Solanaceae*).

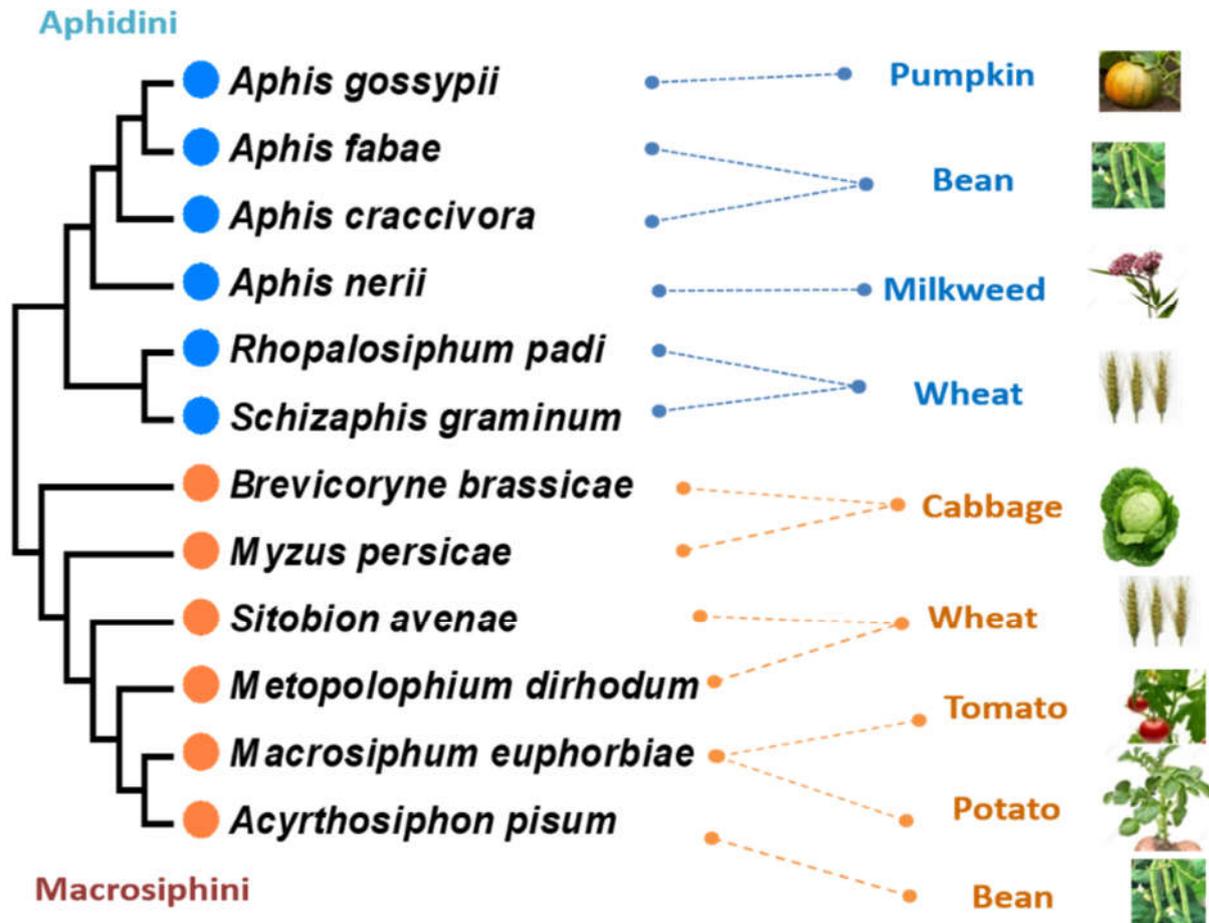


Figure 26. Lists of aphids and the phylogenetical relationship among them

Molecular Phylogenetic analysis by Maximum Likelihood method –the phylogeny of aphid species used in our experiments. The tree was constructed from COI sequences found on GenBank® (<https://www.ncbi.nlm.nih.gov/genbank/>), mostly from European origin aphids.

**Fundamental host ranges of *A. ervi*, *A. abdominalis* and *D. rapae*: laboratory non-choice test**

Laboratory no-choice assays evaluated the fundamental host range in a small area that consists of the behavioral observation and the physiological test (where the test design maximizes the probability of host acceptance by parasitoid) (**Erreur ! Source du renvoi introuvable.**). We noted sequential steps of the host selection process (Wellings 1993) that are 'detect' (antenna touch) – 'accept' (bend abdomen and prepare to attack) – 'successful attack' (inject ovipositor inside aphid hosts), each variable will have the binomial value of yes or no (see **Erreur ! Source du renvoi introuvable..** – preference). The survival/mortality of immature parasitoids inside aphid hosts are evaluated by sequential dissections at different stages: egg (1 hour after parasitism) – larva (4 days) – mummies (10 days) – emerged adults (15 days) (see **Erreur ! Source du renvoi introuvable..** – performance and **Erreur ! Source du renvoi introuvable.**).

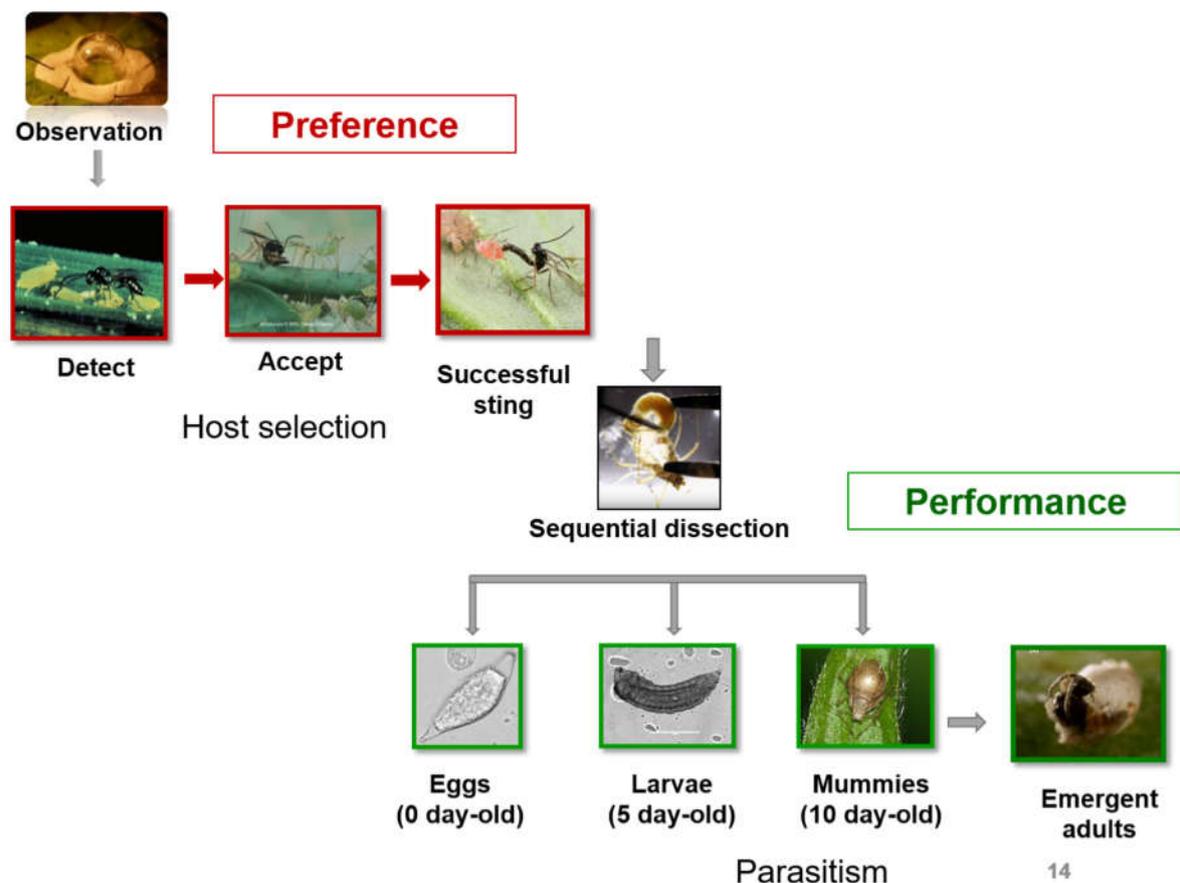
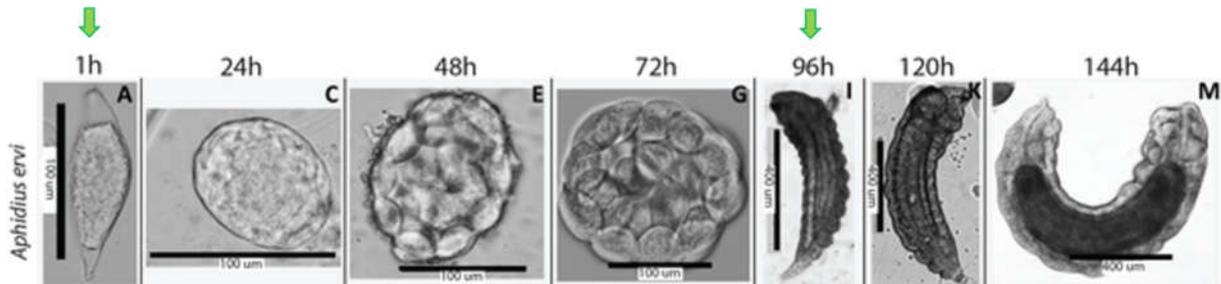


Figure 27. Host specificity testing in the laboratory.

*Parasitoid behavioral traits (preference) are subsequent actions leading to host acceptance or rejection. Physiological host range (performance) is the number of species in which the parasitoid could fully complete its development.*



*Figure 28. Serial dissections of parasitized pea aphids*

*Development of Aphidius ervi (top). (A) Eggs of A. ervi 1 hour after parasitism. (C) The morula of A. ervi shortly after the egg has hatched, revealing the developing embryo surrounded by serosal cells (known as placenta-like structure). (E) The A. ervi morula continues to grow. (G) First instar A. ervi larva. The egg finally hatches between 72–96h. (I) Second instar larvae of A. ervi. (K) Third instar larvae of the wasp (from Martinez et al. 2016)*

The optimal foraging model was statistically analyzed to find the correlation between parasitoid preference and performance, where preference is the acceptance of an aphid as host, *i.e.* parasitoid attack and oviposition) and performance is the survival ratio of parasitoids during each step of its immature life cycle.

### **Results & discussion - The continuum specialist-generalist**

Among six parasitoids (Figure 28), their taxonomic specificity indexes ( $S_{TD}^*$ ) range from 1.17 to 2.55 in order of decreasing specificity: *D. rapae*, *A. abdominalis*, *A. ervi*, *L. testaceipes*, *B. koreanus* and *B. communis*. Their Rhode indexes of specificity ( $S_s$ ) range from 0.37 to 0.70 in order of decreasing specificity: *L. testaceipes*, *A. abdominalis*, *D. rapae*, *A. ervi*, *B. communis* and *B. koreanus*. The correlation preference-performance exist for *A. ervi*, *L. testaceipes* and *B. communis*, which are more specialists, but not for *D. rapae* and *A. abdominalis* which are more generalists based on  $S_{TD}^*$ . The existence of correlation pattern in these parasitoids are therefore relevant to the degree of specificity measured by  $S_{TD}^*$ .

Similarly, we saw a relevance between field host range, laboratory host range and the optimal oviposition pattern. The field host range of *A. ervi*, *A. abdominalis*, and *D. rapae* are 14, more than 10 and 98 species; their ( $S_{TD}^*$ ) are 2.21, 2.37 and 2.55, respectively.

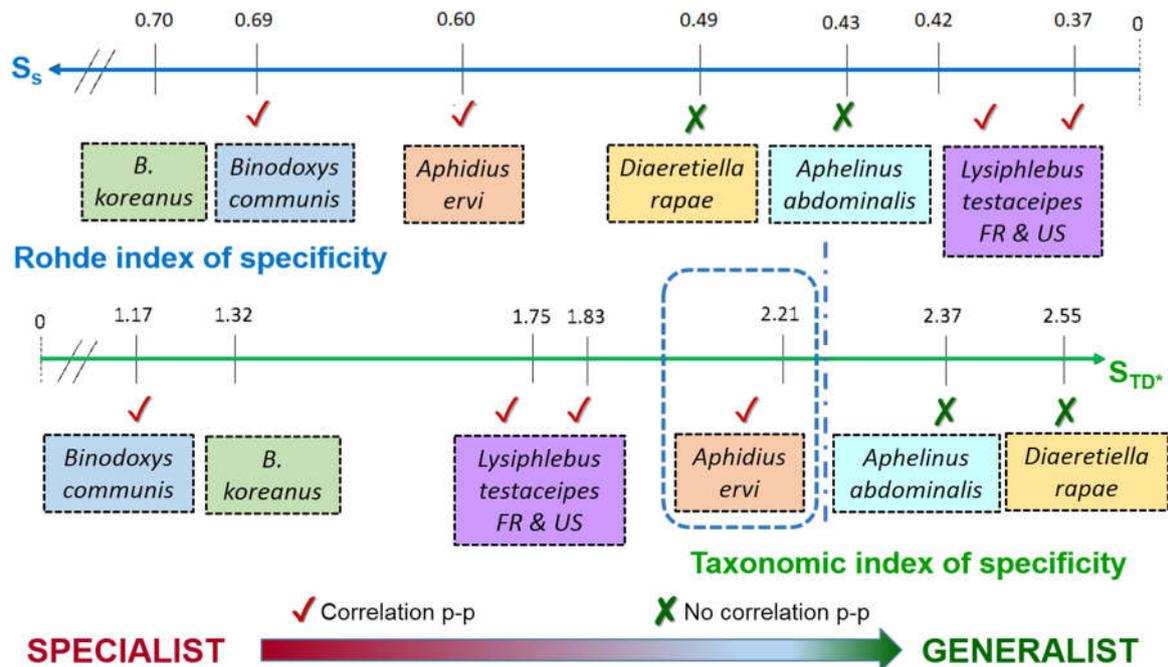


Figure 29. The host specificity indexes and the correlation preference-performance of six parasitoids, *Aphidius ervi*, *Diaeretiella rapae*, *Aphelinus abdominalis* (Monticelli, Nguyen, et al. 2018), *Binodoxys communis*, *B. koreanus* and *Lysiphlebus testaceipes* (data generated in the laboratory). The blue arrow means Rohde index of specificity ( $S_s$ ), the bigger the index, the more specialist parasitoid. The green arrow means the taxonomic index of specificity ( $S_{TD}^*$ ), the smaller the index, the more specialist parasitoid. The red check means the correlation preference-performance exists for that parasitoid. The green X means there is no correlation preference-performance.

From all information, we concluded that the taxonomic specificity index and the correlation preference-performance should be used to predict the host specificity of one parasitoid. The taxonomic indexes, in that case, are sensible enough to classify parasitoid host specificity based on taxonomic distance. The Rhode indexes are not relevant in that case probably because it excludes the phylogenetical difference among hosts. The results prove our hypothesis of selective strategies of specialist parasitoids. We proved that the strains of *A. ervi* we had in the laboratory are intermediate specialists/generalists, whereas *A. abdominalis*

and *D. rapae* are generalists. Also, we reported the three-parasitoid fundamental host specificity. The results mean specialist parasitoid accept hosts with good quality for their offspring development, while generalist parasitoids are less choosy. This result is consistent with the statement of host specificity from Colles *et al.* (2009) that at the individual-choice level, one organism 'decide' to be a specialist (choosy) if they can afford the selection, *i.e.* capable of using different resources, no search-time constraint). The study confirms the optimal reproduction hypothesis in ecology on specialist parasitoids and supports current studies on mechanisms of specialization and resistant evolution of *A. ervi* as a biological model.

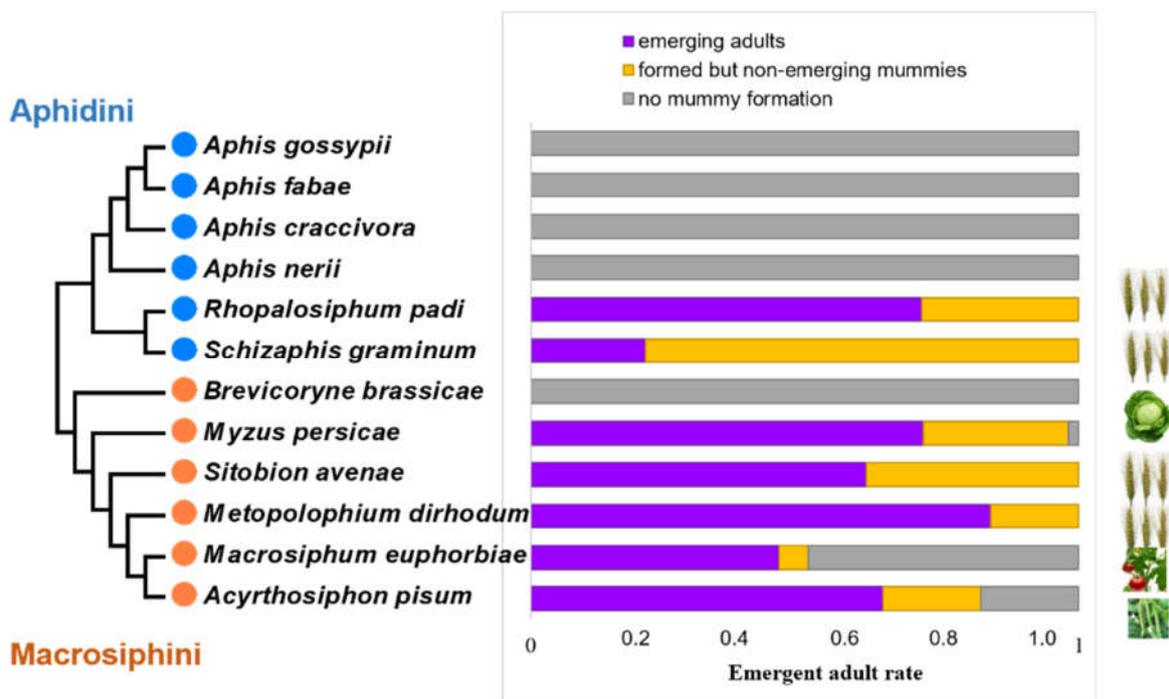
Based on the specificity index and the correlation preference-performance pattern, we could define parasitoid assemblages adapted for biocontrol (Klinken 1999; Poulin and Mouillot 2003; Mills and Wajnberg 2008). For instance, specialist parasitoids are chosen to release in classical and augmentation biocontrol strategies. However, in conservation biocontrol aiming to enhance natural enemy activities by landscape managing, practitioners should consider mix specialist and generalist assemblage (Raymond *et al.* 2015). Parasitoids with optimal patterns would adapt well in case of classical BC, but that characteristic could be a trade-off with host suppression at the local level in inundative BC (Mills and Wajnberg 2008). Host specificity index and behavioral patterns, therefore, plays a vital role in predicting non-target effects of potential agents and host use efficiency in the field.

### **To go further - Evaluation of the "cryptic species" hypothesis**

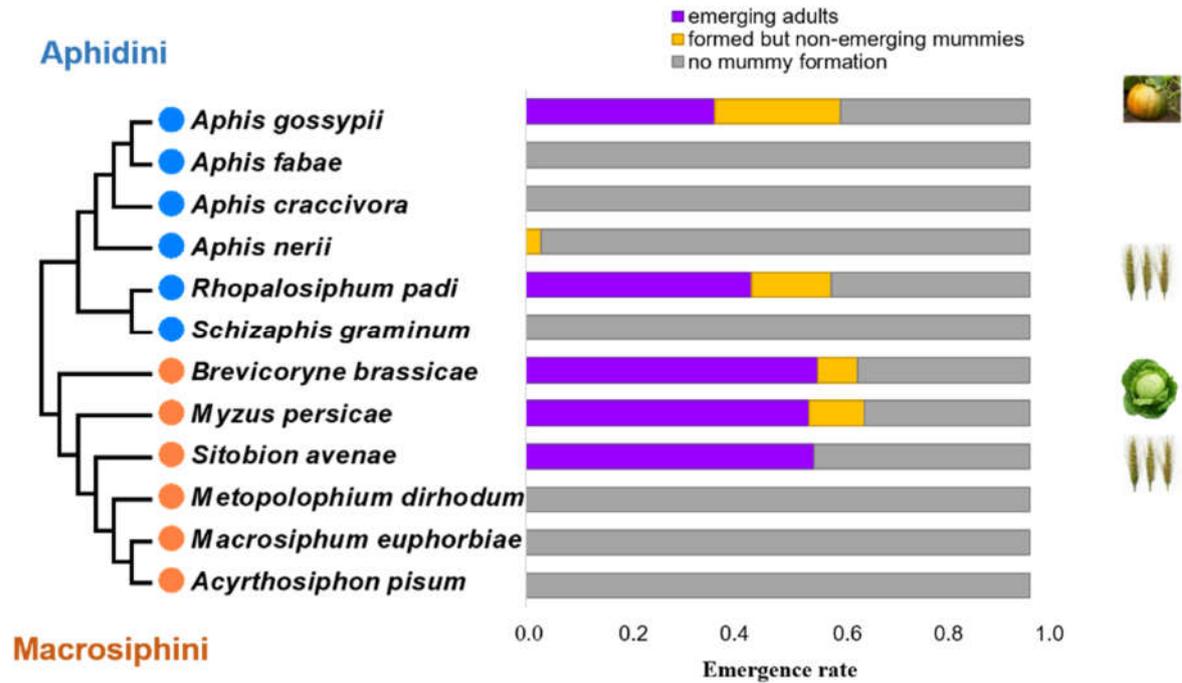
Natural populations of parasitoid adaptation to their local environment and differentiation in host specificity (host species and host exploitation efficiency) are common phenomena (Takada and Tada 2000; Henry *et al.* 2008). Moreover, most of the analyzed generalist morpho-species were composed of subgroups related to the aphid host, some of them revealed cryptic species (Derocles *et al.* 2016). There are hypotheses of cryptic species within the population of both *A. ervi* (Pennacchio *et al.* 1994) and *D. rapae* (Antolin *et al.* 2006; Henry *et al.* 2008; Navasse *et al.* 2017), and very few information of *A. abdominalis*.

We also compared the results from our experiments to other studies on the field and in the laboratory in different geographical areas to test the hypothesis of cryptic species within this

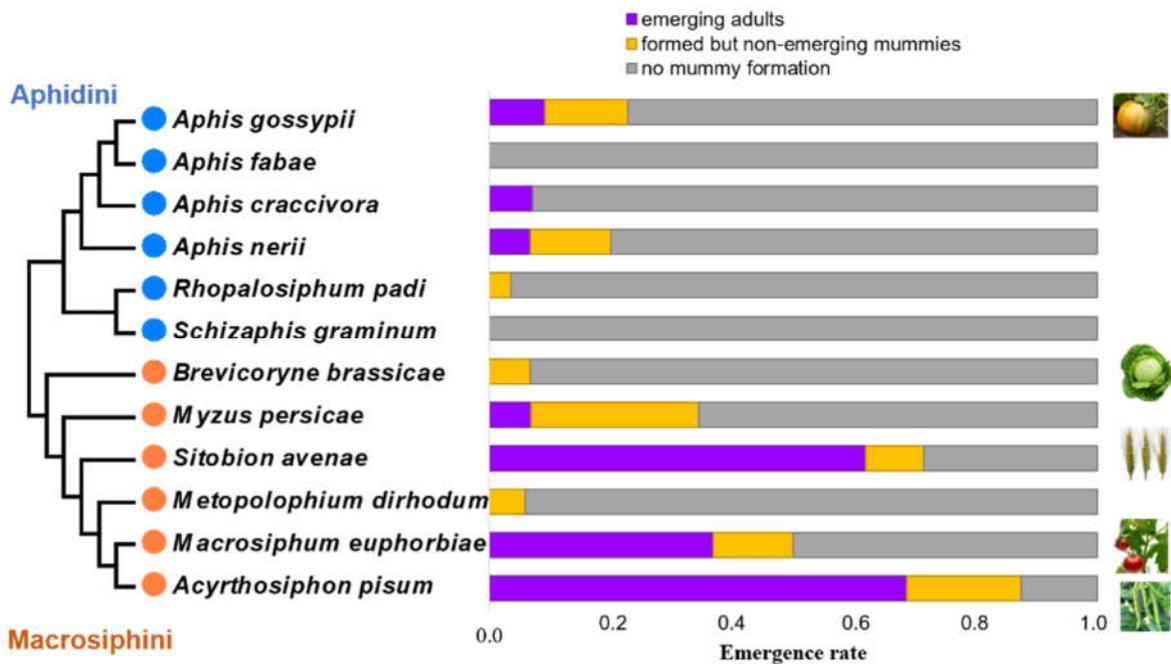
population. Results are quite similar between various studies in the field and under laboratory conditions. Among our three parasitoids, *D. rapae* has a higher specificity index (2.55) than *A. abdominalis* (2.37), which are proved to be highly generalists, and *A. ervi* (2.21), which are shown to be an intermediate specialist. However, when *A. abdominalis* and *A. ervi* expressed generalist behavior, *i.e.* they accepted and attacked all hosts at a high rate (more than 40% of successful oviposition for both species even on low-quality hosts (Erreur ! Source du renvoi introuvable.)).



*A. Aphelinus abdominalis* host specificity



**B. *Diaeretiella rapae* host specificity**



**C. *Aphidius ervi* host specificity**

Figure 30. Host specificity of *Aphelinus abdominalis* (A), *Diaeretiella rapae* (B) and *Aphidius ervi* (C). Results from the non-choice host specificity assay in the laboratory.

*D. rapae* did not accept low-quality hosts like *A. fabae*, *A. craccivora*, and *M. dirhodum* or *M. euphorbiae* and expressed no correlation between preference-performance, even though they have time-limited constraint like *A. ervi*. Antolin *et al.* (2006) found that *D. rapae* from two adjacent fields containing Russian wheat aphids (*Diuraphis noxia*) and cabbage aphids (*Brevicoryne brassicae*) were genetically differentiated and locally adapted by host species. The origin of *D. rapae* in our study came from adjacent fields of cabbages and wheat in Rennes (Britannic region, France) similar to the last research. Regarding the reproduction of *D. rapae* in the laboratory conditions, Hopper *et al.* (2005) found that some allopatric populations of parasitoids are partially or entirely reproductively compatible in laboratory crosses, although they differed in host specificity. The evidence of cryptic species also shows in the case of *Binodoxys* population (Desneux *et al.* 2009b; Mitrovski—Bogdanović *et al.* 2013). Recently, the premise of *D. rapae* being cryptic species is re-proposed by Navasse *et al.* (2017) related to their ecological specialization. The hypothesis of cryptic *D. rapae* population is therefore non-negligible.

Regarding *A. ervi*, our results are quite similar to different studies both in the field and under laboratory conditions in various regions (Zepeda-Paulo *et al.* 2013, Bilodeau *et al.* 2013, Kavallieratos *et al.* 2004, Milne 1986). These shreds of evidence proved that *A. ervi* life history traits are well conserved at geographical levels. Additionally, Henry *et al.* (2008) stated that host specificity is strictly genetically related. Derocles *et al.* (2016) found that among seven generalist species, only *A. ervi* do not have morphological substructure specific to their natal hosts (**Erreur ! Source du renvoi introuvable.**). Moreover, in our study *A. ervi* are instead an intermediate specialist. *A. ervi* populations are therefore less likely to be composed of cryptic species.

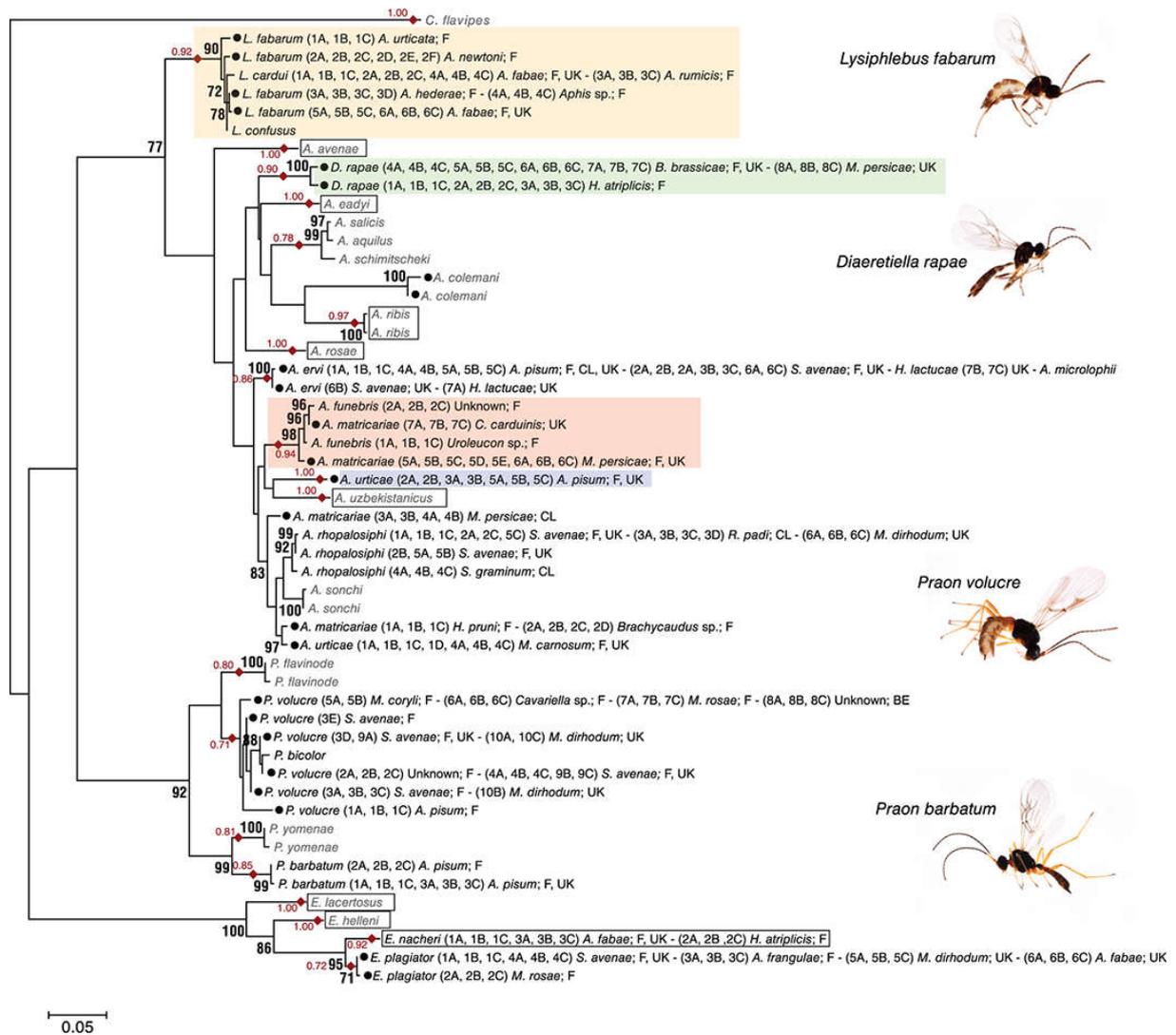


Figure 31. Phylogenetical relationships among Aphidiinae parasitoids

"Maximum likelihood tree obtained from cytochrome c oxidase I fragment. Information is presented in the following order: parasitoid morphospecies name; specimen voucher numbers, aphid host, and sampling location." From Derocles et al. (2016).

# Article I. Preference-performance relationship in host use by generalist parasitoids

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1 **ABSTRACT**

2 Host specificity has been described by the preference-performance hypothesis where  
3 performance (physiological host range) is defined as the sum of all species on which  
4 parasitoids can complete their life cycle and preference is defined as host acceptance.  
5 Generalist behavior (low selectivity when encountering various hosts) associated with  
6 parasitoid fitness, *i.e.* performance, mostly dictated by host suitability for parasitoid  
7 offspring development, may lead to a lack in the preference-performance relationship in  
8 generalist parasitoids. In this context, we assessed under laboratory conditions the  
9 preference – performance relationship in three generalist aphid parasitoids, testing for  
10 twelve hosts over a broad phylogenetic range. The three parasitoids showed low selectivity  
11 (preference), *i.e.* all aphid species were stung by the females. However, depending on the  
12 parasitoid species considered, only 42-58% of aphid species enabled producing offspring.  
13 Also, we did not find the correlation between the preference and the performance of *A.*  
14 *abdominalis* and *D. rapae* while correlation was significant for *A. ervi*. For the later, host  
15 phylogeny is important as females showed higher attack rate on hosts closely related to  
16 optimal hosts (*Acyrtosiphum pisum*, *Macrosiphum euphorbiae*, and *Sitobion avenae*).  
17 Furthermore, the generalists are less affected by specific aphid defenses against them (such  
18 as endosymbionts) whereas they are strongly affected by general aphid defenses, *e.g.* aphid  
19 ability to sequester toxic compounds. Overall, host specificity indexes hinted that *D. rapae*  
20 and *A. abdominalis* are true generalist parasitoids whereas *A. ervi* and *L. testaceipes* are  
21 likely intermediate specialist-generalist, and *B. communis* and *B. koreanus* are specialist  
22 parasitoids.

23 **Keywords:** Host range, generalist parasitoids, specialization, preference-performance  
24 hypothesis, aphid

25  
26  
27

## 28 INTRODUCTION

29 Specialization in parasitoid species is defined as a narrow pattern of hosts selected and  
30 suitable for offspring development (Futuyma and Moreno 1988, Muller *et al.* 1999, Straub *et*  
31 *al.* 2011, Desneux *et al.* 2012). Multiple characteristics related to biological, ecological and  
32 phylogenetic traits are normally used to classify parasitoids as specialists or generalists.  
33 However, all these traits are scarcely documented for most parasitoid species, and the  
34 number of host species successfully parasitized has been used largely as an endpoint for  
35 describing host specificity (Futuyma and Moreno 1988, Shaw 1994). On the one hand,  
36 specialists usually show fitness values that are higher, when using one or few particular  
37 resources, than fitness values showed by generalists that use all resources available (Levins  
38 1962 and 1968). On the other hand, generalists can rely on a wider range of resources and  
39 are more tolerant to environmental changes as well as to poorly diversified systems, *e.g.*  
40 agricultural habitats (Futuyma and Moreno 1988).

41 Host specificity, and more broadly diet breadth, has been described by the preference-  
42 performance hypothesis of Jaenike (1978). It predicts a positive relationship between the  
43 choice of adult females (preference) and the degree of successful development of offspring  
44 (performance). More widely, female preference tends to correlate with host quality for  
45 offspring development (Jaenike 1978, Thompson 1988, Desneux *et al.* 2009a). Various  
46 studies stressed the occurrence of such relationship for specialized phytophagous  
47 arthropods (Craig *et al.* 1989; Nylin and Janz 1993; Gripenberg *et al.* 2010) as well as for  
48 both specialized predators (Sadeghi & Gilbert 1999) and parasitoids (Driessen 1991, Brodeur  
49 *et al.* 1998, Desneux *et al.* 2009a). By contrast, such relationships shall not be famous in case  
50 of generalist arthropods (Eben *et al.* 2000, Gripenberg *et al.* 2010, Chesnais *et al.* 2015)

51 notably presumably owing to their weaker choosiness when encountering different hosts.  
52 Indeed, the behavioral selection of host by parasitoids involves the detection of physical  
53 and/or chemical cues from the other trophic levels (like host species and/or host plants)  
54 (Vinson, 1985, Vet and Dicke 1992, Mackauer and Michaud 1996), and the specificity of  
55 parasitoids may be mainly shaped by info chemicals (Afsheen *et al.* 2008). Specialist  
56 parasitoids more efficiently use specific cues related to their hosts (Barbosa 1988, Vet and  
57 Dicke 1992, McCormick *et al.* 2012). For example,, for *Microplitis croceipes* use host  
58 kairomones from a variety of host-related sources, *e.g.* frass, hemolymph, and salivary  
59 secretions (Jones *et al.* 1971, Alborn *et al.* 1995). By contrast, generalist parasitoids often  
60 use more general cues to identify potential host species (Vet and Dicke 1992). For example,  
61 the generalist parasitoid *Aphaereta minuta* does not use host-derived chemical signals to  
62 select host fly larvae and attacks almost all hosts that are present in encountered decaying  
63 materials (Vet and Dicke 1992). Such a generalist behavior (low selectivity when facing  
64 various hosts) is associated with parasitoid fitness, *i.e.* performance, mostly dictated by  
65 hosts suitability for parasitoid offspring development, which may lead to an overall lack in  
66 the preference-performance relationship in generalist parasitoids. However, several studies  
67 did report positive preference-performance relations in case of generalist parasitoids  
68 (Brodeur *et al.* 1998, Henry *et al.* 2005, Li *et al.* 2009, Kos *et al.* 2012). Still, these studies (i)  
69 tested a few host species only (up to 3), and (ii) the host species belonged to the same tribes  
70 or genus representing a possible bias in assessing preference-performance correlation  
71 (Poulin and Mouillot in 2005). Such reported positive relationships may be false positive as  
72 these studies were not designed *per se* to evaluate the link between the preference of  
73 females and the performance of offspring in the context of the preference-performance  
74 hypothesis (Gripenberg *et al.* 2010).

75 In this study, we assessed under laboratory conditions the preference (behavioral host  
76 range)-performance (physiological host range) relationship in three generalist aphid  
77 parasitoids attacking a broad phylogenetic range of hosts. For this, we calculated a host  
78 specificity index (Poulin and Mouillot 2005) to classify the parasitoids tested depending on  
79 their host specificity and to identify an indicator of the quantifying where these species in a  
80 generalist-specialist continuum. For this, we took into account previously published results  
81 on specialist parasitoids generated by our research group. Also, some side factors  
82 modulating preference and/or performance of parasitoids such as endosymbionts or host  
83 plants. This is why, twelve aphid species spread over six different host plants were tested  
84 and all aphid species were screened for the presence of 9 endosymbionts species.

## 85 **MATERIAL AND METHOD**

### 86 ***Biological materials***

87 Three Eurasia generalist parasitoids were tested: *Aphelinus abdominalis* (Aphelinidae:  
88 Aphelininae), *Aphidius ervi* (Braconidae: Aphidiinae) and *Diaeretiella rapae* (Braconidae:  
89 Aphidiinae). These endoparasitoid species are koinobiont of many aphid species (Honek *et al.*  
90 *al.* 1998, Kavallieratos *et al.* 2004). The description of the aphid species, their color, hosts  
91 plants, the aphid tribe and the number of replications performed in experiments for each  
92 parasitoid species are reported Table 1. Twelve aphid species spread over two different  
93 tribes (aphidini and macrosiphini) were used in this study and were chosen to encompass a  
94 wide phylogenetic range of aphid species (van Emden and Harrington 2007). Among this  
95 aphid species, *Macrosiphum euphorbiae* was maintained on two plant species: *Solanum*  
96 *tuberosum* identified by (P) and *S. lycopersicum* identified by (T) in the text and the other  
97 figure and table. Also, there were two phenotypes of *Myzus persicae* (one green and one

98 red). Parasitoids and aphid species were reared in climatic cabinets ( $23 \pm 2$  °C, RH  $65 \pm 5\%$   
99 and photoperiod 16:8 L: D h) and parasitoids were maintained on their main hosts in the  
100 field: *Acyrtosiphum pisum* for *A. abdominalis* and *A. ervi* and *Brevicoryne brassicae* for *D.*  
101 *rapae*. Before experiments, the parasitized aphids at the mummy stage were retrieved and  
102 isolated in plastic Petri dishes. After the adult emergence, females were mated and fed with  
103 the honey solution (50 % water + 50 % honey) for at least 24 hours. The experiments were  
104 carried out using 24-48 hour-old parasitoid females.

105 Experiment 1: preference.

106 Parasitoid behavioral host ranges were established observing their behavior when they  
107 encountered different aphid species. Three parasitoid behavioral steps were identified:  
108 detection, acceptance, and oviposition (parasitoids attack). Detection was described as the  
109 contact between aphid and parasitoid followed by antenna analysis. Acceptance was  
110 defined as the parasitoid abdomen bent underneath its thorax in the direction to the aphid  
111 for *A. ervi* and *D. rapae* while for *A. abdominalis*, it was described as movement's right and  
112 left behind the aphid. Oviposition was defined as the introduction of the ovipositor in the  
113 aphid followed by an egg deposition. Aphid defensive behaviors were also recorded, and  
114 three reactions were considered as defensive ones: the kick, cornicle secretion (sticky  
115 secretion) and/or escape. For the analyses, all defensive behaviors were grouped.

116 For each replicates, one leaf of one host plant was placed upside down under a binocular  
117 magnifier (8x). One aphid was placed on the leaf with a fine brush. After 5 minutes of the  
118 establishment, one mated female parasitoid was introduced. When the parasitoid touched  
119 the leaf, the experiment began, and the parasitoid behavior was noted during 5 minutes for  
120 *A. ervi* and *D. rapae* (short stinging time) and during 10 minutes for *A. abdominalis* (long

121 stinging time, Wahab 1985). The preference experiment was stopped after the 5 or 10  
122 minutes or when the parasitoid introduced the ovipositor in the aphid suggesting an egg  
123 deposition. Each parasitoid and aphid species was tested randomly every experimental day.  
124 Aphid size is known to have an impact on parasitoid host selection process (Wyckhuys *et al.*  
125 2008). Hence, the aphids used in the experiment were all of the equivalent sizes of 2<sup>nd</sup> instar  
126 *A. pisum* for *A. abdominalis* and *A. ervi* and an equivalent of 4<sup>th</sup> instar *B. brassicae* for *D.*  
127 *rapae*, *i.e.* known instar preferred by parasitoid for oviposition (Sequeira and Mackauer  
128 1994, Hafez 1961).

129 Experiment 2: performance.

130 The physiological host range was established observing the parasitoids development in the  
131 different aphid species. Aphids previously stung in experiment 1 were isolated in plastic  
132 Petri dishes on one leaf of their respective host plant in a climatic room at  $23 \pm 1$  °C, RH  $65 \pm$   
133 5% and photoperiod 16:8 L:D. Because a higher number of replicates was needed in  
134 experiment 2, additional replicates were performed in the same conditions of experiment 1  
135 (without recording the parasitoid behavior).

136 Parasitoid development within the hosts was monitored at four different times. The aphids  
137 were dissected (1) after being stung (monitoring egg survival) under a binocular microscope  
138 at 100x magnification, (2) after 4 days (tracking larvae survival) under a binocular  
139 microscope at 40x magnification, (3) after 7 days to monitor aphid mummification, and (4)  
140 the emergence rate and the sex ratio was finally recorded.

141 Experiment 3: Presence of secondary endosymbionts in aphids.

142 To tested the impact of aphid secondary endosymbionts on the development of juvenile

143 parasitoids, all of the aphid species were screened to detect the presence of 9 facultative  
144 symbionts genera that are known to interact with aphids (Ferrari and Vavre 2011):  
145 *Arsenophonus*, *Hamiltonella defensa* (T-type), *PAXS* (Pea-aphid X-type symbiont), *Regiella*  
146 *insecticola* (U-type), *Rickettsia*, *Rickettsiella*, *Serratia symbiotica* (R-type), *Spiroplasma*,  
147 *Wolbachia*.

148 *Insect sampling and DNA extraction.* 0.01 g of aphids were collected from each aphid colony.  
149 Each sampling was washed in 70 % ethanol for 2 to 5 minutes (aphid size dependent) rinsed  
150 in PBS (phosphate buffer solution) for 1 minute and finally washed in pure water. Samples  
151 were homogenized with a piston (1 piston/sample) in Lysis buffer for DNA extraction. Then,  
152 samples were placed in 10  $\mu$ L of RNase A, 50  $\mu$ L of lysozyme and 20  $\mu$ L of protease K and  
153 incubated at 55 °C for 1 hour. For DNA purification, samples were centrifuged at 3000 rpm  
154 for 5 minutes, and the supernatants were collected. 1mL of absolute ethanol and 50  $\mu$ L of  
155 sodium acetate were added and the mixture was placed in -20°C overnight. Samples were  
156 then centrifuged at 14000 rpm for 20 minutes, and the supernatants were removed. After  
157 adding 1mL of 70 % ethanol, the mixture was homogenized and centrifuged at 14000 rpm  
158 for 5 minutes. After 5 minutes at room temperature to let the pellet dry, 50  $\mu$ L of pure water  
159 was added to the pellet and then stored at -20 °C until used. The quantity and quality of the  
160 DNA were measured with the NanoDrop and diluted to obtain 50 ng of DNA / $\mu$ L for each  
161 sample.

162 *PCR amplification.* Diagnostic PCR reactions with a species-specific primer (Sup material 1)  
163 were conducted in 1.5 % agarose gel stained with ethidium bromide and visualized with UV  
164 light to test the presence of facultative symbiont. Each symbiont was tested with a positive  
165 control (DNA from infected species) and two negative controls (two pea aphid genotypes

166 with only primary endosymbiont *Buchnera aphidicola*). Furthermore, the quality of the  
167 extraction was tested by PCR on the primary endosymbiont: *B. aphidicola*. Finally, bands  
168 showing a signal were removed from the gel, purified (with Min Elute PCR purification kit)  
169 and sequenced to check the symbiont identity (validated when the sequence was at least  
170 95% similar).

171 Index of host specificity ( $S_{TD}^*$ ).

172 The  $S_{TD}^*$  considers the taxonomic and ecological information, and calculates a value for  
173 each parasitoid species (Poulin and Mouillot 2005). This index is inversely proportional to  
174 the host specificity and was computed with the program TaxoBiodiv2 (Poulin and Mouillot  
175 2005) with a taxonomic tree of hosts build on family, tribes, genus, and species (Blackman  
176 and Eastop 2006). The index was computed for each parasitoid species tested and for three  
177 other specialist parasitoid species: *Binodoxys communis* (Desneux *et al.* 2009a), *Binodoxys*  
178 *koreanus* (Desneux *et al.* 2009b) and *Lysiphlebus testaceipes* (from France and USA; Desneux  
179 & Heimpel, unpublished data).

## 180 **Data analysis**

181 All statistical analyses were carried out using R version 3.2.2. A generalized linear model  
182 (GLM) with a binomial distribution and followed by a multi-comparison test (Tukey, package  
183 'multcomp') was used to (i) compared each parasitoid behavior recorded (detection,  
184 acceptance and stinging rate) on the rearing host with the parasitoid behavior on all other  
185 aphid species, (ii) analyzed the effect of the aphid colors, the aphid host plants, the aphid  
186 tribe and the presence of secondary endosymbiont on the proportion of stung aphids by  
187 each parasitoid species in each aphid species, (iii) compared the parasitoid mortality among

188 the different stage (egg, larvae, mummy and adult) in every aphid species, and (iv) analyzed  
189 the relationship between parasitoid stinging rate and (1) the aphid defensive behavior or (2)  
190 the parasitoid physiological hosts range (emergence rate). The deviation from a 0.5 sex ratio  
191 was tested with permuted Fisher's Exact test (with the Bonferonni adjustment method).

## 192 **RESULTS**

### 193 Experiment 1: Preference.

194 For *A. abdominalis*, the proportion of aphids detected in each aphid species was not  
195 significantly different than the proportion of *A. pisum* (the rearing host) detected, ( $X^2_{13} =$   
196 15.53,  $P > 0.05$ ) (Table 2). The proportion of detected aphids in each aphid species ranged  
197 from 0.91 to 1.00. Two aphid species (*A. fabae* and *A. gossypii*) were less accepted  
198 compared to the proportion of *A. pisum* accepted ( $X^2_{13} = 112.47$ ,  $P < 0.001$ ). The proportion  
199 of aphids accepted in each aphid species ranged from 0.31 to 1.00. These species being less  
200 accepted were also less stung by the parasitoids compared to the proportion of *A. pisum*  
201 stung ( $X^2_{13} = 93.37$ ,  $P < 0.001$ ). The proportion of stung aphid species ranged from 0.25 to  
202 0.94. Due to the low number of *A. fabae* and *A. gossypii* stung by *A. abdominalis*, these  
203 aphid species were not used in experiment 2.

204 For *A. ervi*, the proportion of aphid species detected in each aphid species was not  
205 significantly different than the proportion of *A. pisum* (the rearing host) detected ( $X^2_{13} =$   
206 31.76,  $P < 0.01$  but there were no differences between the proportion of rearing host  
207 detected and the proportion of the other aphid species in the multi-comparison test, Table  
208 2). *Aphidius ervi* detected a proportion of aphids in each aphid species that ranged from 0.91  
209 to 1.00. Four aphid species (*A. craccivora*, *A. fabae*, *B. brassicae* and *R. padi*) were less

210 accepted compared to the rearing host ( $X^2_{13} = 155.84, P < 0.001$ ). The proportion of  
211 accepted aphids in each aphid species ranged from 0.48 to 0.95. The same four less  
212 accepted species were also less stung compared to the rearing host ( $X^2_{13} = 144.89, P <$   
213  $0.001$ ) and their proportions ranged from 0.42 to 0.95.

214 For *D. rapae*, the proportion of aphid species detected in each aphid species was not  
215 significantly different than the proportion of *B. brassicae* (the rearing host) detected ( $X^2_{13} =$   
216  $72.05, P < 0.001$  but there were no differences between the proportion of rearing host  
217 detected and the proportion of the other aphid species in the multi-comparison test, Table  
218 2). The detection proportion ranged from 0.58 to 1.00. Six aphid species (*A. craccivora*, *A.*  
219 *fabae*, *A. gossypii*, *M. euphorbiae* (T and P), *M. dirhodum* and *R. padi*) were less accepted  
220 compared to the rearing host ( $X^2_{13} = 157.68, P < 0.001$ ) and the proportion of aphids  
221 accepted in each aphid species ranged from 0.30 to 0.98. These six less accepted aphid  
222 species and two other aphid species (*A. nerii* and *M. persicae* red clone) were less stung  
223 compared to the rearing host ( $X^2_{13} = 190.94, P < 0.001$ ). *M. dirhodum*, *A. craccivora*, and *A.*  
224 *fabae* were not used in experiment 2 due to the insufficient number of stung aphids.

225 When all aphid defensive behaviors were grouped, there was a negative relationship  
226 between the proportion of aphid species stung by *A. abdominalis* and the proportion of  
227 aphid defenses ( $X^2_1 = 34.42, P < 0.01$ , dispersion parameter: 4.8) (Figure 1). There was no  
228 relationship between the proportion of stung aphid species by *A. ervi* and *D. rapae* and the  
229 proportion of aphid defenses ( $X^2_1 = 20.48; 6.49$ , dispersion parameter = 9.5; 13.5,  $P > 0.05$ ,  
230 respectively). The aphid defensive behavior varied depending on the parasitoid species and  
231 the aphid species ( $X^2_2 = 270.94, = P < 0.01$  and  $X^2_{13} = 101.26, P < 0.001$ , respectively).

232 Specifically, *D. rapae* induced the highest aphid defensive rate (on average 62% species of

233 the aphid reacted), followed by *A. abdominalis* (on average 45% of the aphid species  
234 reacted) and *A. ervi* (on average 20% of the aphid species reacted).

235 Experiment 2: Performance.

236 The highest adult survival rate for *A. abdominalis* was in *A. pisum*, *M. euphorbiae* (potato  
237 and tomato plants), *M. dirhodum*, *M. persicae* (green and red clones), *R. padi* and *S. avenae*  
238 and the proportions of adults emerged ranged from 0.61 to 0.9 (Figure 2, A). The other  
239 aphid species could be separated by the stages at which the parasitoid development failed.  
240 Firstly, a lower proportion of parasitoid eggs were deposited in *A. craccivora* compared to  
241 the rearing host ( $P < 0.01$ ). Then, a high parasitoid mortality was observed between egg and  
242 larval stage when *A. abdominalis* developed on *A. nerii* ( $P < 0.01$ ) and the proportion of  
243 larvae in this aphid species was different compared to the proportion of larvae in the rearing  
244 host ( $P < 0.01$ ). The parasitoid mortality between the larval and the mummy stage was  
245 observed in *B. brassicae* and *S. graminum*, (all  $P < 0.01$ ) and the proportions of mummies  
246 were significantly different compared to the proportion in the rearing host (all  $P < 0.01$ ).  
247 Finally, in *S. avenae*, parasitoid mortality was observed after aphid mummification ( $P =$   
248 0.023). However, the proportion of adult parasitoids emerged from this aphid species was  
249 not different compared to the proportion emerged from the rearing host. The *A.*  
250 *abdominalis* sex ratio varied from the 50:50 depending on the aphid species. It was male-  
251 biased on *M. dirhodum*, *M. persicae* green and red clones and *R. padi* (all  $P < 0.001$ ) and  
252 female-biased in *M. euphorbiae* on tomato ( $P < 0.05$ ) (Table 3). We found no relationship  
253 between the preference (sting rate) of *A. abdominalis* and its performance (emergence rate)  
254 ( $X^2_1 = 23.53$ ,  $P > 0.05$ , dispersion parameter = 11.71, Figure 3 and S1, A).

255 The highest adult survival rate for *A. ervi* was in *A. pisum*, *M. euphorbiae* (tomato plant) and  
256 *S. avenae*. The proportions of adults emerged ranged from 0.43 to 0.69 (Figure 2, B). The  
257 other aphid species could be separated by the stages at which the parasitoid development  
258 failed. Firstly, fewer eggs were deposited in *B. brassicae*, and *S. graminum* compare to the  
259 proportion of egg deposited in the rearing host ( $P < 0.01$ ;  $P = 0.043$ , respectively). Then, a  
260 significant parasitoid egg mortality was observed in *M. euphorbiae* (potato plant) ( $P < 0.01$ )  
261 but the proportion of parasitoid larvae in this aphid species was not different compared to  
262 the proportion of larvae in the rearing host ( $P > 0.05$ ). The parasitoid mortality between the  
263 larval and the mummy stage were observed in *A. craccivora*, *A. fabae*, *A. gossypii*, *A. nerii*,  
264 *M. dirhodum* and *R. padi*, (all  $P < 0.045$ ); and the proportion of mummies was significantly  
265 different than the proportion of mummies in the rearing host ( $P < 0.01$ ). Finally, for *M.*  
266 *persicae* green and red clone, parasitoid mortality was observed after aphid mummification  
267 ( $P = 0.01$ ) and the proportion of adults emerged from these species was significantly  
268 different than the proportion of adults emerged from the rearing host ( $P < 0.01$ ). The *A. ervi*  
269 sex ratio was similar from 50:50 in all aphid species (all  $P > 0.05$ ) (Table 3). We found a  
270 positive relationship between the *A. ervi* preference (sting rate) and its performance  
271 (emergence rate) ( $X^2_1 = 33.89$ , dispersion parameter = 4.8,  $P < 0.01$ , Figure 3 and S1, B).

272 The highest adult survival rate of *D. rapae* was observed in *A. gossypii*, *B. brassicae*, *M.*  
273 *persicae* (green and red clones), *R. padi* and *S. avenae* and the proportions of adults  
274 emerged from these species ranged from 0.38 to 0.61 (Figure 2, C). The other aphid species  
275 could be separated by the stages at which the parasitoid development failed. Firstly, a  
276 significant parasitoid mortality was observed between egg and larval stage in *A. pisum* and  
277 *M. euphorbiae* (on potato and tomato plants) (all  $P < 0.01$ ) and the proportion of parasitoid

278 larvae in these aphid species was different than the proportion of parasitoid larvae in the  
279 rearing host ( $P < 0.01$ ). The parasitoid mortality between the larval and the mummy stage  
280 was observed in *A. nerii* and *S. graminum* (all  $P < 0.01$ ) and the proportion of mummies was  
281 significantly different than the mummy proportion in the rearing host ( $P < 0.01$ ). Finally, the  
282 parasitoid mortality was observed after the aphid mummification in *B. brassicae*, *M.*  
283 *persicae* green and *R. padi* (all  $P < 0.04$ ). However, their proportion of adults was not  
284 significantly different than the proportion of emerged adult in the rearing host ( $P > 0.05$  for  
285 the three aphid species). The *D. rapae* sex ratio was similar from 50:50 in all aphid species  
286 (all  $P > 0.05$ ) (Table 3). We found no relationship between the preference (sting rate) of *D.*  
287 *rapae* and its performance (emergence rate) ( $\chi^2_1 = 11.49$ , dispersion parameter = 9.56,  $P >$   
288 0.05, Figure 3 and S1, C).

289 Experiment 3: Presence of secondary endosymbionts in aphids.

290 The primary endosymbiont *Buchnera aphidicola* was found in all aphid samples.  
291 *Arsenophonus*, PAXS, *Rickettsia*, *Rickettsiella*, *Serratia symbiotica*, *Spiroplasma*, and  
292 *Wolbachia* were not found in the aphid species screened. *Hamiltonella defensa* was found  
293 6 times out of 6 in *A. fabae* (6/6) and 4 times out of 6 in *M. dirhodum* (4/6), and *Regiella*  
294 *insecticola* was found 6 times out of 6 in *M. dirhodum* (6/6).

### 295 **Index of host specificity.**

296 *Binodoxys communis* and *B. koreanus* were the most specialized species considered in our  
297 study, and they stung only the *Aphis* genus ( $S_{TD}^*$  are respectively 1.17 and 1.32) (figure 4).  
298 *Lysiphlebus testaceipes* (France and USA origin) stung more aphid species, but they only  
299 came from the Aphidini tribes ( $S_{TD}^*$  are respectively 1.75 and 1.83). *A. ervi* stung the

300 Macrosiphini tribes and some species with small prevalence in Aphidini tribes and its  $S_{TD}^*$  is  
301 2.21. *A. abdominalis* and *D. rapae* stung almost the same quantities of species in both tribes  
302 with high prevalence, and their  $S_{TD}^*$  are 2.37 and 2.55, respectively.

### 303 **DISCUSSION**

304 In this study, we tested the preference-performance relationship for three generalist  
305 parasitoids on twelve aphid species and used previous results on specialist parasitoids. We  
306 showed no relationship for *A. abdominalis* and *D. rapae* while a significant relationship was  
307 found for *A. ervi*. Overall, the three parasitoid species showed a low behavioral selectivity  
308 (preference traits) whereas their performances, and specifically for *A. ervi*, were strongly  
309 linked to actual suitability for offspring development in the parasitized host species. The two  
310 secondary endosymbionts *H. defensa* and *R. insecticola* were detected in only two host  
311 species (*M. dirhodum* and *A. fabae*) and the host specificity index indicated that *D. rapae*  
312 and *A. abdominalis* are true generalist parasitoids whereas *A. ervi* and *L. testaceipes* are  
313 likely intermediate specialist-generalist, and *B. communis* and *B. koreanus* are specialist  
314 parasitoids (Desneux *et al.* 2009a, 2009b, unpublished data).

#### 315 ***Preference traits***

316 As expected for generalist parasitoids, the three species tested showed low host selectivity,  
317 and they stung mostly all aphid species encountered at high rates. However, preference was  
318 modulated by different factors (1) *A. abdominalis* and *A. ervi* had less stung the black aphids  
319 compared to the other aphid colors (respectively,  $X^2_3 = 49.44$ ; 69.4, dispersion parameter =  
320 4.3; 7.1,  $P < 0.02$ ), (2) *A. abdominalis* and *A. ervi* stung mainly the aphids from the  
321 macrosiphini tribe (respectively,  $X^2_1 = 31.86$ ; 55.36, dispersion parameter = 4.9; 7.75,  $P <$

322 0.01) and (3) *A. abdominalis* had less stung the aphids on squash ( $X^2_3 = 60.5$ , dispersion  
323 parameter = 4.32,  $P = 0.03$ ). The presence of endosymbiont did not modulate the parasitoid  
324 preference (respectively for *A. abdominalis*, *A. ervi* and *D. rapae*  $X^2_1 = 14.24$ ; 2.21; 32.9,  
325 dispersion parameter = 6.88; 10.9; 11.6,  $P > 0.05$ ). Aphid defensive behaviors are known to  
326 potentially affect oviposition behavior of various aphid parasitoids and reduce the parasitoid  
327 host range (Kouamé and Mackauer 1991, Wyckhuys *et al.* 2008, Desneux *et al.* 2009a). In  
328 line with these studies, no relationship was found between aphid stung rates by *A. ervi* and  
329 *D. rapae* and the proportion of aphid defenses observed, suggesting that their 'quick' sting  
330 syndrome avoid aphid defenses (Desneux *et al.* 2009c, Bilodeau *et al.* 2013,). By contrast,  
331 there was a negative relationship between the proportion of aphid species stung by *A.*  
332 *abdominalis* and the proportion of aphid defensive behaviors. *Aphelinus abdominalis*  
333 showed stinging time ranging between 20 and 60 seconds, so about four times more than  
334 the two other parasitoid species tested. This behavioral pattern suggests that aphid  
335 defensive behaviors may disturb females during their stinging event (De Farias and Hopper  
336 1999, Wahab 1985). Secondly, the success of aphid defenses depends on the relative size of  
337 attacking parasitoid vs. aphid. *A. abdominalis* is two times smaller than *A. ervi* and *D. rapae*  
338 which may attack aphids more easily (Le Ralec *et al.* 2010). Finally, *A. abdominalis* did not  
339 show a particular behavior enable to lower occurrence of aphid defenses, as observed in  
340 several other aphid parasitoid species, *e.g.* antennal tapping mimicking the behavior of  
341 aphid-mutualistic ants (Völkl and Kroupa 1997).

#### 342 Performance traits

343 The three generalist parasitoids showed higher host specificity index values compared to the  
344 specialized species considered in this assessment. Indeed, *Binodoxys communis* and *B.*

345 *koreanus* are specialized on the *Aphis* genus (Desneux *et al.* 2009 a, b) whereas *L.*  
346 *testaceipes* is specialized on the *Aphidini* tribe (Desneux & Heimpel, unpublished data, figure  
347 4). By contrast, *A. abdominalis* and *D. rapae* had a successful development in both tested  
348 tribes and in different genus tested. However, *A. ervi* showed a lower host specificity index  
349 than the two other generalist species because its performance was more efficient on host  
350 from *Macrosiphini* tribe (Zepeda-paulo *et al.* 2013, Raymond *et al.* 2015), indicating that *A.*  
351 *ervi* could be considered as an intermediate specialist-generalist, *i.e.* it has the same host  
352 range than a generalist one but differ in their relative performance (Klinken *et al.* 2000).

353 Different physiological and ecological factors could give aphid resistance against immature  
354 parasitoids and modify parasitoid host range. The primary sources of resistance are poor  
355 parasitoid ability to control the host metabolism, the presence of secondary endosymbionts  
356 in aphids, and the aphid ability to sequester toxic compounds and/or the host quality itself.  
357 Generalist organisms have a successful development in a wide host range through  
358 phenotypic plasticity, *i.e.* the ability to express different phenotypes depending on the  
359 environment (Agrawal 2001) and transgenerational phenotypic plasticity, *i.e.* the offspring  
360 would be primed to develop in the host in which their mother developed (Mousseau and  
361 Fox 1998). The generalist behavior of the three parasitoid species in association with their  
362 phenotypic plasticity may rapidly develop an adaptation to novel host species (Fox and  
363 Mousseau 1998). However, becoming acclimated to its host may be costly for the  
364 parasitoids (Uller 2008).

365 The facultative endosymbionts present in aphids may compromise the successful  
366 development of parasitoids and reduce their host ranges (Ferrari *et al.* 2004, Oliver *et al.*  
367 2005, McLean and Godfray 2015). Specifically, *Hamiltonella defensa* and *Regiella insecticola*

368 are known to protect aphids against different natural enemies such as parasitoids (Oliver *et*  
369 *al.* 2003, von Burg *et al.* 2008). In this study, *A. abdominalis* was not impacted by the  
370 presence of secondary endosymbionts in aphids and had 84% of successful parasitism in *M.*  
371 *dirhodum*. The impact of *H. defensa* in the *D. rapae* development cannot be discussed  
372 because *A. fabae* and *M. dirhodum* are low parasitized. However, a high parasitoid larval  
373 mortality of *A. ervi* was observed when it encountered *A. fabae* and *M. dirhodum*, whereas  
374 *H. defensa* was detected in *A. fabae* and *M. dirhodum* and *R. insecticola* was also detected in  
375 *M. dirhodum* (as reported by Henry *et al.* 2015). However, *A. ervi* is well known to parasite  
376 Macrosiphinae species such as *A. pisum*, *M. euphorbiae*, *S. avenae* and *M. dirhodum* (Stary  
377 *et al.* 1993, Kavallieratos *et al.* 2004), suggesting that the presence of *H. defensa* and/or *R.*  
378 *insecticola* reduces the *A. ervi* host range. Several studies have shown that endosymbionts  
379 confer protection only against the more specialized natural enemies and not against  
380 generalist ones (Parker *et al.* 2013, Asplen *et al.* 2014, Hrcek *et al.* 2016, Kraft *et al.* 2017),  
381 which consolidate the hypothesis whereby *A. ervi* is an intermediate specialist-generalist.

382 Aphid ability to sequester toxic secondary metabolites when feeding on toxic plants  
383 (Mooney *et al.* 2008, Pratt *et al.* 2008) might also impact the parasitoid host range (Helms *et*  
384 *al.* 2004). The specialist aphid species *A. nerii* and *B. brassicae* are known to sequester  
385 cardenolide (*Asclepias*) and glucosinolate (cabbage) respectively (Desneux *et al.* 2009a,  
386 Jones *et al.* 2001) and these toxic allelochemical molecules have a drastic impact on  
387 immature parasitoid survival (Mooney *et al.* 2008, Pratt *et al.* 2008, Desneux *et al.* 2009a,  
388 Kos *et al.* 2011). The three generalist parasitoids cannot successfully parasitize *A. nerii*  
389 despite a high sting rate (ranged from 0.55 to 0.84). They all reached the larval stage and  
390 then died. Similarly, *A. abdominalis* and *A. ervi* cannot successfully parasitize *B. brassicae*

391 despite a high sting rate (0.73 and 0.56 respectively). However, *D. rapae* is well known to  
392 have a successful development in *B. brassicae*; suggesting the success of the acclimation  
393 through phenotypic plasticity for this parasitoid. By contrast, *M. persicae* is not a  
394 glucosinolate-sequestering aphid whether it feeds on cabbage too. It excretes the  
395 glycosinolates in its honeydew, and the impact on parasitoid offspring development is low  
396 (Weber *et al.* 1986, Merritt 1996, Francis *et al.* 2001). In our study, *A. abdominalis* has a  
397 successful development in *M. persicae* (0.73 adults in the next generation) compared to no  
398 development at all in *B. brassicae*, indicating that *A. abdominalis* is strongly affected by  
399 glycosinolates. However, *A. ervi* cannot parasitize *M. persicae* whereas it is a suitable host  
400 (Bruce *et al.* 2008, Kavallieratos *et al.* 2004, Colinet *et al.* 2005), suggesting that the aphid  
401 genotype could be involved in this failure (Bilodeau *et al.* 2013). Aphid ability to sequester  
402 the toxic compounds from their plant requires a high specialization of these aphid species  
403 (Mooney *et al.* 2008) and only a few (up to four) parasitoid species can parasitize *A. nerii*  
404 and *B. brassicae* (Kavallieratos *et al.* 2004); suggesting that robust circumventing  
405 mechanisms are needed for a parasitoid to adapt to aphid defense. Furthermore, by  
406 contrast with endosymbionts, this is a general aphid defensive against natural enemies in  
407 general and not only against parasitoids (Omkar and Mishra 2005, Toft and Wise 1999),  
408 general defenses confer a stronger protection against generalist parasitoids compared to  
409 the specialized defenses.

410 Finally, host quality could also contribute to a reduction in aphid parasitoid host range (high  
411 mortality of the older parasitoid larvae until emergence) or at least modulate their sex ratio  
412 (male-biased) (Thompson 1985, Mackauer 1986, Kouamé and Mackauer 1991, Godfray  
413 1994). The host species and the host's age are the two main components of host quality for

414 parasitoid development. However, generalist parasitoids have a weaker choosiness when  
415 encountering different hosts as shown in the behavioral results of this study. For example, *S.*  
416 *graminum* caused a high larval mortality of the three parasitoid species (consistent with  
417 Desneux *et al.* 2009a) and a high value of un-emerged parasitoids of *A. ervi* were observed in  
418 *R. padi* despite they are stung mainly by the parasitoids, indicating *S. graminum* and *R. padi*  
419 to be poor hosts for these parasitoid species. Furthermore, some parasitoids tend to place  
420 male eggs in unfavorable hosts (King 1990, Kochetova 1978). For example, the sex ratios of  
421 *Aphidius colemani* emerging adults were more male-biased from *R. padi* than from the three  
422 other aphid species (*M. persicae*, *S. graminum*, and *A. gossypii*), suggesting that *R. padi* is a  
423 poor-quality host for *A. colemani* (Ode *et al.* 2005). In *A. abdominalis*, a male-biased sex  
424 ratio was observed in *M. dirhodum*, *M. persicae* (green and red), *R. padi* and *S. graminum*;  
425 but no link among the host plant, the presence of endosymbiont, the color or the host size  
426 could explain these results except the low quality of these hosts for *A. abdominalis*.

#### 427 ***The preference-performance relationship in generalist parasitoids***

428 The meta-analysis of Cripenberg *et al.* (2010) of the preference-performance relationship in  
429 phytophagous insects described a relationship between the preference and the  
430 performance of specialists and intermediate specialists / generalists and no relationship for  
431 generalists and these results are consistent with those obtained in our study, there was no  
432 relationship between the preference and the performance of *A. abdominalis* and *D. rapae*  
433 whereas a strong relationship was observed for *A. ervi*. The phenotypic plasticity is more  
434 critical in generalist parasitoids as well as the transgenerational phenotypic plasticity, and  
435 these abilities could explain the lack of the preference-performance relationship in *A.*  
436 *abdominalis* and *D. rapae*, due to their low host selectivity and their high performance

437 among the hosts. *A. ervi* is considered as an intermediate specialist-generalist because it  
438 showed a successful development only in three of the aphid species stung; and its low  
439 selectivity can be explained by its strategy to avoid aphid defenses (highly aggressive and  
440 quick oviposition when it encountered hosts; Bilodeau *et al.* 2013). Furthermore, a possible  
441 phylogenetical signal could exist among its hosts (Zepeda-Paulo *et al.* 2013); suggesting a  
442 host phylogenetic specialization (as for *B. communis*, Desneux *et al.* 2012).

443 We demonstrated that the preference-performance relationship does occur for specialist  
444 and intermediate specialist-generalist parasitoids but not for true generalist ones; likely  
445 owing to combined effects of low selectivity and the phenotypic plasticity in generalist  
446 parasitoids. The generalists are less affected by specific aphid defenses against them (such  
447 as endosymbionts) whereas they are strongly affected by general ones that are used against  
448 natural enemies, *e.g.* aphid ability to sequester the toxic compounds (Desneux *et al.* 2009a).  
449 The preference of generalists is not an accurate proxy of actual parasitoid realized host  
450 range, *i.e.* performance. The occurrence (or lack thereof) of such relationship, as well as the  
451 host specificity index, may provide a reliable indicator of actual generalism – specialism in  
452 parasitoids.

453

454

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Table 1. Aphid species, their color, host plants and the number of replicates for each experiment (1, 2 or 3). Specifically, for the experiment 1 and 2, the number of experiment is followed by the number of replicates in the whole experiment for *A. abdominalis*, *A. ervi* and *D. rapae* respectively.

Species	Aphid color	Host plant species	Experiments (replication)			Tribe
<i>Aphis fabae</i>	Black	Bean ( <i>Vicia faba</i> )	1(32,52,30),	2(n/a,64,n/a),	3(3)	Aphidini
<i>Aphis gossipy</i>	Yellow	Squash ( <i>Cucurbita moschata</i> )	1(32,47,30),	2(n/a,69,59),	3(5)	
<i>Aphis craccivora</i>	Black	Bean ( <i>Vicia faba</i> )	1(31,70,31),	2(41,45,n/a),	3(5)	
<i>Aphis nerii</i>	Yellow	<i>Asclepias sp.</i>	1(37,63,31),	2(58,46,70),	3(5)	
<i>Rhopalosiphum padi</i>	Black	Wheat ( <i>Hordeum vulgare</i> )	1(33,67,32),	2(66,59,73),	3(4)	
<i>Schizaphis graminum</i>	Green	Wheat ( <i>Hordeum vulgare</i> )	1(32,58,40),	2(63,53,68),	3(5)	
<i>Brevicoryne brassicae</i>	Green, powder	Cabbage ( <i>Brassica oleracea</i> )	1(33,109,46),	2(65,56,76),	3(5)	Macrosiphini
<i>Myzus persicae</i>	Green or Red	Cabbage ( <i>Brassica oleracea</i> )	1(66,127, 80),	2(181,99,171),	3(10)	
<i>Sitobion avenae</i>	Green	Wheat ( <i>Hordeum vulgare</i> )	1(37,59,45),	2(82,54,78),	3(5)	
<i>Metopolophium dirhodum</i>	Yellow	Wheat ( <i>Hordeum vulgare</i> )	1(32,55,30),	2(80,52,n/a),	3(4)	
<i>Macrosiphum euphorbiae</i>	Green	<i>Solanum sp.</i>	1(64,107,60),	2(221,118,118),	3(10)	
<i>Acyrtosiphum pisum</i>	Green	Bean ( <i>Vicia faba</i> )	1(32,41,30),	2(80,42,61),	3(6)	

All aphid species belong to the family Aphididae and subfamily Aphidinae and their morphological characteristics were described by Blackman and Eastop (2006). All aphids were collected in the field in France during 2013-2014 on their respective host species and maintained in their host plant in ventilated cage (60 x 60 x 60 cm) covered by mesh under controlled conditions (23 ± 2 °C, RH 65 ± 5% and photoperiod 16:8 L:D). n/a means that data are non-available due to the unsuccessful development of the parasitoids in these aphid species.

Table 2. Proportions of aphid detected, accepted, and stung by *A. abdominalis* (Aa), *A. ervi* (Ae) and *D. rapae* (Dr) respectively when they encountered different aphid species (experiment 1).

Aphid species /Parasitoid species	Proportion of aphids detected			Proportion of aphids accepted			Proportion of aphids stung		
	Aa	Ae	Dr	Aa	Ae	Dr	Aa	Ae	Dr
<i>Acyrtosiphum pisum</i>	1	1	1	0.97	0.95	0.83	0.91	0.95	0.77
<i>Aphis craccivora</i>	1	1	0.58	0.48	0.5**	0.19***	0.48	0.49**	0.13***
<i>Aphis fabae</i>	0.94	0.92	0.83	0.34***	0.48**	0.3**	0.31***	0.42**	0.17***
<i>Aphis gossypii</i>	0.91	0.96	0.93	0.34***	0.77	0.47*	0.25***	0.77	0.37***
<i>Aphis nerii</i>	1	0.98	0.97	0.89	0.68	0.74	0.84	0.68	0.55*
<i>Brevicoryne brassicae</i>	0.97	0.96	1	0.73	0.57*	0.98	0.73	0.56*	0.96
<i>Macrosiphum euphorbiae</i> (P)	0.97	1	0.77	0.94	0.96	0.43*	0.94	0.92	0.17***
<i>Macrosiphum euphorbiae</i> (T)	0.97	1	0.93	1	0.88	0.37**	0.91	0.71	0.17***
<i>Metopolophium dirhodum</i>	0.97	0.96	0.77	0.81	0.93	0.23***	0.69	0.87	0.2***
<i>Myzus persicae</i> (Green)	0.97	0.97	1	0.84	0.94	0.79	0.77	0.94	0.67
<i>Myzus persicae</i> (Red)	0.97	1	0.93	0.69	0.93	0.63	0.69	0.91	0.54*
<i>Rhopalosiphum padi</i>	1	0.92	0.94	0.82	0.55*	0.47*	0.67	0.52*	0.38***
<i>Schizaphis graminum</i>	0.97	0.91	0.98	0.81	0.71	0.95	0.81	0.64	0.95
<i>Sitobion avenae</i>	1	1	1	0.89	0.92	0.84	0.86	0.9	0.76

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  means a significant difference compare to the rearing host (*A. pisum* for *A. abdominalis* and *A. ervi* and *B. brassicae* for *D. rapae* (in italic)) by GLM followed by multi-comparison test.

Table 3. Female sex ratio (proportions females) for each parasitoid species developing on different hosts.

Female sex ratio (proportion females)			
Aphid species	<i>Aphelinus abdominalis</i>	<i>Aphidius ervi</i>	<i>Diaeretiella rapae</i>
<i>Acyrtosiphum pisum</i>	0.67	0.73	n/a
<i>Aphis gossypii</i>	n/a	n/a	0.67
<i>Brevicoryne brassicae</i>	n/a	n/a	0.59
<i>Macrosiphum euphorbiae</i> (P)	0.44	0.60	n/a
<i>Macrosiphum euphorbiae</i> (T)	0.76*	0.56	n/a
<i>Metopolophium dirhodum</i>	0.04***	n/a	n/a
<i>Myzus persicae</i> (red)	0***	n/a	0.50
<i>Myzus persicae</i> (green)	0.09***	n/a	0.61
<i>Rhopalosiphum padi</i>	0.05***	n/a	0.59
<i>Sitobion avenae</i>	0.32	0.54	0.55
<i>Aphis fabae</i>	n/a	n/a	n/a
<i>Aphis craccivora</i>	n/a	n/a	n/a
<i>Schizaphis graminum</i>	n/a	n/a	n/a
<i>Aphis nerii</i>	n/a	n/a	n/a

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$  (deviation from a 0.5 sex ratio). n/a means that data are non-available due to the unsuccessful development of the parasitoids in these aphid species.

1 **FIGURE LEGENDS**

2 Figure 1: Relationship between the stinging rate (preference) and the aphid defensive  
3 behaviors when three generalist parasitoids (*A. abdominalis*, *A. ervi* and *D. rapae*)  
4 encountered twelve aphid species.

5  
6 Figure 2. Proportion of stinging aphids that: contained an egg (dissection after stung),  
7 contained a larva (dissection after 4 days), mummified (after 10 days) and produced an adult  
8 parasitoid for (A) *A. abdominalis*; (B) *A. ervi* and (C) *D. rapae* (experiment 2). For each aphid  
9 species, bars followed by the same letter are not significantly different (GLM followed by  
10 multi-comparison test).

11  
12 Figure 3. Relationship between the stinging rate (preference) and the emergence rate  
13 (performance) when three generalist parasitoids (*A. abdominalis*, *A. ervi* and *D. rapae*)  
14 encountered twelve aphid species.

15  
16 Figure 4. Host specificity index ( $S_{TD}^*$ ) values and ranking of the parasitoids according to their  
17 degree of specialization.

18 Figure 1.

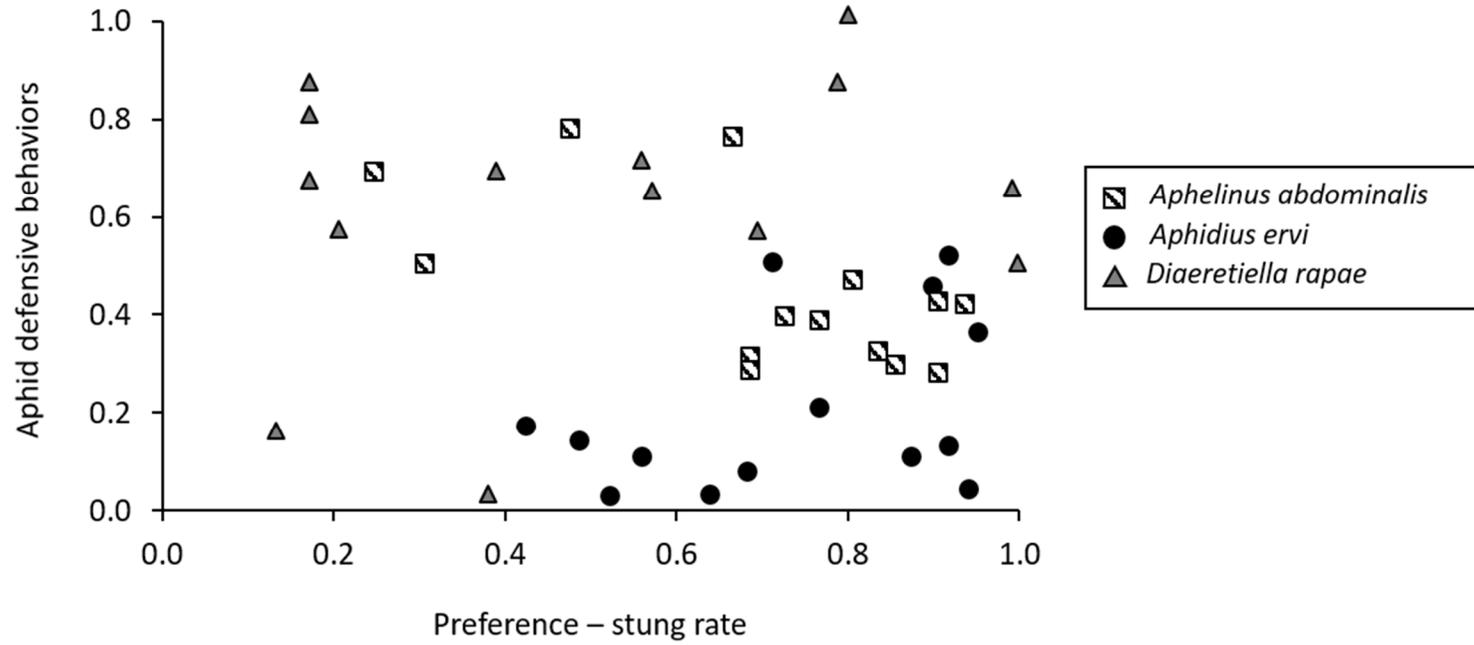
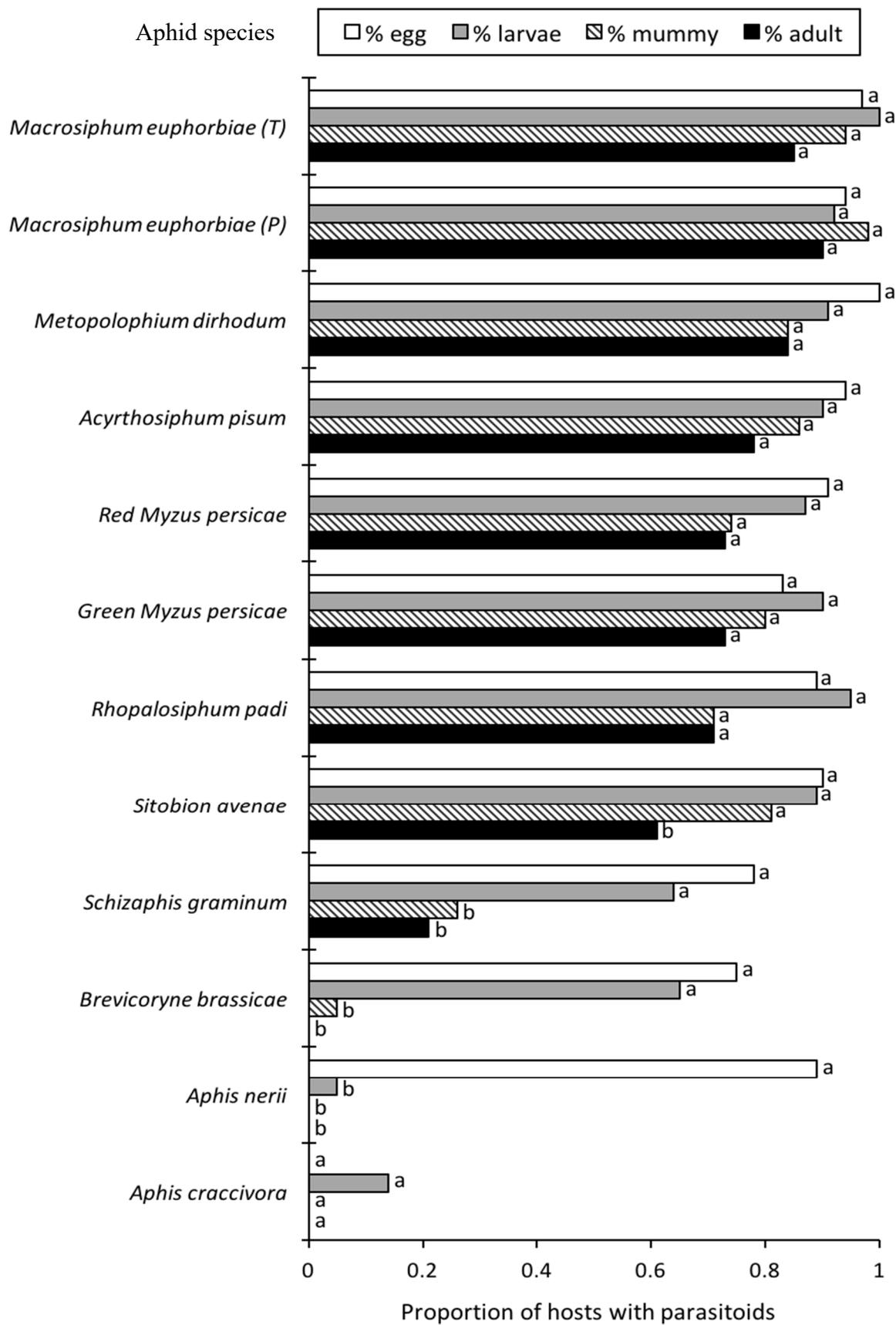
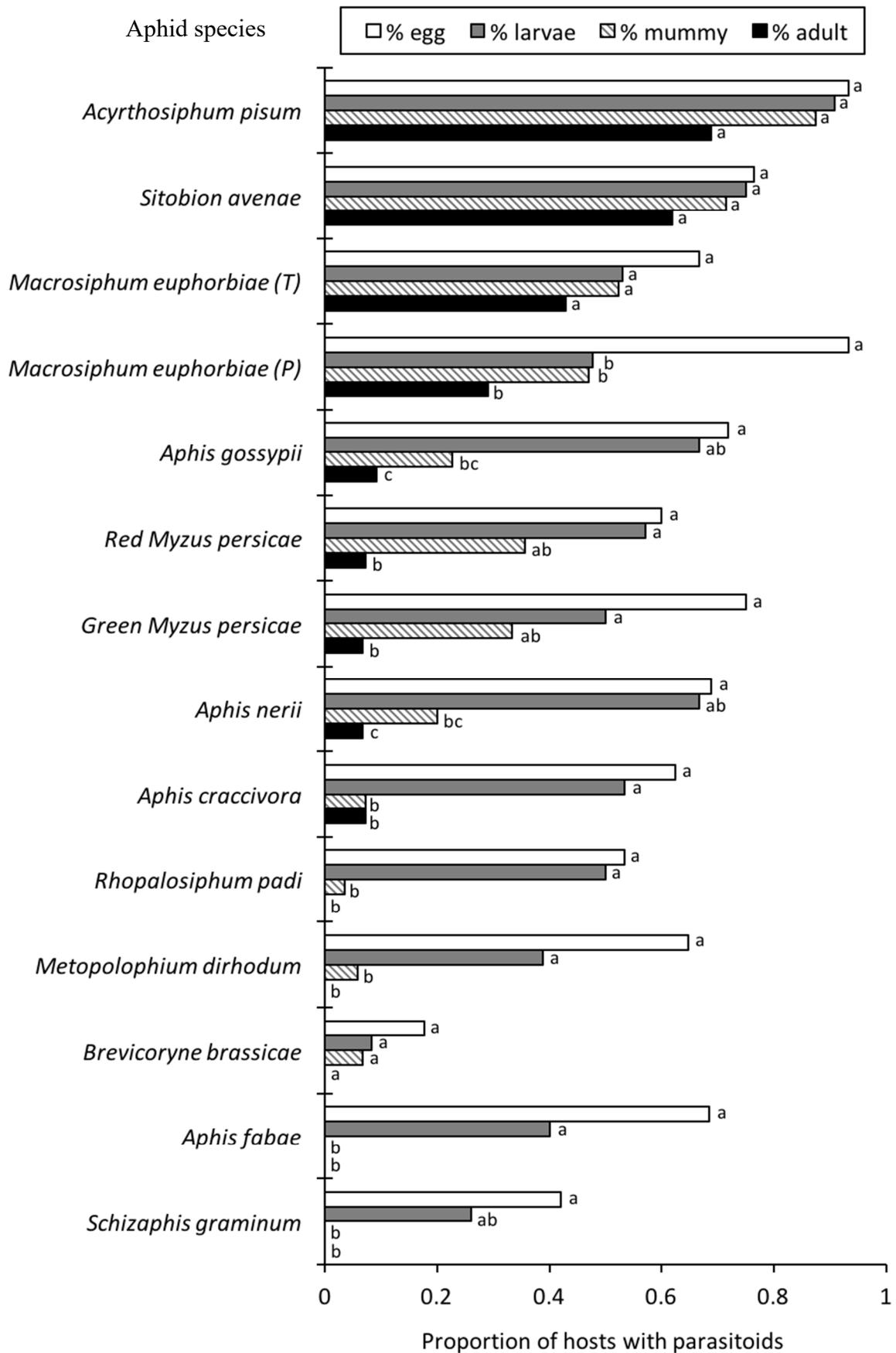


Figure 2. A. *Aphelinus abdominalis*



**Figure 2. B. *Aphidius ervi***



**Figure 2. C. *Diaeretiella rapae***

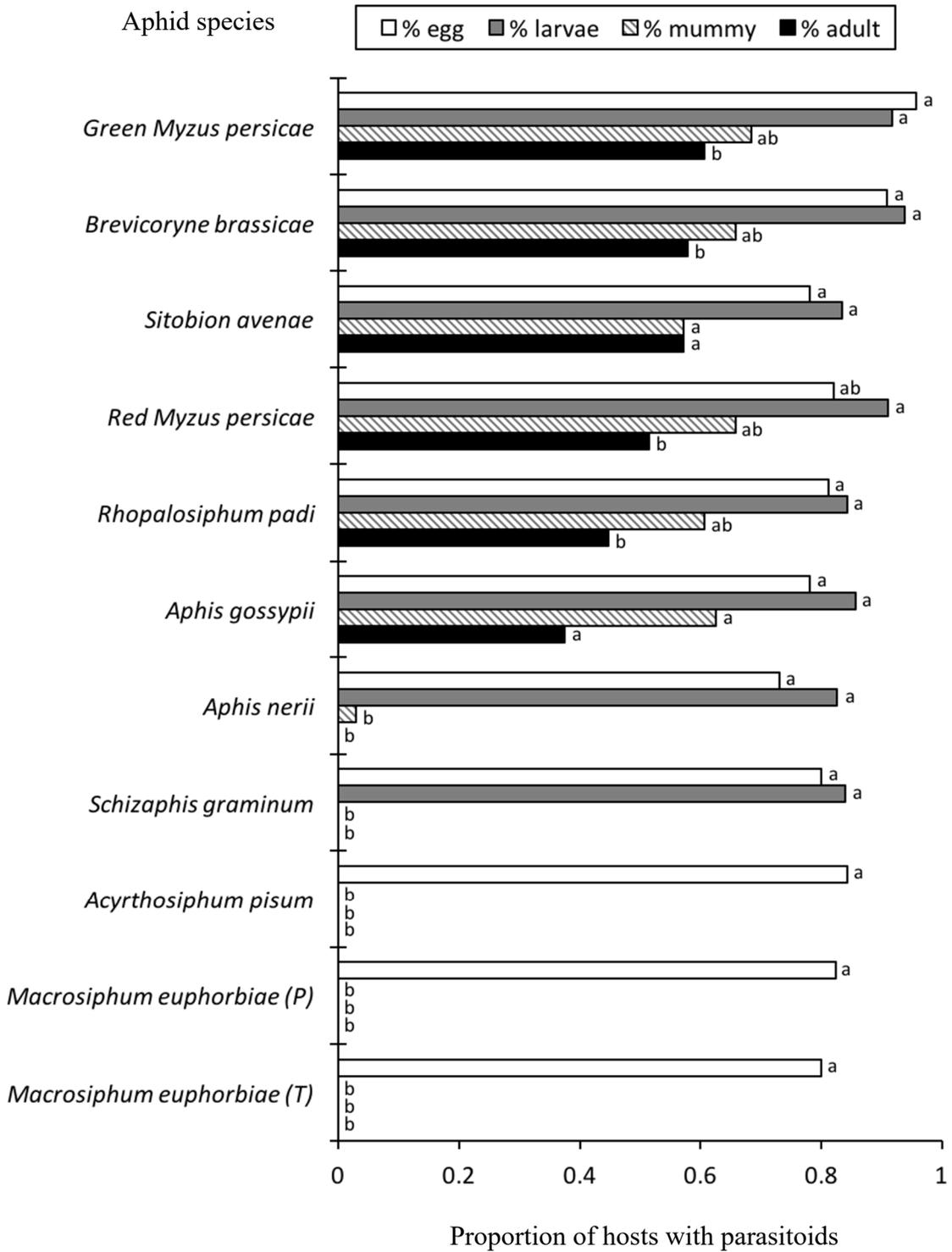
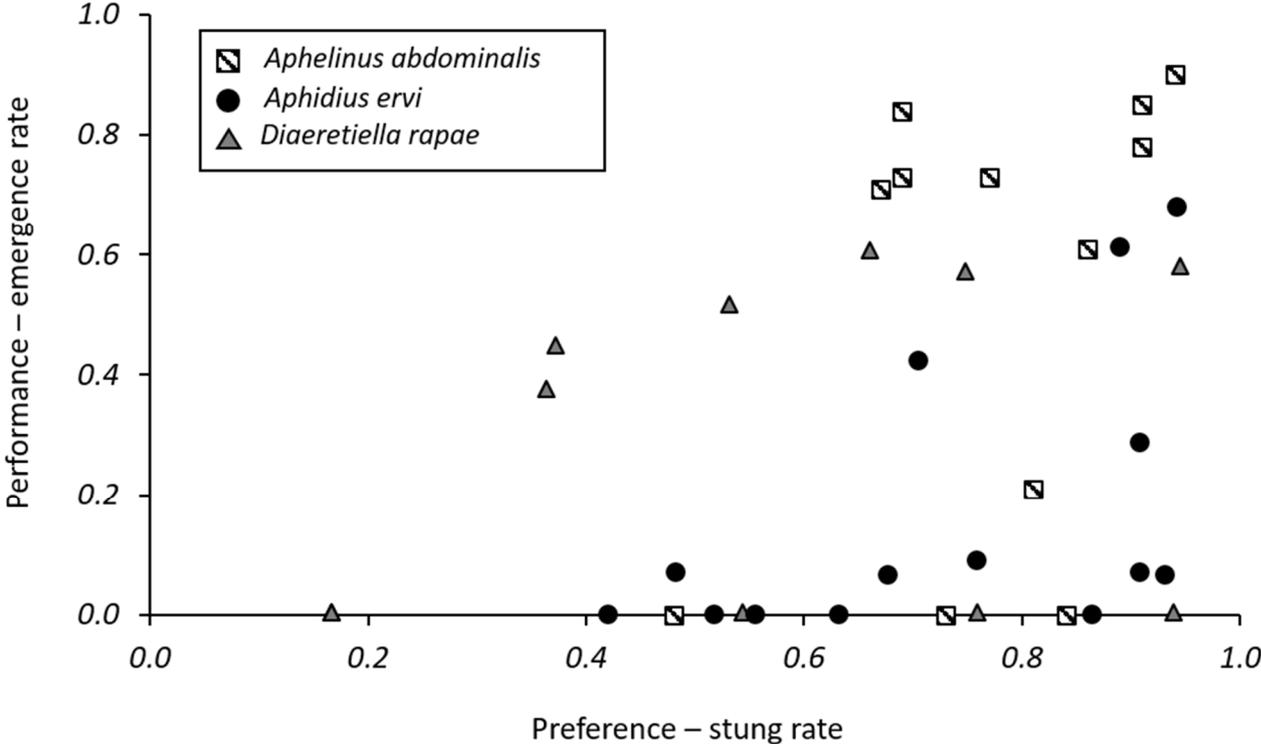


Figure 3.



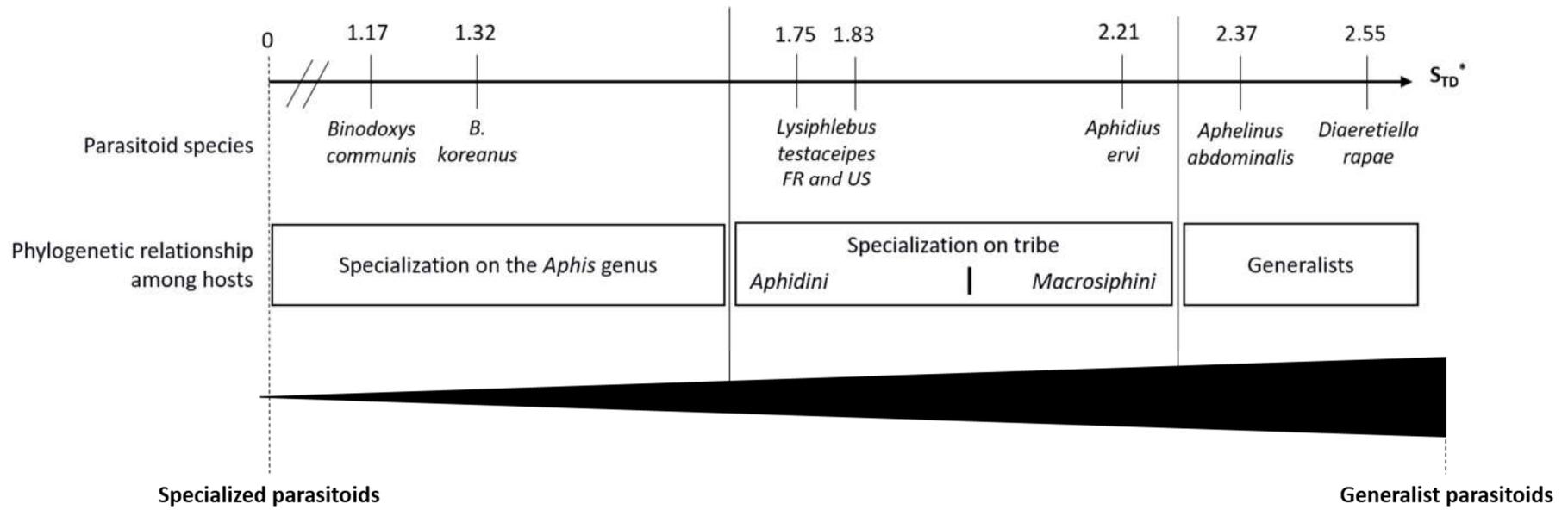


Figure 4.

**SUPPLEMENTARY TABLE AND FIGURE.**

**Figure S1.** Relationship between the stinging rate (preference) and the emergence rate (performance) when three generalist parasitoids (*A. abdominalis* (A), *A. ervi* (B) and *D. rapae* (C)) encountered twelve aphid species.

Supplementary material 1. Endosymbiont targeted, the target gene, the primer name, the primer sequence (5'-3'), the expected product size (in bases), the temperature of melting (TM) and the references.

Target	Target gene	Primer name	Sequence (5'-3')	Expected product size (bases)	Tm	References
<i>Hamiltonella defensa</i> (T-type)	16S rDNA	16S-8F 16S-480R		480	53	
<i>Buchnera</i>	<i>DnaK</i>	BuchDnaK_12F BuchDnaK_162R		150	53	
<i>Regiella insecticola</i> (U-type)	16S rDNA	16S-8F 16S-R2		1000	56	
<i>Rickettsiella</i>	16S rDNA	P136F-16S P136Ric-470R-16S		300	60	
PAXS	16S rDNA	PAXS F-16S PAXS R-16S		500	58	
<i>Serratia symbiotica</i> (R-type)	16S rDNA	16S-8F PASS1140R		1140	54	
<i>Rickettsia</i>	16S rDNA	ricCsA-318-F-GltA ricCsA-318-R-GltA		318	54	
<i>Spiroplasma</i>	16S rDNA	Spi 618834-F-16S Spi 618834-R		234	54	
<i>Wolbachia</i>	<i>FtsZ</i>	Wol-FtsZ-F Wol-FtsZ-R		400	53	
<i>Arsenophonus</i>	<i>yaeT</i>	Ars-yaeT-F Ars-yaeT-R		438	59	

Figure S1. A. *Aphelinus abdominalis*

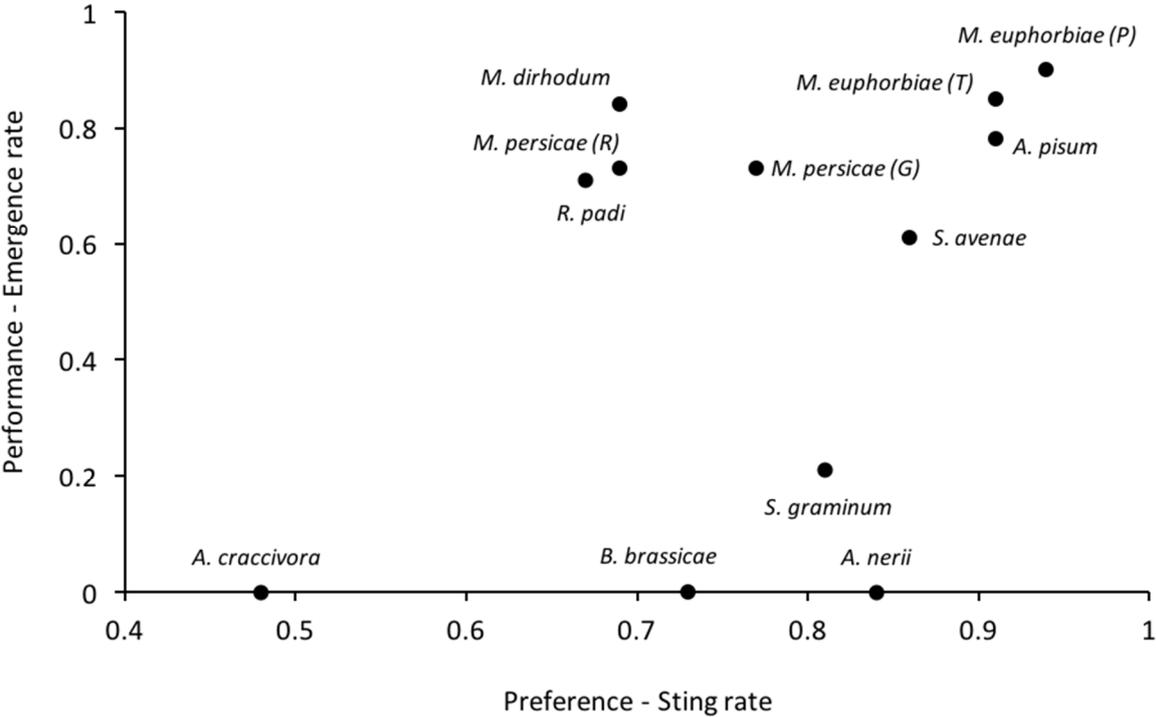


Figure S1. B. *Aphidius ervi*

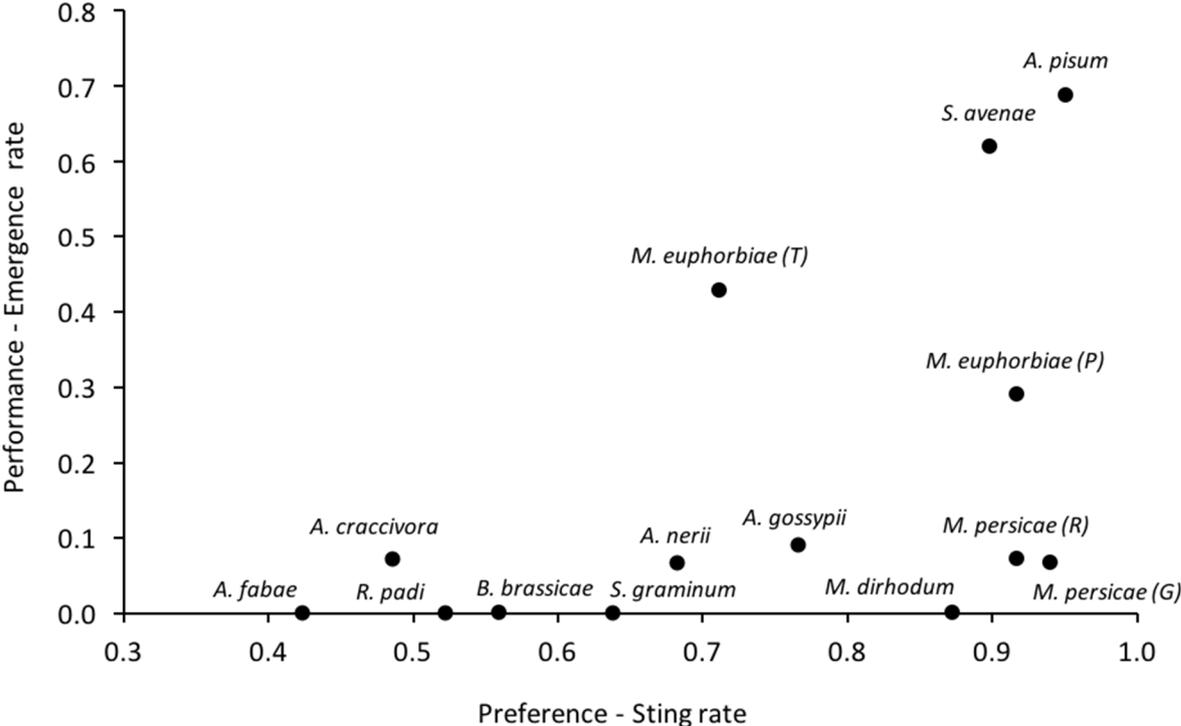
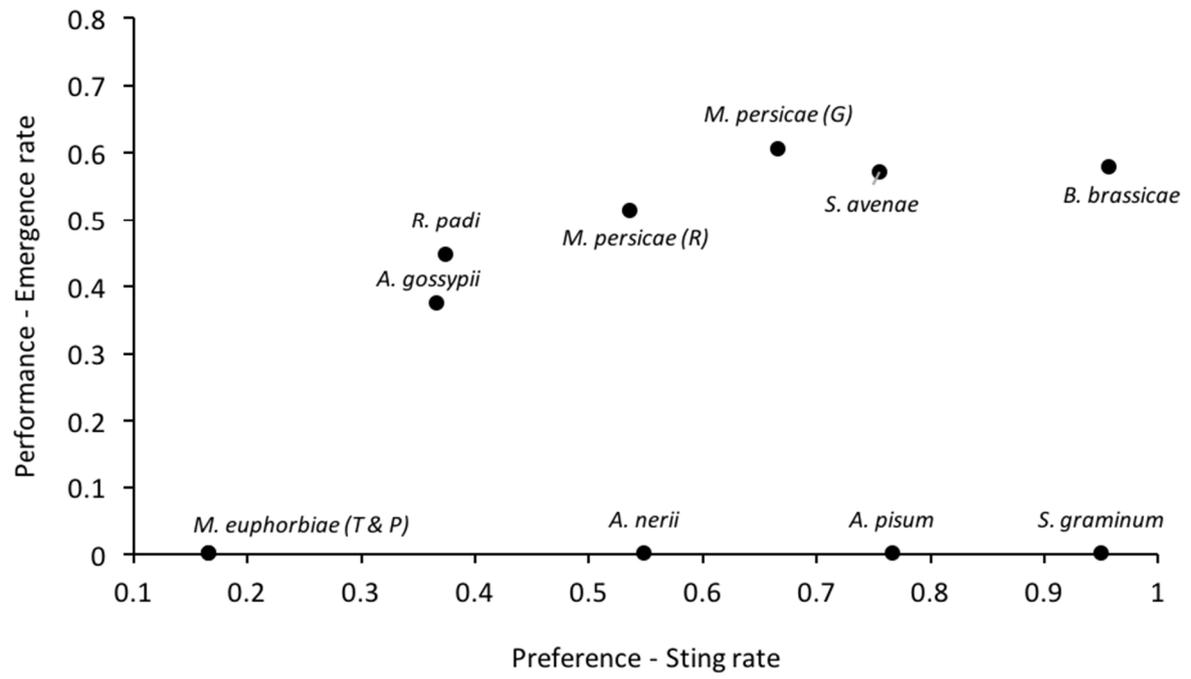


Figure S1. C. *Diaeretiella rapae*



## Chapter 5. Water stress-mediated bottom-up effects on aphid parasitoid diet breadth

### Context

In the previous chapter, we investigated the fundamental host ranges of three parasitoids: *A. ervi*, *A. abdominalis* and *D. rapae* under laboratory conditions (Figure 32). However, as seen before, the fundamental host range could differ from the field host range. For example, the field inefficiency of *A. abdominalis* is well known despite its good parasitism rate in the laboratory (Holler and Haardt 1993). Our next question is to disentangle the difference between fundamental and field host range by defining which environmental factors influence the parasitoid host specificity and how? Within the plant-aphid – parasitoid tritrophic system, the determinants of the host specificity could come from biotic interactions among them and with other trophic levels, *e.g.* endosymbionts (see article 1) or from abiotic environmental conditions ().

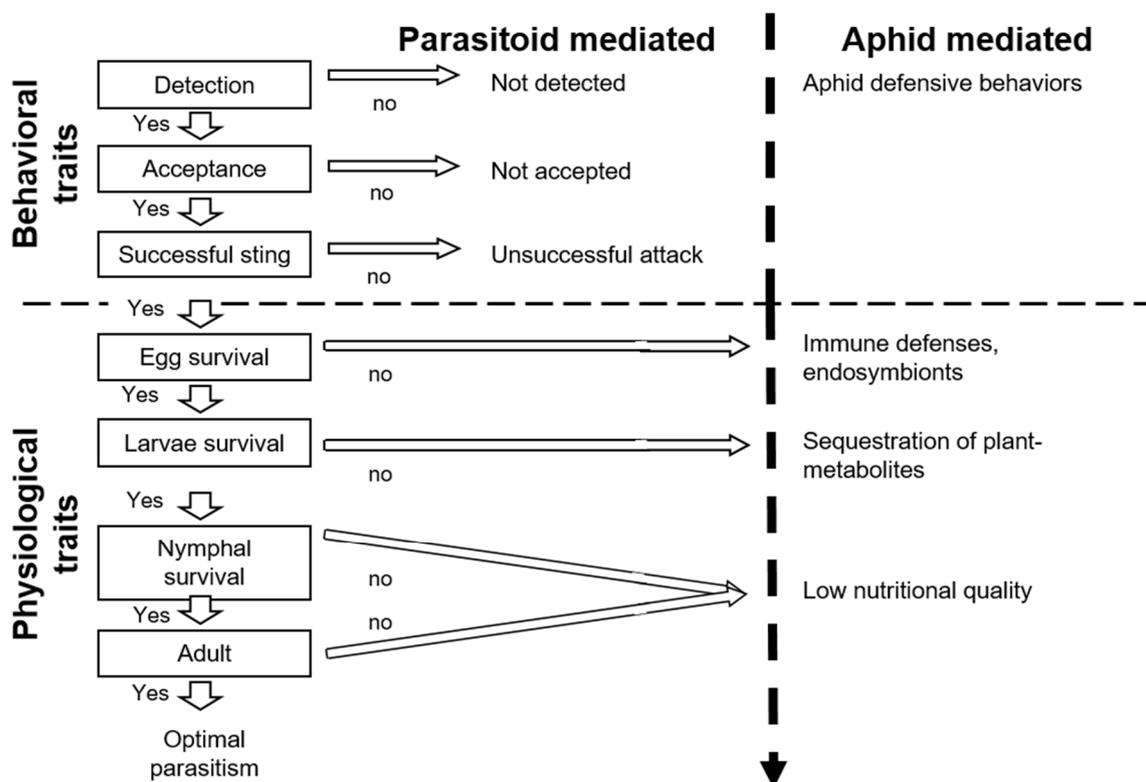


Figure 32. Parasitoid responses at each step of parasitism process and possible mechanisms of their mortality (from Desneux 2009a).

Among these factors, plant stress causes the most chronic harmful effects on parasitoid performance in greenhouses compare to the other biotic factors (, Prado *et al.* 2015). In the field, bottom-up effects of abiotic factors on plants are significantly stronger than biotic forces (Schuldt *et al.* 2017). Environmental abiotic stressors, *i.e.* water supply, salt or nutrition may affect plant quality including, morphology, nutritional quality or defense. Those impacts may reach parasitoids by plant-mediated or aphid-mediated bottom-up effects (, Hunter 2003). For example, the acceptance, *i.e.* parasitoid attack and oviposit on) and suitability of an aphid as parasitoid host depends on both aphid host quality (nutritional quality and behavior) and aphid host density (the probability of encounter) (Mackeur *et al.* 2012).

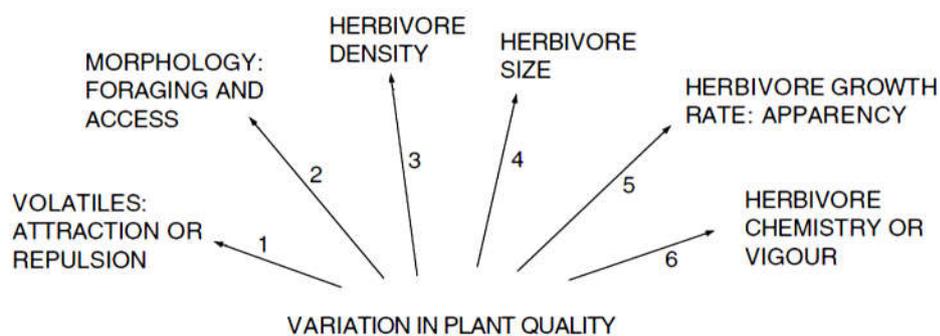


Figure 33. Synthesis of bottom-up effects of plants on parasitoid community (from Hunter 2003)

We focused on the bottom-up effect of abiotic stresses on the host specificity of parasitoids. Firstly, we performed an analytic review on the bottom-up effects of all abiotic stresses on the tri-trophic plant-aphid-parasitoid to define the most relevant factor for our experimental set-up. Secondly, we chose one parasitoid among our three parasitoids based on previous results (chapter 4). Thirdly, we designed experiments to question the ability of such abiotic factor to modulate the host range of our parasitoid (**Erreur ! Source du renvoi introuvable.**).

## 1. Choice of a relevant abiotic factor to analyze impacts of bottom-up effect on the host specificity of parasitoids

### ***Gathering data***

To gather all articles on the subject 'bottom-up effects of abiotic stress on aphid parasitoids', we based on the process of meta-analysis review (Koricheva *et al.* 2013). The first step of the process consisted of the construction of a database of all relevant articles based on Web of Science<sup>®</sup>.

We chose the following combination of keywords for searching on Web of Science<sup>®</sup>: *((aphid\* OR apheli\*) AND parasitoid AND (stress\* OR abiotic OR drought OR water OR inundation OR logged OR dry OR dessic\* OR sal\* OR temperature OR winter OR cold OR heat OR cool OR thermal OR nutri\* OR fertili\* OR nitrog\* OR potassium OR phosphat\* OR light OR UV OR ozone OR elevated OR climat\* OR weather OR plant condition OR plant quality OR bottom-up OR humidity OR wind)) NOT whitefly NOT moth NOT coccine\* NOT ladybeetle*.

To eliminate irrelevant studies, we considered only studies that question the bottom-up effect of abiotic factors on the tritrophic system 'plant-aphid – parasitoid'. These studies contain data sets from both optimal and stress conditions (average +/- variance). Finally, the following set of criteria were applied:

- a. Research year: all, between 1990 and 2016
- b. Studies on tritrophic: plants – aphids - parasitoids
- c. Data: related to the performance of species or population under stress condition versus optimal conditions.
- d. Direct impacts of temperature on parasitoids, *e.g.* storage temperature without plant or aphid presence are not considered.

Based on these keywords, 746 studies were found. By reading titles, abstracts or if necessary, articles, 230 articles that followed our criteria were chosen (annex 1, figure 36). However, only 18 studies provide the required information, *i.e.* the parameters of three trophic under optimal conditions and abiotic stress; the number of replications for each trophic. Those are studies of Garratt *et al.* (2010); Bannerman *et al.* (2011); Johnson *et al.* (2011); Wu *et al.*

(2011); Gillespie *et al.* (2012); Aslam *et al.* (2013); Cayetano and Vorburger(2013; Ismail *et al.* (2013); Romo and Tylianakis(2013; Tariq *et al.* (2013); Le Lann *et al.* (2014); Meisner *et al.* (2014); Aqueel *et al.* (2015); Jerbi-Elayed *et al.* (2015); Mace and Mills(2015; Sanders *et al.* (2015); Flores-Mejia *et al.* (2016); Moiroux *et al.* (2016).

In one the case study of meta-analysis review (chapter 5, p. 48, Koricheva *et al.* 2013), initial results were 2845 studies found by keywords, they reduced to 124 relevant papers, and finally, only 20 documents providing necessary information. The process of our data research was hence appropriate. However, more studies should be added to complete the data analysis.

### ***Data extraction and statistical analysis***

We extracted all data related to the modifications on different parameters of life-history traits of the three trophic levels: plant-aphid-parasitoids. The parameters for plants were morphology, primary metabolism, and secondary metabolism. The parameters for both aphids and parasitoids were the preference, performance, and population dynamics. The data were extracted from tables or figures using ImageJ. Three experimental scales have been taking on: laboratory, greenhouse or on the field. We quoted the stress type (drought, nutrients, temperature) and the ways those stresses were applied (continuous or pulsed). The data were analyzed by Pearson's Chi-squared test with Yate continuity correction to compare the performance of plants, aphids, and parasitoids between optimal and stress conditions. The purpose was to find if abiotic factors have a significant impact on the third trophic level, *i.e.* parasitoids. We counted the number of parameters of performance that reduced (optimal>stress), increased (optimal<stress) or did not change (optimal = stress) under stress conditions.

### ***Results***

Abiotic factors have significant impacts on the whole system (,  $p$  value < 0.001). Among all types of abiotic stress, continuous water limitation adversely affected parasitoid life-history traits ( $p$  value < 0.001) and plants ( $p$  value = 0.013). However, aphids were only marginally impacted ( $p$  value = 0.056). There are few data on how pulsed water stress affected the tri-

trophic system. Huberty and Denno (2004) suggested that pulsed water stress could indirectly benefit aphids as senescence plants release nutrients to the phloem.

The other stressors such as light and temperature imply both bottom-up effects and direct effects on the other trophic levels (). Light conditions did not cause significant impacts on plants or aphids ( $p$  value  $> 0.05$ ) but significant impacts on parasitoids ( $p$  value = 0.02). Temperatures have negative impacts on all organisms (plants:  $p$  value = 0.001; aphids:  $p$  value = 0.0098; parasitoids:  $p$  value = 0.032). However, it is not clear whether impacts of temperatures on insects are direct or indirect because aphids and parasitoids are temperature sensible (Godfray 1994; van Emden and Harrington 2007). There was no evidence of bottom-up effects of nutrient stress on the whole system or at each trophic level.

Table 2. Bottom-up effects of abiotic factors including water supply, nutrient supply, light, and temperature. The data were analyzed by Pearson's Chi-squared test with Yate continuity correction (test of significance) to compare the performance of plants, aphids, and parasitoids between optimal and stress conditions. Code of the threshold to reject the null hypothesis of no difference between optimal and stress condition:

\*  $p$  value < 0.05, \*\*  $p$  value < 0.01, \*\*\*  $p$  value < 0.001, N/A: not enough data to conclude

Factor	Trophic	Impacts of abiotic stress (Numbers of variables of organism's performance)			$\chi^2$	$p$ value	Statistical significance
		positive	negative	not significant			
		(control < treat)	(control > treat)	(control = treat)			
1. All stress	All	192	409	16	39.72	< 0.001	***
2. All drought	All	25	86	1	16.89	< 0.001	***
3. Continuous drought	All	18	71	1	15.95	< 0.001	***
4. Pulsed drought	All	7	15	0	0.85	0.358	
5. Light	All	35	80	1	8.32	0.004	**
6. Nutrients	All	42	46	0	0.02	0.880	
7. Temperature	All	90	197	14	19.87	< 0.001	***
8. Continuous T°	All	20	31	0	0.79	0.373	
9. Pulsed T°	All	70	166	14	19.53	< 0.001	***
10. All stress	Parasitoids	113	219	12	16.72	< 0.001	***
11. All drought	Parasitoids	14	41	0	5.99	0.014	*

<b>12. Continuous drought</b>	Parasitoids	7	29	0	6.13	0.013	*
<b>13. Pulsed drought</b>	Parasitoids	7	12	0	0.23	0.630	
<b>14. Light</b>	Parasitoids	18	40	1	5.15	0.023	*
<b>15. Nutrients</b>	Parasitoids	28	42	0	1.04	0.310	
<b>16. Temperature</b>	Parasitoids	53	91	11	4.58	0.032	*
<b>17. Continuous T°</b>	Parasitoids	14	27	0	1.49	0.220	
<b>18. Pulsed T°</b>	Parasitoids	39	64	11	2.59	0.011	**
<b>19. All stress</b>	Aphids	53	111	3	9.87	0.002	**
<b>20. All drought</b>	Aphids	1	12	0	3.64	0.056	* (marginally)
<b>21. Continuous drought</b>	Aphids	1	9	0	2.14	0.056	* (marginally)
<b>22. Pulsed drought</b>	Aphids	N/A					N/A
<b>23. Light</b>	Aphids	17	33	0	2.01	0.156	
<b>24. Nutrients</b>	Aphids	N/A					
<b>25. Temperature</b>	Aphids	29	66	3	6.66	0.010	**

<b>26. Continuous T°</b>	Aphids	6	4	0	N/A		
<b>27. Pulsed T°</b>	Aphids	23	62	3	8.45	0.004	**
<b>28. All stress</b>	Plants	26	79	1	13.17	< 0.001	***
<b>29. All drought</b>	Plants	10	33	1	6.06	0.014	*
<b>30. Continuous drought</b>	Plants	10	33	1	6.06	0.014	*
<b>31. Pulsed drought</b>	Plants	N/A					N/A
<b>32. Light</b>	Plants	N/A					N/A
<b>33. Nutrients</b>	Plants	8	4	0	0.17	0.679	
<b>34. Temperature</b>	Plants	8	40	0	10.55	0.001	***
<b>35. Continuous T°</b>	Plants	N/A					N/A
<b>36. Pulsed T°</b>	Plants	8	40	0	10.55	0.001	***

For this study, we focused on water limitation. Firstly, water stress is one of the most common abiotic factors that adversely affected the agriculture, perturbed the agrosystem and cause severe economic and social damage (FAO 2015; Ziolkowska 2016). Secondly, water limitation could have bottom-up effects (indirect impacts starting from lower trophic level) on parasitoids: however, the incomes are both negative and positive, varying with stress nature and herbivore species (Price 1991; Huberty and Denno 2004; Ramegowda and Senthil-Kumar 2015).

There are so far six articles relevant to our subject of “bottom-up effects of water limitation on aphid parasitoids” (table 5). In general, all studies suggest a decrease of parasitoid efficiency in host suppression (Johnson *et al.* 2011; Shipp *et al.* 2011; Amini *et al.* 2012; Tariq *et al.* 2013; Aslam *et al.* 2013; Romo and Tylianakis 2013).

*Table 3. Articles on the subject: “Impacts of water stress on the tritrophic plant-aphid-parasitoid system.” Results were found from the database of Web of Science ®. Codes of experimental scales: laboratory: L, Greenhouse: G, Field: F, Observation in the field: O. NE stands for all parasitoids.*

Year	Scale	Parasitoid species	Reference
2012	O	<i>Diaeretiella rapae</i>	Amini <i>et al.</i> (2012)
2013	L	<i>Aphidius ervi</i>	Aslam <i>et al.</i> (2013)
2011	L	<i>Aphidius ervi</i>	Johnson <i>et al.</i> (2011)
2013	L	<i>Diaeretiella rapae</i>	Romo and Tylianakis (2013)
2011	G	<i>Aphelinid spp.</i>	Shipp <i>et al.</i> (2011)
2013	L	<i>Aphidius colemani</i>	Tariq <i>et al.</i> (2013)

**Explanations of possible bottom-up impacts**

Effects on parasitoids may be modulated by the herbivorous interactions between aphids and their host plant (). Water deficiency in plants may decrease the emission of plant volatiles which serves as cues for parasitoids (Weldegergis *et al.* 2015) resulting in parasitoids less prefer infested plants (Aslam *et al.* 2013, Tariq *et al.* 2013). Herbivore density and size could be modulated by the stress tolerance of plants, which result in affected plant nutritional quality and/or immune system. One scenario of plant stress tolerance is their secondary pathways activated producing insecticidal toxins like phenolic compounds (Caretto *et al.* 2015). Those toxins to protect infested plants could delay insect growth and make them more susceptible to natural enemies by diminishing the herbivorous immune response or performance (Ibanez *et al.* 2012). On the contrary, the plant insecticidal compounds may act like “arms race” of aphids by deterring the performance of parasitoids (Züst and Agrawal 2015) if aphids could sequester them. More specifically, aphids can sequester polar toxic compounds or tolerate apolar induced compounds at low concentration (Züst and Agrawal 2016). Morphological modification in plants can influence the overall parasitic efficacy. The structural morphology of plants may be enhanced (Couture *et al.* 2015) that cause difficulty for herbivores in foraging. The altered plant quality is accompanied by the reduction in aphid population and the loss in a number of survival parasitoids. In another case, the increase in flower-head size provides shelter for herbivores and reduce the parasitism (Dias *et al.* 2010). Another critical factor is the presence of symbionts on aphids. Plant host’s stresses can impact the bacterial population on aphids following by the alter the resistance of aphid to parasitism (Cayetano and Vorburger 2013). Overall, the effects of plant hosts quality under stresses on parasitoids are mutually determined by several factors (). It thus hard to predict the trend of the host range of parasitoids under bottom-up effects.

## **2. Choice of a relevant ‘plant-aphid-parasitoid’ tritrophic system to analyze the host range modulation**

Among our three tested parasitoids, we interest in *A. ervi*. Firstly, *A. ervi* are intermediate (host) specialist. This intermediate position may allow a shift toward a more generalist or specialist pattern in a variable environment. There is a hypothesis on intermediate specialists/generalists which extinct due to their low efficient adaptation strategy (Colles *et al.* 2009, Buchi and Vuilleumier (2014). We would like to test the adaptability of *A. ervi* to

modulate its host range under environmental stresses. Moreover, *A. ervi* is commonly used as a biological model to study ecological concepts and evolution mechanisms (annex chap5 table 8). These studies may provide hints for mechanisms underlying the results of bottom-up effects we observed.

Based on previously established host range part for *A. ervi* (chap 4, **Erreur ! Source du renvoi introuvable.**), we chose six aphid species assemblage which is different on taxa and biological traits. Three relatively good aphid hosts (more than 40% emerging adults) were selected: *Sitobion avenae* on wheat and *Acyrtosiphon pisum* on faba beans and *Macrosiphum euphorbiae* on potato. *Myzus persicae* on cabbage were also selected as medium host (10% emerging adults). All of them belong to the Macrosiphini tribe as the host aphid phylogeny was described previously as a significant factor to explain the host range (chap 4). For the other aphid hosts, *A. ervi* accepted at low ratio and were not capable of forming mummies inside the rest hosts. We excluded them except for *Aphis nerii* on Asclepias and *Rhopalosiphum padi* on wheat to also test our hypotheses on bad hosts from the Aphidini tribe.

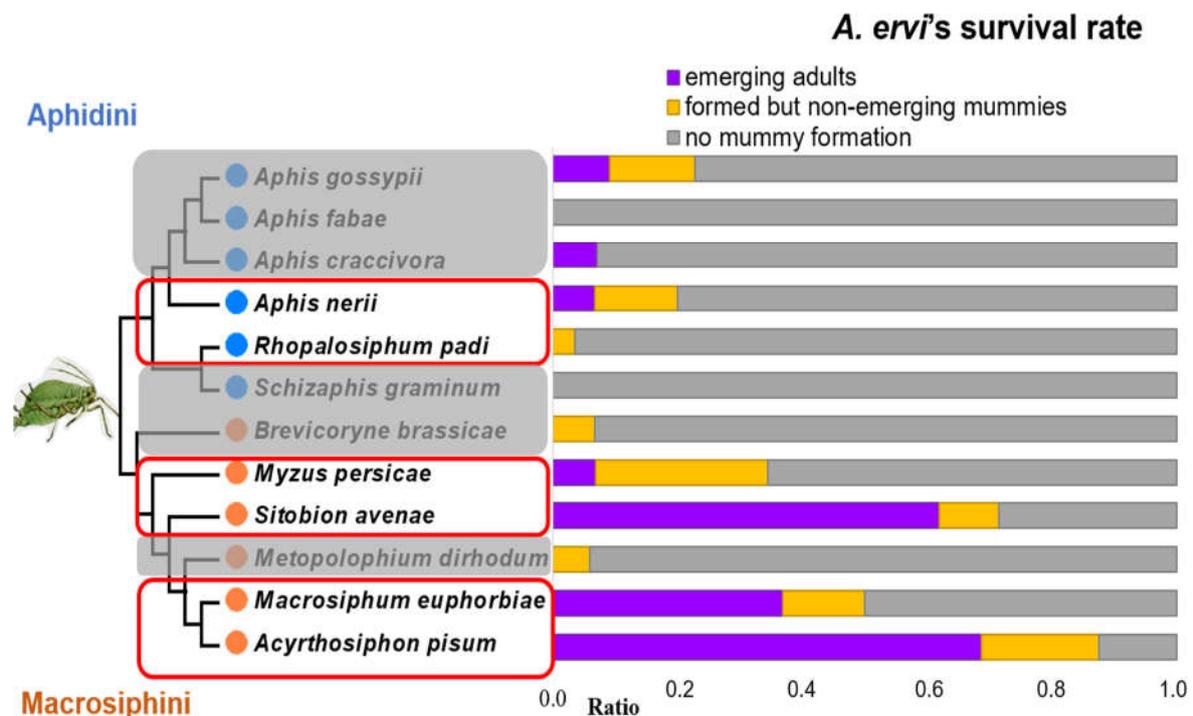


Figure 34. Host range testing of *Aphidius ervi* under water limitation condition. The red-boxed aphid names were chosen for the previous experiment (chapter 4): *Sitobion avenae*

*and Acyrthosiphon pisum (good hosts), Myzus persicae and Macrosiphum euphorbiae (medium hosts), Rhopalosiphum padi (reported as host in the field), and Aphis nerii (attacked at high rate but unsuitable for A. ervi development).*

### **3. Experimental set-up: Does water limitation bottom-up effect modulate *A. ervi* host specificity?**

To disentangle the effect of environmental conditions on the host range modulation, we wanted to test the effect of abiotic factors on our host range indexes previously described (chap 4): the host specificity index and the correlation preference-performance. Our question is whether these indexes would change under water limitation conditions. Firstly, we tested the eventuality of bottom-up effects on two equally good hosts for *A. ervi* (article 2), *i.e.* whether the impact of water limitation could reach and influence the preference and performance of *A. ervi*. Secondly, we increased the diversity of aphid hosts in quality and quantity to test the impact of bottom-up effect on the correlation preference-performance and host specificity. Moreover, if there is an impact, what happens at the lower trophic level that could explain such result (articles 3)? Our hypothesis was that plant water limitation could affect the preference and performance of *A. ervi* due to modifications at the plant levels such as defense, morphology or nutritional quality as suggested by Becker *et al.* (2015). As a result, *A. ervi* host specificity would be impacted by water limitation.

In this study, we chose to apply a long-term and continuous water stress treatment (30% of soil saturation level) compare to optimal conditions (100% of soil saturation in all plants except 70% in cabbage). To define the relevant level of water, we monitored a pre-experiment to test the effect of different water conditions on plant and aphid biological traits. The threshold of 30% was a compromise between an apparent effect of water on plant traits compare to optimal conditions and an acceptable rate of aphid survival when reared on plants submitted to water limitation.

We applied the same host range testing method as previous chapter 4. The biological traits of both plants, aphids, and parasitoids were measured to evaluate the impacts of water limitation. We also calculated two host specificity indexes: the ***Taxonomic index of specificity*** (Poulin & Mouillot 2005) which put weigh of specificity on the taxonomic distance among hosts; and the ***Rohde index of specificity*** (Rohde & Rohde 2008), which measures host specificity based on the parasitism rates on hosts (Chapter 1.4.1).

#### **Water limitation impact preference and performance of good host (article 2)**

We were able to show that the impact of water limitation can reach the higher trophic level of natural enemies even when plants and aphids tolerate the applied stress but this effect is not similar in different plant-aphid complexes, yet the relative host qualities are identical. Plant and aphid traits were negatively affected by water limitation, which might be related to the reduction of host use efficiency of *A. ervi*. The next question is: whether water limitation impacts on *A. ervi* performance on sub-optimal hosts or host feeding on toxic plants? Would the results be similar across all plant-aphid combinations?

### **Water conditions modulate *A. ervi* host specificity (article 3)**

We observed that water limitation has negative impacts on parasitoid development in medium and good host quality (*M. persicae*, *M. euphorbiae*, and *S. avenae*). The mortality of parasitoids on low-quality hosts like *R. padi* or *A. nerii* remains high which is not different under both water conditions. Our explanation comes from different defense strategies of plants and aphids under combined stresses, and the nutritional quality of both plant and insect. Under severe and/or continuous drought conditions, plants' nutrient resources reduce as a trade-off for stress tolerance which reduces herbivore fitness (Price 1991, Huberty and Denno 2004). At the same time, the hardened structure of plants, the stomatal closure or the increase of plant trichome under stress may cause difficulty for herbivores in foraging (Couture *et al.* 2015). The two mechanisms probably cause the decrease of *A. ervi* performance on *M. persicae*, *M. euphorbiae* and *S. avenae*.

However, on native host species (*A. pisum*), both preference and performance of *A. ervi* were unchanged. The resistance of *A. ervi* developed on *A. pisum* under cascade impacts of drought could be explained by the effectiveness of the placenta-like structure of larval parasitoid which drives adequate nutrients for larvae, the efficiency of plant symbioses (rhizobacteria) in protecting beans from combined stress.

Besides, we observed that the optimal strategy for *A. ervi* is not efficient under water limitation *i.e.* the correlation between preference and performance is lost under stressed conditions compared to optimal conditions. Our study provides evidence for the model of the trade-off between host range breadth and host use efficiency as suggested by Straub *et al.* (2011).

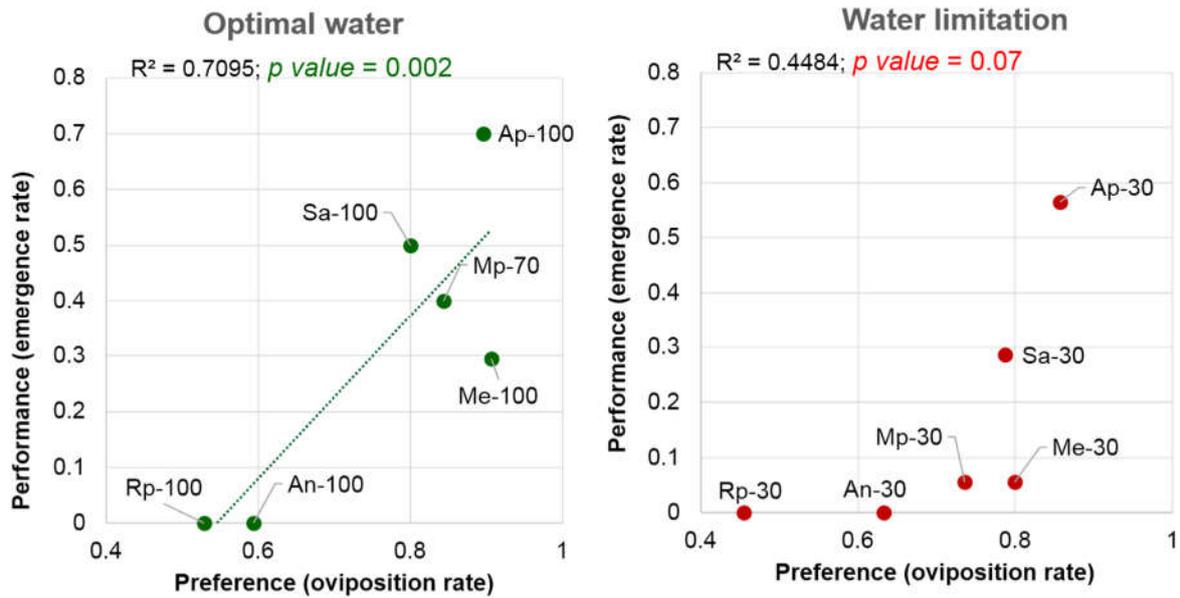


Figure 35 Impacts of soil water limitation on the relation preference – performance of *Aphidius ervi*

Interestingly, the impacts of water limitation on the preference and performance of *A. ervi* were reflected on the shift of host specificity indexes. Among two indexes, the  $S_{TD}^*$  similar, but the LW  $S_s$  decreased in compare to OW (0.61 and 0.77, respectively). The result means that *A. ervi* became more specialist under water limitation as they could develop well on only one aphid host, *A. pisum*. The decrease of host specificity is relevant to the model of Klinken (1999) (see chapter 1.4). The Rhode index, in that case, is more relevant than the  $S_{TD}^*$  as it could detect the subtle change in host specificity through parasitoid performance and *A. ervi*, under both LW and OW, had the same host range.

In this study, we highlight the environmental context-dependent of outcomes of abiotic stress effects. The information of abiotic factors then should be considered before choosing and releasing on BCA on the field. This study also helps to predict the efficiency of one BCA on the field, which also depends on the host range of both herbivores and parasitoids.

Table 4. Biotic and abiotic factors affecting the host specificity of aphid parasitoids (adapted from Hunter 2003, Prado et al. 2015)

Impacts of abiotic factors	Impacts of plant hosts	Impacts of aphids hosts	Impacts of parasitoid life-history traits	Impacts of other interactions
Water supply Fertilizer Temperature Light Wind Humidity Precipitation Season	Volatile organic compounds (cues for parasitoid host finding) Defenses Nutritional quality Phylogeny	Cues for parasitoid host finding Size Nutritional quality Defenses Phylogeny Density	Cues from their leagues (altruism) Behavior pattern (optimal strategy, generalist strategy) Learning Size Egg load Age Defenses	Plant mutualists (endophyte, rhizobacteria) Aphid mutualists (bacterial symbionts, bacteriophage) Parasitoid mutualists (plant) Parasitoid competitors (intra- and inter-competitions, <i>i.e.</i> Other natural enemies of aphids)

1 **Article II. Bottom-up effect of water**  
2 **stress on the aphid parasitoid *Aphidius***  
3 ***ervi* (Hymenoptera: Braconidae)**

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12 **Abstract:** Natural enemies inhabiting agro-ecosystems such as parasitoids may be primarily  
13 affected by stresses inducing bottom-up effects that in turn modulate their preference (host  
14 acceptance) and/or their performance (host suitability). The availability of water is one of  
15 the most influential forces that impact plant quality and determines population changes and  
16 community structure. In the present study, we have examined the impact of the bottom-up  
17 effect of water stress on host specificity of the aphid parasitoid *Aphidius ervi*. The cascade  
18 impact of abiotic stress on plant hosts varies depending on the aphid-plant system  
19 considered. Water stress applied to beans did not impact the performance of *A. ervi* on  
20 *Acyrtosiphum pisum* whereas there was a negative impact on *Sitobion avenae* on wheat.  
21 The wheat leaf mass per area was higher on water-stressed plants than on the well-watered  
22 ones. Various mechanisms, notably related to the production of plant toxins during water  
23 stress and host quality, are discussed to explain the bottom-up effect observed in  
24 parasitoids.

25 **Keywords:** host range, oviposition, tritrophic interactions, abiotic stress, drought

## 26 Introduction

27 Arthropod communities are influenced by both bottom-up and top-down forces in wild and  
28 agricultural ecosystems, with bottom-up forces being characterized by effects occurring  
29 from lower trophic levels to higher ones while the top-down forces show the reverse  
30 (Hunter and Price 1992, Johnson 2008). Natural enemies inhabiting agro-ecosystems such as  
31 parasitoids may be largely affected by bottom-up forces because herbivore hosts represent  
32 the entire nutritional and physiological environment during immature parasitoid  
33 development, and such herbivores are often strongly impacted by bottom-up effects (Han *et*  
34 *al.* 2014, 2016). Parasitoid performance depends mainly on host quality, which in turns is  
35 modulated by the host plant and abiotic factors (Vinson, 1990; Godfray, 1994). Also, adult  
36 female parasitoid preference, *i.e.* selection of hosts for laying eggs, is intervened by both  
37 their host recognition and acceptance (Godfray 1994). Female choice primarily bases on  
38 host-related, contact, and volatile cues (Vet & Dicke 1992). Therefore, stresses inducing  
39 bottom-up effects on hosts may, in turn, modulates parasitoid preference (host acceptance)  
40 and/or their performance (host suitability) as these are critical determinants of the  
41 parasitoid host range (Desneux *et al.* 2009a; 2009b; 2012). For example, plant vigor could  
42 modulate dispersal of parasitoids presumably through changes in parasitoid preference  
43 when selecting hosts (Kher *et al.* in 2014) and plant characteristics mediated by growing  
44 conditions can impact parasitoid ability to attack host aphids (Desneux and Ramirez-Romero  
45 2009). Availability of critical nutrients to plants, *e.g.* nitrogen, could affect as well the  
46 development of aphid parasitoids (Chesnais *et al.* in 2016, Aqueel *et al.* 2015) but effects  
47 vary in function of host species considered. All in all, variations in host plant quality may  
48 affect directly herbivorous and parasitoid arthropods as well as their relationships.

49           Among abiotic stresses, availability of water is one of primary constraint impacting  
50 plant quality; it may trigger changes in multi-trophic interactions, population dynamics as  
51 well as community structure (Hunter and Price 1992, Schoonhoven *et al.* 2005; Han *et al.*  
52 2015a; 2015b). Plant water content affects its nutritional value which, in turn, has an impact  
53 on insect behavior. For example, herbivorous insect choosiness when encountering host  
54 plants is influenced by plant quality (Schoonhoven *et al.* 2005, Metcalfe *et al.* 2010,  
55 Weldegergis *et al.* 2015), *e.g.* *Mamestra brassicae* (moth) preferred to lay their eggs on  
56 drought-stressed plants than on control ones. Furthermore, severe drought decreases the  
57 emission of herbivore-induced plant volatiles that plays a crucial role in host detection by  
58 parasitoids and modifies their host selection (Becker *et al.* 2015). Plant quality has an  
59 impact also on the higher trophic level performance through three potential mechanisms:  
60 (1) drought stress could promote toxin production by the plant which interferes with the  
61 development of parasitoid larvae inside the host, *e.g.* through sequestration of toxins by the  
62 hosts (Malcolm 1989; Ode 2006; Desneux *et al.* 2009a, (2) hosts could be qualitatively  
63 suboptimal in terms of nutritional requirements for parasitoid larvae (Desneux *et al.* 2009a),  
64 and (3) plant toxins may modulate host immunity enabling higher parasitoid performance  
65 (Kaplan *et al.* 2016).

66           Potential bottom-up effect of drought stress in both preference and performance of  
67 parasitoids has scarcely been documented. Such knowledge on the impact of bottom-up  
68 forces on tritrophic interactions *plant-herbivore – parasitoid* in agroecosystems may help to  
69 improve biological control programs (Hunter 2003). To evaluate the effect of water stress on  
70 the third trophic level, we studied the preference and performance of *Aphidius ervi*, an

71 aphid parasitoid, when parasitizing its two aphid hosts *Acyrtosiphum pisum* and *Sitobion*  
72 *avenae* when host plants were subjected to drought.

## 73 **Material and Methods**

### 74 Biological materials

75 Two aphid species were tested: *Acyrtosiphon pisum* on the fava bean (*Vicia faba* L.) and  
76 *Sitobion avenae* on the common wheat (*Triticum aestivum* L.). Both colonies were initiated  
77 from individuals collected in Brittany, France. They tested negative for secondary bacterial  
78 symbionts (Monticelli, Nguyen & Desneux, unpublished data) when screened for main ones  
79 known to provide stress adaptability in aphids (Oliver *et al.* 2012). The endoparasitoid  
80 *Aphidius ervi* (Haliday) was reared on *Acyrtosiphon pisum*, and both aphid and  
81 parasitoid species were reared in a growth chamber at  $22 \pm 2$  °C,  $65 \pm 5$  % relative humidity  
82 (RH) and 16:8-h light:dark (L:D). Mummies of *Aphidius ervi* were collected and kept in the  
83 dark at 22°C until adult emergence. New emergent parasitoids were captured and  
84 transferred into a 3-cm diameter cylindrical tube in a 1:1 ratio and were fed with a water  
85 solution containing 50% honey. After 24 hours, the mated females were isolated in gelatin  
86 capsules before the no-choice test (see below).

### 87 Plant water treatment and infestation by aphids

88 Plants were grown from seeds in a climatic chamber ( $24 \pm 1$ °C,  $65 \pm 5$ % RH, 12:12-h L:D) in  
89 plastic pots (9 × 9 × 10 cm) containing organic soil and limestone grains using a 1:1 ratio. A  
90 nutrient solution was used to water plants. For a 100-L stock solution, we added 12.5kg  
91  $\text{Ca}(\text{NO}_3)_2$ , 0.5kg  $\text{NH}_4\text{NO}_3$ , 7.5kg  $\text{KNO}_3$ , 3.5kg  $\text{K}_2\text{HPO}_4$ , 1kg  $\text{K}_2\text{SO}_4$ , 1.5kg  $\text{MgSO}_4$ , 3L  $\text{HNO}_3$ , 1.5L

92 H<sub>3</sub>PO<sub>4</sub>. Micronutrients were provided in the form of 3L Kanieltra 6 Fe (Hydro Azote,  
93 Nanterre, France), and iron was supplied by 2.8L of EDTA-Fe. The stock solution was then  
94 diluted with tap water using a ratio of 5L per 100L final volume to obtain the final irrigation  
95 solution. One week after sowing, bean and wheat seedlings reaching four to eight  
96 centimeters in height, were transferred under laboratory conditions (23 ± 2 °C, 65 ± 5% RH  
97 and 16:8-h L:D). One-week-old bean and wheat plants were randomly assigned two water  
98 levels: 30% and 100% water volumes (referred to as water stress and control conditions).  
99 Both stressed and control plants received the same amount of the necessary nutrient  
100 solution for the highest level stressed plants; Control plants then received tap water to  
101 reach their irrigation levels. The purpose was to maintain the same amount of nutrients and  
102 only to vary the volume of water each plant received during the experiments.

103         Three weeks after the beginning of the water treatment, wheat and bean plants  
104 were offered to aphid colonies in well aerated 60x60x60cm mesh cages. New experimental  
105 colonies were initiated by introducing fourth-instar aphids into the control and water stress  
106 plant cages until new aphid generations appeared. Aphid parents were then removed. Aphid  
107 colonies were maintained from five to ten generations until the experiments ended. New 3-  
108 week treated wheat or beans were added each week and stayed from one to two weeks in  
109 the cages before being replaced. The aphids were used for no-choice host specificity testing  
110 as described by Desneux *et al.* (2009a).

#### 111 **Plant traits: height and leaf mass area**

112 Plant height and leaf mass area (LMA) were recorded before infestation. The LMA (g.m<sup>-2</sup>) is  
113 calculated as the dry leaf mass divided by the leaf area. To calculate the leaf area, we cut off

114 leaves, flattened them between transparent plastic sheets, scanned (Sharp MX-3140  
115 scanner) and measured with the ImageJ freeware. The leaves were then put in an oven for  
116 24 h at 70°C and were weighted.

#### 117 Experiment 1: Host acceptability and preference

118 We used a no-choice bioassay (adapted from Desneux *et al.* 2009, 2012) to study parasitoid  
119 female host selection behavior, *i.e.* preference). Female preference was divided into three  
120 action steps, from the first contact with the host to the actual stinging of the host. These  
121 actions were defined to categorize female parasitoid behaviors when encountering tested  
122 hosts : (1) detection – when the parasitoid touched the aphid with its antenna; (2)  
123 acceptance – when the female bent its abdomen and attacked aphid hosts (3) successful  
124 stinging – when the female inserted its ovipositor inside the aphid and withdrew it (often  
125 resulting in aphid movement). To observe parasitoid behavior, we placed one aphid, and  
126 one female parasitoid in a 3-cm diameter and 1-cm high dome. They were both naive and  
127 had never been in contact with their counterparts to avoid learning-by-experience impacts.  
128 All insect behaviors were noted for 5 minutes or until successful stinging had taken place.  
129 The standard aphid size was chosen based on the size of the 2<sup>nd</sup> *Acyrtosiphon pisum* instar,  
130 known as the preferred instar host of *Aphidius ervi* (Sequeira and Mackauer 1994). 30-36  
131 replicates were performed for each aphid species and each watering conditions in  
132 experiment 1.

#### 133 Experiment 2: Host suitability and performance

134 Innate parasitoid performance is determined by the survival of the immature parasitoid  
135 stages (egg, larvae, and pupae) inside aphid hosts. To follow up stung aphid development,

136 the aphids previously stung during *Experiment 1* (see above) were reared individually in clip  
137 cage system on leaflets of water stress or control plants (according to the sources of host  
138 aphids tested) for 15 days or until mummification. The clip cages made from 100- $\mu$ m-pore-  
139 size Corning® cell strainer (Corning, Inc) were adapted from standard clip-cages (*e.g.*  
140 Mouttet *et al.* 2011). Additional replicates were carried out without behavioral observations  
141 to obtain sufficient replicates for the follow-up survival test. The number of mummies,  
142 adults and the sex ratio of parasitoids was recorded. 51-89 replicates were performed for  
143 each aphid species and each watering conditions in experiment 2.

#### 144 Statistical analyses

145 All statistical analyses were performed using R.3.3.3 software (R Core Team, Vienna, Austria  
146 2009). Effect of water treatment on plant height and plant leaf mass area was tested using  
147 ANOVA. The proportion of aphids detected, accepted and successfully stung were compared  
148 per aphid species using pairwise Fisher tests, with Bonferroni adjustment for multiple  
149 comparisons. The proportion of each parasitoid developmental stage and the sex ratio was  
150 also analyzed per aphid species using pairwise Fisher tests, with Bonferroni adjustment for  
151 multiple comparisons.

## 152 **Results**

### 153 **Impact of water stress on plant traits: height and leaf mass area (LMA).**

154 Bean and wheat heights were significantly impacted by water stress treatment. Bean height  
155 was severely reduced by 27.5% (37.47cm  $\pm$  1.53 vs. 27.16cm  $\pm$  0.88) ( $F_{1,18} = 35.61$ ,  $P < 0.01$ )  
156 and wheat height was decreased by 9% (35cm  $\pm$  1.48 vs. 32cm  $\pm$  0.78) ( $F_{1,26} = 5.8$ ,  $P = 0.02$ )

157 (Figure 1, A). Moreover, the wheat LMA was reduced by 15% in comparison to control  
158 samples ( $F_{1,23} = 7.2$ ,  $P = 0.013$ ) (Figure 1, B). However, there was no evidence of impact of  
159 water stress on the bean LMA ( $F_{1,54} = 0.5$ ,  $P = 0.825$ ).

## 160 **Impact of water stress on *A. ervi* preference and performance**

161 **Experiment 1: Preference** - Detection, acceptance and successful sting rates of *A. ervi* on  
162 aphids *A. pisum* and *S. avenae* were not impacted by the water stress treatment (Fisher  
163 exact test:  $P > 0.05$ ) (Table 1). The proportions of *A. pisum* detected, accepted or stung by *A.*  
164 *ervi* were always higher than 0.9 regardless of water treatment. The proportions of *S.*  
165 *avenae* detected, accepted or stung by *A. ervi* were consistently higher than 0.80 regardless  
166 of water treatment.

167 **Experiment 2: Performance** - When *A. ervi* parasitized *A. pisum*, the number of eggs and  
168 larvae found during dissections, as well as mummies produced and adults emerging did not  
169 change significantly in function of water stress (Fisher exact test: all  $P > 0.05$ ) (Figure 2A).  
170 When *Aphidius ervi* encountered *S. avenae* on well-watered plants, there was no parasitoid  
171 mortality (Fisher exact test: all  $P > 0.05$ ) (Figure 2B). By contrast, there was parasitoid  
172 mortality at the mummy stage as adult emergence significantly reduced under water stress,  
173 from 0.63 aphids containing a parasitoid egg to 0.29 adults emerging (Fisher exact test:  $P <$   
174  $0.01$ ). The sex ratio of parasitoid adults emerging from *A. pisum* (control: 0.88, water stress:  
175 0.74) or *S. avenae* (control: 0.72, water stress: 0.79) did not differ as function of water  
176 treatments ( $P = 0.22$  and  $0.35$ , respectively).

## 177 **Discussion**

178 The bottom-up effect of water stress on the aphid parasitoid *Aphidius ervi* was assessed  
179 when encountering two different aphid species on two host plant species. The experimental  
180 design efficiently enabled the water stress to affect the plants; plant height was decreased  
181 for both plants, as well as leaf mass area in the case of wheat. The cascade impact of this  
182 abiotic stress, through host plant of aphid hosts, varied depending on the aphid-plant  
183 system considered. Successful parasitoid offspring development reduced when *A. ervi* was  
184 tested on *S. avenae* reared on water-stressed wheat vs. well water wheat plant. By contrast,  
185 no impact of such abiotic stress was detected when comparing offspring development of *A.*  
186 *ervi* on *A. pisum* on stressed vs. well-watered bean plants. Also, there was no bottom-up  
187 effect on parasitoid preference (behaviors) when parasitoid encountered the two aphids on  
188 water-stressed plants vs. well-watered ones; parasitoid females did not adjust their  
189 behavior according to potential bottom-up effect occurring in the host-plant systems they  
190 were subjected.

191 Typical parasitic behaviors of pro-ovigenic parasitoids *A. ervi*, *i.e.* short lifespan and  
192 initial large egg load at adult emergence such as *A. ervi* (Dieckhoff *et al.* 2014) may explain,  
193 to some extent, the low choosiness of parasitoid female when encountering aphids on  
194 water-stressed plants. Pro-ovigenic parasitoids tend to accept stinging in most encountered  
195 host species belonging to the tribe of their preferred host (Desneux *et al.* 2009a; 2009c;  
196 Monticelli *et al.* 2018). Water stress applied to bean plant did not impact parasitoid  
197 offspring performance on *Acyrtosiphum pisum*. Therefore the parasitoid females did not  
198 need to lower their oviposition rate when encountering hosts despite that these hosts were  
199 feeding on plants under suboptimal growth conditions (*e.g.* see Figure 1). By contrast,  
200 offspring development was affected when *Aphidius ervi* parasitized *S. avenae* on water-

201 stressed wheat plants (decreased survival at pupae stage), but parasitoid females did not  
202 lower their oviposition on these potentially suboptimal hosts. It remains unclear whether  
203 parasitoid females were not able to identify *S. avenae* on water-stressed wheat as  
204 suboptimal hosts or if female parasitoids recognized them as suboptimal ones but decided  
205 to sting these hosts anyway. *A. ervi* is an intermediate specialist (Monticelli *et al.* 2018) and  
206 is partially able to avoid suboptimal hosts. The lower rate of eggs recovered during  
207 dissections in stung *S. avenae* on water-stressed wheat vs. on those on regular wheat plants  
208 may hint that *A. ervi* females did identify the suboptimal hosts and adjusted their  
209 selectiveness partially.

210           Few studies have evaluated the impact of aphid nutrition status on immature  
211 parasitoid development and field observations suggested lower parasitoid performance,  
212 notably reduced offspring production, of aphids and parasitoid populations under  
213 drought stress (Aslam *et al.* 2013, Romo and Tylianakis 2013). Three potential mechanisms  
214 may explain bottom-up effects of water stress on parasitoid performance (Kaplan *et al.*  
215 2016): (i) increased sequestration of plant toxins in hosts, owing to a shift in resource  
216 allocation from primary to secondary metabolism in water-stressed plants (Mewis *et al.*  
217 2012); (ii) reduced resource availability for parasitoid offspring development; such effect  
218 may cascade from the first mechanism as primary plant metabolism reduced in stressed  
219 plants, and it may cascade to lower resources for aphids, and (iii) modulation of host  
220 immunity owing to presence of plant toxins.

221           The two first mechanisms may explain, in part, the lower performance of *A. ervi* on *S.*  
222 *avenae* when developing on water-stressed wheat plants. Both *Acyrtosiphum pisum* and *S.*  
223 *avenae* use general and specific proteins that interfere with plant defensive pathways

224 during feeding (Urbanska *et al.* 1998, Rao *et al.* 2013). However, *A. pisum* produces  
225 metalloproteases in saliva, and this does not occur in the case of *S. avenae* (Carolan *et al.*  
226 2009, Will *et al.* 2013). These proteases break down plant phloem proteins into smaller  
227 nitrogen compounds used for both modulation-suppression of plant defensive hormones  
228 and plant feeding (Furch *et al.* 2014, Furch *et al.* 2015); they may lower potential adverse  
229 bottom effects toward parasitoid developing in *A. pisum* on water-stressed plants. It might  
230 contribute to *A. pisum* resistance to plant nitrogen depletion under drought conditions and  
231 may have enabled *Aphidius ervi* to develop well in this host whereas parasitoid offspring  
232 development in *S. avenae* may have been impaired owing to accumulated secondary  
233 metabolites and/or reduced proteins availability in this aphid. Such observation still may  
234 have to be confirmed by measures of toxins and/proteins content in *S. avenae* developing  
235 on water-stressed plants vs. wheat cropped in well-watered conditions.

236           Reduced aphid size, as well as general resource availability in host aphids, could also  
237 be a factor underneath suboptimal development of parasitoid offspring in *S. avenae*. There  
238 is a positive relationship between plant vigor and herbivore weight in phytophagous  
239 arthropods as well as between their weight and potential parasitoid size (Teder and  
240 Tummaru 2002). Parasitoids could fail to develop in small hosts owing to low-poor resource  
241 availability (Godfray 1994). *Sitobion avenae* size may be caused by poor plant quality and  
242 could be responsible for the reduction of *A. ervi* parasitism rate under drought stress.  
243 However, aphid length data are lacking to validate this hypothesis in our study. Also, host  
244 size may impact parasitoid fitness by modulating sex ratio, *i.e.* inducing a male-biased sex  
245 ratio; parasitoid females lay preferentially more female eggs in large hosts and males in  
246 small ones (Godfray 1994). Sex ratio did not vary when *A. ervi* parasitized the two aphid

247 species on well-watered plants and water-stressed ones, suggesting that *A. ervi* did not  
248 discern or consider the variability in host quality. All in all, a shortage of resources needed to  
249 complete parasitoid development in aphid is thought to affect parasitoid offspring mostly at  
250 the pupae stage, notably at the time the larvae produce silk for mummy cocoon (Desneux *et*  
251 *al.* 2009a) whereas sequestration of toxins by aphids proved to be lethal mostly for younger  
252 offspring (from egg to larvae or from larvae to pupae). Therefore, reduced development of  
253 *A. ervi* in *S. avenae* may be more likely linked to diminished host food quality and/or  
254 quantity rather than sequestration of toxins by this aphid on the water-stressed wheat  
255 plant.

256 LMA is an important trait in predicting plant adaptability strategies and/or mortality  
257 pattern under changing environments (Poorter *et al.* 2009, Anderegg *et al.* 2016). Wheat  
258 plants under stress had a lower height, and higher LMA than well-watered plants (*e.g.* Blum  
259 and Sullivan 1997) and changes in leaf chemical composition mediated by LMA might reflect  
260 the change(s) occurring in the vascular system on which aphids fed (Auclair 1963, Will *et al.*  
261 2013). LMA in herbaceous plant correlates positively to leaf carbon concentration but  
262 negatively to leaf nitrogen concentration, organic acids and protein concentration (Poorter  
263 *et al.* 2009, De La Riva *et al.* 2016). Plants with higher LMA are associated with lower N  
264 content, and it may lower aphid feeding efficiency and subsequently its quality as host for  
265 parasitoid. By contrast, bean height was lower, and its LMA did not alter under the water  
266 stress. Beans tend to avoid drought by reducing evaporation surface and leaf stomatal  
267 conductance which is the most significant morphological adaptation in this species (Lizana  
268 *et al.* 2006, Lonbani and Arzani 2011, Beebe *et al.* 2013). Beans did not show increased LMA,  
269 suggesting a lower impact of water stress on plant physiology in bean; it may explain the

270 lack of bottom-up effect on *A. ervi* parasitism when encountering *Acyrtosiphum pisum* on  
271 water-stressed host plants. However, the use of the LMA trait for drought adaptability is  
272 insufficient and controversial because of plant diversity and the nature of the stress  
273 (Marechaux *et al.* 2015, He and Dijkstra 2014). Further research will require more plant  
274 physiological traits to be measured, *e.g.* photosynthesis and C/N ratio, to deepen our  
275 understanding of mechanisms underlying plant stress survival and potential cascading  
276 effects toward second and third trophic levels.

277 The present study stressed the importance of abiotic conditions in plant-herbivore-  
278 parasitoid interactions and notably host use by parasitoids. Bottom-up effects may cascade  
279 to third trophic level and modulate performance of parasitoids when parasitizing their  
280 hosts. Such effects may have a broad impact on insect communities, *e.g.* it may affect diet  
281 breath of parasitoids through narrowing their host range making suitable hosts to turn into  
282 poorly suitable or unsuitable ones.

283

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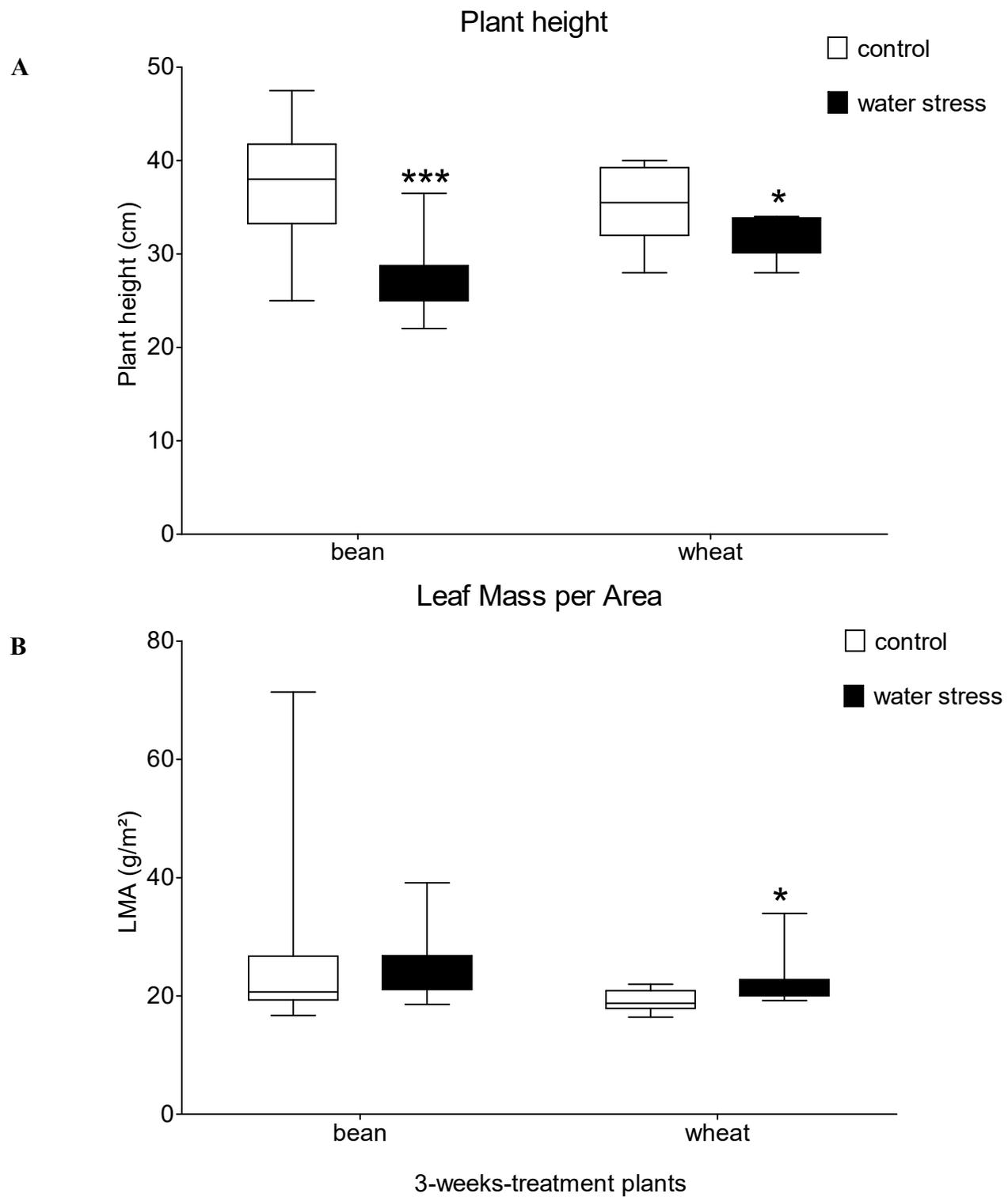
450 **Figure legend.**

451 **Figure 1.** (A) Plant height and (B) leaf mass per area (mean  $\pm$  SEM, N = 13–28) of beans and  
452 wheat under drought conditions versus well-watered ones. The treatment durations were  
453 three weeks for both plants. The bottom and the top part of the plots indicate the 25th and  
454 75th percentile, respectively, the two whiskers the 10th and the 90th percentile, respectively,  
455 and the horizontal line within the box the median value. \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001  
456 (significantly different between drought conditions and well-watered ones).

457 **Figure 2.** The proportion of successfully stung aphids [*Acyrtosiphum pisum* on Bean (A),  
458 *Sitobion avenae* on Wheat (B)] *whether an egg (immediately after being stung), a larva (after*  
459 *four days), a mummy (after ten days) or an adult were observed* (experiment 2). In each aphid  
460 species, *bars followed by the same letter are not significantly different (pairwise Fisher test*  
461 *exact with Bonferroni adjustment method).*

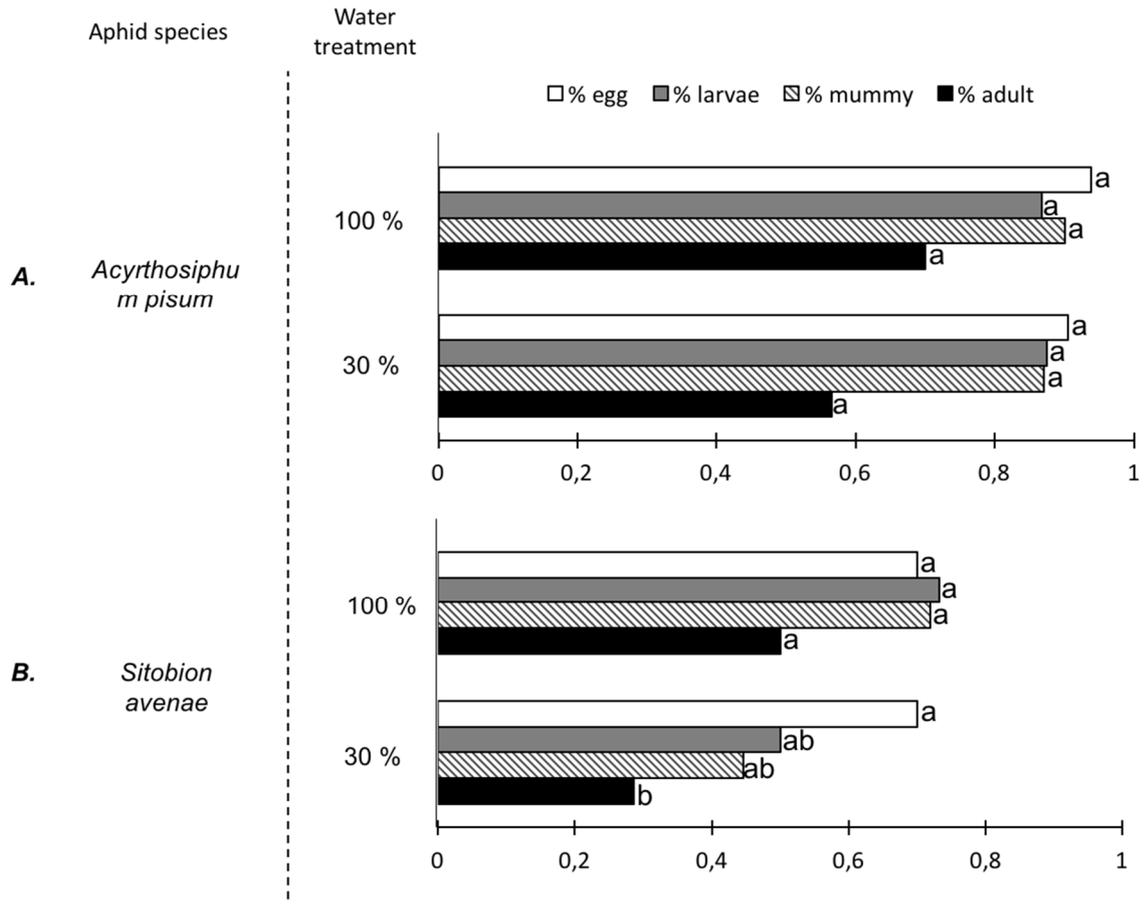
462

463 **Figure 1**



464

465



Aphid species	Water treatment	Proportion of aphids detected	Proportion of aphids accepted	Proportion of aphids stung
<i>Acyrtosiphum pisum</i>	100%	1	0.9	0.9
	30%	1	0.9	0.9
<i>Sitobion avenae</i>	100%	1	0.87	0.81
	30%	0.97	0.83	0.78

468

469 **Table 1.** The proportion of aphids detected, accepted and successfully stung by *A. ervi* when  
 470 encountering *A. pisum* or *S. avenae* under two different water treatment (Experiment 1).

471

472

1 **Article III. Water stress-mediated bottom-**  
2 **up effect on aphid parasitoid diet breadth**

3

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12

13 **ABSTRACT**

14 Shift in the ecological specialization of herbivorous and predatory species may occur  
15 through the indirect impact of abiotic stresses arising at lower trophic levels, *e.g.* in plants  
16 (effects so-called bottom-up effects). A tritrophic system "plant-aphid (sap-feeding  
17 herbivores) – parasitoid (*Aphidius ervi*, Hymenoptera: Braconidae: Aphidiinae)" was used as  
18 a biological model to study such potential shift in parasitoid host specificity owing to  
19 bottom-up impact; we measured possible effects on both behavioral and physiological  
20 parasitoid traits. It was investigated using six host plant-aphid complexes, and water  
21 limitation were used as abiotic stress inducing the bottom-up effect. Also, the impact of  
22 water stress on host plants and aphid life-history traits were assessed. We demonstrated  
23 that bottom-up effects effectively occurred on parasitoid host specificity and that it can  
24 modulate its actual host range. The parasitoid choosiness was not drastically affected by  
25 bottom-up effect while aphid host suitability for parasitoid offspring development was  
26 decreased in three out of the six aphid species tested. Besides, water stress negatively  
27 affected plant primary metabolism-related mechanisms, *e.g.* leaf transpiration rate and  
28 stomatal conductance, and it cascaded to aphids; their development speed and growth  
29 were decreased for half of aphid species considered. Adverse bottom-up effects observed  
30 on aphid hosts were linked to subsequent parasitoid performance on these hosts; except for  
31 one aphid species, those showing reduced survival, generation time and intrinsic rate of  
32 population increase ( $r_m$ ) proved to be suboptimal hosts for the parasitoid when plants were  
33 suffering water stress. This research highlights the potential impact of abiotic-related stress  
34 on actual host specificity in parasitoids.

35 **Keywords:** host specificity, preference-performance hypothesis, tritrophic interactions,  
36 water limitation, biological control, biological control agents

37

38

## 39 INTRODUCTION

40 Patterns of resources utilization of one species, or ecological specialization, are determined  
41 by its functional traits during interactions with other organisms and abiotic factors in an  
42 ecosystem. Shifts in ecological specialization may be caused by abiotic stresses occurring  
43 from lower trophic levels and reaching the top through direct and indirect interactions  
44 among organisms. The understanding of such bottom-up effects of abiotic stresses is  
45 essential to predict one organism responses under fluctuating environmental conditions  
46 (Wiens 2016); the community shift direction and quantitative impacts of community shift on  
47 the wild and agricultural ecosystems (Devictor *et al.* 2010; Moe *et al.* 2013). The tri-trophic  
48 plant-aphid-parasitoid system is a good biological model in both ecology and application  
49 because of the biodiversity of insects in the terrestrial ecosystem, the tight co-evolution of  
50 organisms within the complex and the importance of parasitoid in biological OW as natural  
51 enemies against aphids (Loxdale *et al.* 2011). The host specificity of a parasitoid is its ability  
52 to exploit aphid hosts. It is shaped by parasitoid preference (host acceptance) and parasitoid  
53 performance (host suitability) which are influenced by aphid quality, aphid food source,  
54 plant quality and interactions within this system (Desneux *et al.* 2009; Desneux *et al.* 2012;  
55 Godfray 1994; Klinken 1999; Poulin and Mouillot 2005). The diet of aphid hosts can affect  
56 host suitability for immature aphid parasitoid, however, evidences are scarce. Soil nitrogen  
57 fertilizer could improve parasitoid fitness at moderate quantity (Aqueel *et al.* 2015).

58 Water stress is among most severe abiotic stresses in current decades. It affects 45%  
59 of global farming lands, is predicted to increase at both intensity and frequency (Long and  
60 Ort 2010), causes nearly 20% agriculture damage (FAO 2015) and biodiversity loss (Archaux  
61 and Wolters 2006). Field observations of aphid and their parasitoid populations under water

62 stress suggest a depletion in parasitoid performance (Aslam *et al.* 2013; Romo and  
63 Tylianakis 2013). The water availability mediated by plants triggers a change in population  
64 and community structure at the top level (Han *et al.* 2015a; Han *et al.* 2015b; Hunter and  
65 Price 1992). The outcomes of stress-based modifications at natural enemy level may be  
66 predicted by variations in plants which directly affect natural enemies or mediate the  
67 variations in aphid quality as hosts, *e.g.* through reduction of plant volatiles such as  
68 synomones under water deficiency (Aslam *et al.* 2013; Dias *et al.* 2010; Tariq *et al.* 2013;  
69 Weldegergis *et al.* 2015). Impacts of abiotic stress on parasitoid may also be mediated by  
70 aphids such as modifications in aphid availability (density), nutritional quality (size and  
71 content), defenses (by morphology, immune system or symbionts), and growth rate, *i.e.*  
72 lower host density) because of plant morphological, physiological and chemical  
73 modifications (Hunter 2003). The overall effects may be either negative or positive on aphid  
74 performance but often remain unclear for parasitoids. Several studies reported no impact of  
75 fruit fly (Martinez-Ramirez *et al.* 2016) and leaf miner (Dong *et al.* 2018) parasitoids. On the  
76 negative side, plant biomass loss and plant poor nutrient contents relate to the reduction of  
77 aphid population and performance (Johnson *et al.* 2011; McVean and Dixon 2001; Mewis *et*  
78 *al.* 2012; Simpson *et al.* 2012). Plant trichome increase contributes to plant resistance  
79 against herbivores (Glas *et al.* 2012; Handley *et al.* 2005). In the positive side, stomatal plant  
80 closure improves aphid feeding under elevated CO<sub>2</sub> (Sun *et al.* 2015). The plant traits  
81 variations are determined by plant defense strategies under a combination of stresses and  
82 their nature such as intensity and frequency. Under abiotic stress and aphid infestations,  
83 plants can produce both more or less defensive allelochemicals. For example, glucosinolate  
84 concentration in cabbage and cardenolide in milkweed are reduced under water stress,  
85 respectively (Khan *et al.* 2010; Mewis *et al.* 2012). By contrast, the secondary pathways in

86 plants could also be activated under stress to produce more insecticidal toxins, *e.g.* phenolic  
87 compounds (Caretto *et al.* 2015). Those toxins could delay the growth of phytophagous  
88 insects as well as making them more susceptible to natural enemies (Ibanez *et al.* 2012).  
89 Bottom-up effects may also impair endosymbionts harbored by aphids, thus possibly making  
90 them more vulnerable to parasitism (Cayetano and Vorburger 2013). However, these  
91 allelochemicals can even be sequestered by specialist herbivores and be used as protection  
92 against parasitism and/or predation (Züst and Agrawal 2015). So far, previous studies hinted  
93 that bottom-up effects on host-parasitoid relationships could not be readily generalized and  
94 inferred from plant responses to a specific individual stress (Suzuki *et al.* 2014); the studies  
95 assessing potential bottom-up effects should be carried out using a range of tri-trophic  
96 complexes under well-defined stress conditions to enable providing broad significance.

97         In the present study, we studied the impact of a bottom-up force, the water stress,  
98 on critical determinants of host specificity (Desneux *et al.* 2009) of the specialist-generalist  
99 aphid parasitoid *Aphidius ervi*. Based on a previous study on *A. ervi* diet breath (Monticelli  
100 *et al.* 2018), we selected six aphid – host plant complexes to assess the impact of water  
101 stress on the parasitoid host specificity: *Acyrtosiphon pisum* - bean, *Sitobion avenae* –  
102 wheat, *Rhopalosiphum padi* - wheat, *Myzus persicae* - cabbage, *Aphis nerii* - milkweed, and  
103 *Macrosiphum euphorbiae* - potato. They were chosen as meeting one the following criteria  
104 in the absence of water stress (Monticelli *et al.* 2018): (i) high quality host, *i.e.* high  
105 parasitoid offspring survival until adulthood, or (ii) suboptimal host, *i.e.* average mortality  
106 occurring before adult emergence. These two conditions should enable detecting possible  
107 adverse effects (case *i*) and positive effects (case *ii*) on parasitoid offspring development,  
108 notably owing potential modifications in plant biochemistry and/or host aphid physiology

109 (which is known to impair parasitoid development at larva stage, Desneux *et al.* 2009). Also,  
110 life-history traits of aphids and plants were recorded to further depict results on parasitoid  
111 host specificity under bottom-up force conditions. The central hypothesis was tested: (i)  
112 parasitoid females may show lower preference toward hosts under bottom-up force owing  
113 to decreased quantity and/or quality of chemical cues from host aphids and/or plants, (ii)  
114 parasitoid performance would increase on generalist aphids fed on toxic plants and  
115 decrease on aphids fed on non-toxic plants, (iii) the relationship preference-performance  
116 could change under water stress impacts.

## 117 **MATERIELS AND METHODS**

### 118 ***Biological system***

119 The parasitoid *Aphidius ervi* (Haliday) was reared on *Acyrtosiphon pisum* for 20 generations  
120 in a growth chamber (23 ± 2 °C, 65 ± 5 % RH, 16:8-h L: D). The host specificity of *A. ervi* was  
121 tested in six aphid-plant complexes under two water regimes: optimal water supply (OW)  
122 and limited water supply (LW), the irrigation volumes were 100% and 30% of saturated soil  
123 volume for five species except for *Myzus persicae* 70% and 30% of saturated soil volume  
124 was applies. The six complexes were: *Acyrtosiphon pisum* (Harris) on fava bean, *Vicia faba*  
125 *L.* (referred as Ap100 and Ap30 for OW and LW); *Sitobion avenae* (Fabricius) and  
126 *Rhopalosiphum padi* (Linnaeus) on common wheat, *Triticum aestivum L.* (Sa100 and Sa30, *R.*  
127 *padi*100 and *R. padi*30, respectively); *Myzus persicae* (Sulzer) on cabbage, *Brassica oleracea*  
128 *var. capitata* (*M. persicae*70 and *M. persicae*30); *Aphis nerii* (Boyer de Fonscolombe) on  
129 milkweed, *Asclepias incarnata* (An100 and An30) and *Macrosiphum euphorbiae* (Thomas )  
130 on potato, *Solanum tuberosum* (Me100 and Me30).

131 ***Impacts of water stress on plants***

132 *Plant water stress treatment* – The water stress treatment was applied from the previous  
133 study of Nguyen, LTH, *et al.*, (2018, in prep). The experimental plants were grown from  
134 seeds in a climatic chamber ( $23 \pm 2$  °C,  $65 \pm 5$  % RH, 12:12-h L:D) in plastic pots ( $9 \times 9 \times 10$   
135 cm) containing organic soil (Terreau Horticole Bio Tonusol, Agriver, France) and limestone  
136 grains (Perlite Italiana Srl, Corsico, Italy) in ratio 1:1. The quantity per pot was five seeds/pot  
137 for bean, ten seed/pot for wheat, one seed/pot for other plants. The term 'stres is used here  
138 when, for any reason, plant performance in module growth is reduced below that achieved  
139 under optimal conditions. The water supply volume for OW plants was determined during  
140 preliminary experiments where we LW plants with four water levels: 30%-, 50%-, 70%- and  
141 100% of soil-saturated volume and then we measured plant parameters to find the optimal  
142 conditions showing highest plant biomass and metabolism. One week after sowing, plant  
143 germinations of 4-8 cm height were transferred under laboratory conditions ( $23 \pm 2$  °C,  $65 \pm$   
144 5 % RH, 16:8-h L:D). One-week-old bean, wheat, milkweed, and potato were randomly  
145 assigned to two water levels: 30% and 100% of soil-saturated volumes (referred as water  
146 stress and OW or 30% and 100%). The exceptional case is cabbages of which the OW was  
147 70% of soil-saturated volume because cabbage metabolism decreased at 100% volume  
148 irrigation similar to the water stress symptom. The treatments were started three weeks  
149 before aphid infestation and was maintained continuously. LW and OW were kept on  
150 tested plants during all experiments as well.

151 *Plant morphology measurements* - Plant morphological parameters including height and leaf  
152 mass area were measured each week. Plant height and number of nodes or stem leaves  
153 were measured from the soil surface. Leaf mass per area (LMA) was calculated by dry mass

154 divided by leaf area. The leaves were cut off and flattened between transparent plastic  
155 leaflets and then scanned by a Sharp MX-3140 scanner. Leaf area (cm<sup>2</sup>) was calculated using  
156 the freeware ImageJ.

157 *Leaf gas exchange measurement* - Non-destructive measurements of leaf photosynthesis  
158 rate based on net CO<sub>2</sub> assimilation ( $A_N$ ), transpiration rate (E) and stomatal conductance ( $g_s$ )  
159 were performed. We chose the 4<sup>th</sup> or 5<sup>th</sup> young leaves from the stem which provides  
160 optimal aphid feeding and proved suffering water limitation long enough during preliminary  
161 experiments.

162 One leaflet per plant was analyzed using a photosynthesis system (Li-6400, Li-Cor, Lincoln,  
163 NE, USA) equipped with a light source (6200-02B LED, LiCor). Leaflets first were acclimatized  
164 in the chamber for more than 20 min under controlled conditions: leaf temperature of 27.0  
165  $\pm$  (SE) 0.1 C, CO<sub>2</sub> air concentration of  $500 \pm 0.04 \mu\text{mol mol}^{-1}$ , and saturating photosynthetic  
166 photon flux density (PPFD) of  $700.04 \pm 0.05 \mu\text{mol hv m}^{-2}\text{s}^{-1}$ . The light intensity of  $700 \mu\text{mol}$   
167  $\text{m}^{-2}\text{s}^{-1}$  PAR is high enough to stimulate leaf transpiration and is closer to the laboratory light  
168 condition. Relative humidity was maintained between 10% and 50% in the cuvette for all  
169 measurements.

170 After detecting a significant difference in at least one of morphological or metabolic  
171 parameters, we transferred plants to aphid-feeding cages. Infestation periods were  
172 determined for each plant by preliminary tests. Intrinsic water use efficiency ( $A_N/g_s$ ) was  
173 calculated as the ratio between leaf photosynthesis rate ( $A_N$ ) and leaf stomatal conductance  
174 ( $g_s$ ) as the study of Medrano *et al.* (2015).

175 ***Bottom-up effect of water stress on aphids***

176 *Plant infestation* – LW and OW plants were offered to aphid colonies in a cage of the  
177 dimension 60x60x60cm covered by mesh placed in a climatic chamber ( $23 \pm 2$  °C,  $65 \pm 5$  %  
178 RH, 16:8-h L:D). We initiated new colonies by introducing 4<sup>th</sup> instar aphids into the cage of  
179 OW and LW plants until the reproduction of new generations. Aphid parents were then  
180 removed. Aphid colonies were maintained for 5 to 10 generations until experiments ended.  
181 New plants were added every week and stayed from 1 to 2 weeks in the cages before being  
182 removed. All plant metabolism and morphology were measured (see above) prior aphid  
183 infestation to make sure LW plants were effectively under water stress.

184 *Aphid performance: survival rate, generation time (D), and the intrinsic rate of increase ( $r_m$ ).*

185 We evaluated aphid performance on LW and OW plants on three parameters: The survival  
186 rate, the generation time (D), and the intrinsic rate of increase ( $r_m$ ) was calculated as  
187 described by (Wyatt and White 1977; van Emden and Harrington 2007). We placed ten 4<sup>th</sup>  
188 instar aphids on LW and OW plants on a Petri-dish cage system of 85mm-diameter covered  
189 by mesh. When second aphid generations were born, we removed aphid parents and used  
190 offspring aphids for evaluating aphid performance. 1-day-old aphids from the same cohort  
191 were then individually confined into clip-cages attached to the experimental leaves in all  
192 plants from LW and OW conditions, ten clip-cages per plant, three plants per treatment. We  
193 measured the *survival rate as the number of aphids* surviving after seven days in clip-cages  
194 per total clip-caged aphids. The generation time (D) was determined by recording duration  
195 from aphid to their first reproduction. The intrinsic rate of the increase relates the fecundity  
196 of an individual aphid to its development time:  $r_m = (\ln M_d \times 0.738) / D$ , where  $M_d$  is the  
197 number of nymphs produced by the adult in the first D days of reproduction after the adult  
198 molt (van Emden and Harrington 2007).

199 ***Bottom-up effect of water stress on parasitoids***

200 Parasitoid preference: no-choice test - We conducted the parasitoid specificity test as  
201 previously described by Desneux *et al.* (2009) to test behavioral and physiological traits of  
202 parasitoids on potential aphid hosts. This test design included observing the behaviour of  
203 aphids and parasitoids when they individually encounter in a small area of 3-cm diameter, 1-  
204 cm height –dome. Parasitoids were one-day-emerged, mated and naive. Aphids were  
205 standardized by size equal the second instar of *A. pisum*, the natal parasitoid host. The  
206 standard size was chosen based on relative size of different aphid colonies and the  
207 preferable host instar of *A. ervi* while parasitizing *A. pisum*.

208 The host selection process, *i.e.* female preference) was divided into 3 steps, each with a  
209 perceptible representative sign: (1) detect (when the parasitoid touched the aphid either by  
210 antenna or leg) – accept (when the female bent its abdomen and attacked aphid hosts,  
211 following or not by aphid defense) – successful sting (when the female inserted its  
212 ovipositor inside the aphid and withdrew it resulting in aphid movement). After one  
213 successful sting, aphids were removed from the dome immediately for not being super  
214 parasitized by *A. ervi*. Aphid defensive behaviors were recorded as antennal push, cornicle  
215 secretion, kick or rotation (Desneux *et al.* 2009). All insect actions were noted as described  
216 above until 5 minutes or until successful sting, depending on what happened first. *A. ervi*  
217 females were aggressive toward aphids during our experiments, so 5-minute length is  
218 enough to complete their host selection process in a small dome.

219 *Parasitoid performance: sequential dissection* - To follow up immature parasitoid  
220 development, stung aphids from plants under limited water supply and optimal water

221 supply conditions (from the previous behavioral assay, see above) were individually reared  
222 in the clip cage system on leaflets belonging to their respective plant treatment, *i.e.* LW or  
223 OW). Two third of stung aphids were then sequentially dissected to find the egg and larval  
224 survival at 1- and 5-day after being stung, respectively. The remaining 1/3 were kept in clip-  
225 caged for up to 15 days, or until mummy formed, the emergence rate and the survival  
226 aphids from parasitism were then recorded. We repeated the dome experiment without  
227 actual behavioral observations to increase the number of replications for this assay. To  
228 analyze the correlation between preference and performance for *A. ervi*, we considered the  
229 successful stung ratio per total observed aphids as a proxy of parasitoid preference and the  
230 adult emergence rate per stung aphids as a proxy of parasitoid performance.

### 231 **Statistical analysis**

232 Impact of the water limitation on plant height, plant leaf mass area and leaf gas exchange  
233 was analyzed using factorial ANOVA. The impact of water stress on aphid generation time  
234 and intrinsic rate of development was examined using factorial ANOVA. The impact of water  
235 stress on aphid survival rate and other life history traits was analyzed using Fisher exact test.  
236 Each trait was compared in pairs between LW and OW plants. The relationship between  
237 parasitoid preference for and performance on aphids feeding on LW or OW plants was  
238 analyzed using logistic regression with a binomial distribution. Detection, acceptance and  
239 sting rates were compared, per species for each water treatment, using pairwise compared  
240 using permuted Fisher Exact test with Bonferonni adjustment method. Similar analyze  
241 method was used to compare the proportion of aphids containing an egg, larvae, producing  
242 a mummy and adult. All tests were performed using R software (R Core team). All graphics  
243 were processed using Prism 5 software (GraphPad Software Inc 2007).

244 RESULTS

245 **Impact of stress on plant morphological and metabolic traits:**

246 ***Plant height, the number of nodes and leaf mass area (LMA) (Figure 1A, B, C)*** - Plant height  
247 was significantly reduced under water stress for all plants tested; still, the impact was not  
248 similar among plant species. Bean, milkweed, and potato showed severe height reduction  
249 by up to 34% (Figure 1A,  $p$  value  $< 0.001$ ) whereas the height of wheat was slightly  
250 decreased ( $p$  value = 0.02). There was no evidence of the difference of cabbage height  
251 between OW and LW ( $p$  value  $> 0.05$ ); however the number of cabbage leaves was  
252 significantly lower than in optimal water supplied plants which reduced by 23% under LW ( $p$   
253 value = 0.007). There was no evidence water limitation impact on LMA of all plants ( $p$  value  
254  $> .05$ ) except wheat with LMA increased by 15% ( $p$  value = 0.013).

255 ***Leaf photosynthesis, conductance, transpiration rate and the intrinsic water use efficiency***  
256 **(Figure 2A, B, C)** - Leaf stomatal conductance of all plants ranged from 0.05 to 0.19  
257  $\text{molH}_2\text{Om}^{-2}\text{s}^{-1}$  (N = 24-68) in OW plants and from 0.02 to 0.08 in LW plants, which decreased  
258 significantly under water stress conditions despite plant species.  $p$  value  $< 0.001$  for all  
259 plants except potato  $p$  value = 0.018. Leaf transpiration rate ranged from 1 to 3.6  $\text{mmol}$   
260  $\text{H}_2\text{Om}^{-2}\text{s}^{-1}$  in OW plants and from 0.5 to 1.7  $\text{H}_2\text{Om}^{-2}\text{s}^{-1}$  in LW plants. Similar to the variation of  
261 stomatal conductance, leaf transpiration rate decreased significantly under water stress  
262 despite plant species. ( $p$  value = 0.003 for bean,  $p$  value = 0.01 for potato and  $p$  value  $<$   
263 0.001 for three other plants).

264 Leaf intrinsic water use efficiency ( $W_{UE}$ ) of bean, wheat, and cabbage increased  
265 significantly under LW ( $p$  value = 0.005 for bean,  $p$  value  $< 0.001$  for two other plants (Figure

266 2D). Water use efficiency  $W_{UE}$  of milkweed and potato only marginally increased ( $p$  value =  
267 0.059 for both plants).

### 268 **Impact of water limitation on aphid performance: survival rate, generation time and** 269 **intrinsic rate of development**

270 The life-history traits of *A. pisum* and *A. nerii* including survival rate, generation time (D),  
271 and intrinsic rate of development ( $r_m$ ) were not significantly different between LW and OW  
272 ( $p$  value > 0.05) (Figure 3A, B, C). The generation time of three species *S. avenae*, *M.*  
273 *persicae* and *M. euphorbiae* were significantly reduced in LW plants (factorial ANOVA tests  
274 for *S. avenae*:  $p$  value = 0.0036,  $F_{1,19} = 11$ ; for *M. persicae*:  $p$  value = 0.026,  $F_{1,28} = 5.56$ ; for *M.*  
275 *euphorbiae*:  $p$  value < 0.001,  $F_{1,30} = 33.41$ ). The intrinsic rate of development of three  
276 species *R. padi*, *M. persicae* and *M. euphorbiae* were significantly reduced in LW plants (*R.*  
277 *padi*:  $F_{1,43} = 7.16$ ,  $p$  value = 0.01; *M. persicae*:  $F_{1,30} = 4.29$ ,  $p$  value = 0.047; *M. euphorbiae*:  
278  $F_{1,49} = 33.41$ ,  $p$  value < 0.001).

### 279 **Impact of water limitation on the parasitoid *A. ervi* (Figure 4A, B)**

280 *Parasitoid survival rate* - The survival of parasitoid at mummy stage and adulthood was  
281 significantly reduced when developing on *S. avenae*, and *M. persicae* reared on water stress  
282 plants (LW) when compared to those reared on optimal water conditions (OW) (Table 3:  
283 survival until mummy stage: *S. avenae*,  $p$  value = 0.006, *M. persicae*,  $p$  value = 0.038; survival  
284 at adulthood: *S. avenae*,  $p$  value = 0.029, *M. persicae*,  $p$  value = 0.030). The survival until  
285 adulthood was notably reduced by 85% and 40% when developing in *M. persicae* and *S.*  
286 *avenae* subjected to water stress-related bottom-up effect, respectively. The similar pattern  
287 was observed in *M. euphorbiae* though it was only marginally significant (survival until

288 mummy stage:  $p$  value = 0.075, survival at adulthood:  $p$  value = 0.088). The water stress did  
289 not show a significant effect on parasitoid development in other aphid species tested (all  $p$   
290 value > 0.05).

291 *Correlation preference – performance* (table 5) - There was a significant preference-  
292 performance correlation when *A. ervi* was parasitizing aphids reared in optimal watering  
293 conditions (OW,  $p$  value = 0.002,  $R^2$ = 0.71). By contrast, this relationship was weaker when  
294 aphids were reared on plants suffering water stress ( $R^2$ = 0.45), and there was no significant  
295 correlation anymore ( $p$  value = 0.071).

## 296 **DISCUSSION**

297 In the present study, testing six aphid species as potential hosts and generating bottom-up  
298 effects on host aphids through varying water stress in host plants, we demonstrated that  
299 bottom-up effects effectively occurred on parasitoid host specificity and that it can  
300 modulate its actual host range. The parasitoid choosiness was not drastically affected by  
301 bottom-up effect while host suitability for parasitoid offspring development was decreased  
302 in three out of the six aphid species tested. Water stress did negatively affect plant primary  
303 metabolism-related mechanisms, *e.g.* leaf transpiration rate and stomatal conductance, and  
304 it proved to cascade to the second trophic level, *i.e.* the aphids; their development speed  
305 and growth were decreased for half of aphid species considered. Adverse bottom-up effects  
306 observed on aphid hosts were linked to subsequent parasitoid performance on these hosts,  
307 except for some aphid species, those showing reduced survival, generation time and/or  
308 intrinsic rate of population increase ( $r_m$ ) proved to be suboptimal hosts for the parasitoid  
309 when plants were suffering water stress. This research highlights that actual parasitoid diet

310 breath observed in wild conditions largely depend on abiotic factors impacting parasitoids  
311 themselves but also through less intuitive effects occurring through both host plants and  
312 hosts owing to bottom-up forces.

### 313 **Parasitoid preference under bottom-up force**

314 We demonstrated that preference traits of the aphid parasitoid *A. ervi* toward hosts might  
315 be only slightly modulated by bottom-up force occurring through water stress applied to  
316 actual plants bearing the host aphids. No drastic difference was observed in detection,  
317 acceptance and stinging rates of *A. ervi* when parasitizing five of the six aphid species tested  
318 (*R. padi*, *M. euphorbiae*, *A. nerii*, *A. pisum* and *S. avenae*) on LW vs. OW plants. The host  
319 selection behavior in Aphidiine aphid parasitoids relies on host-associated cues, both from  
320 the host external and internal, *e.g.* haemolymph quality assessed during insertion of the  
321 ovipositor (Larocca *et al.* 2007). The present study hinted that such traits were not modified  
322 in the tested aphid species, at least not enough for changing the parasitoid host selection  
323 pattern. However, it could not be excluded that potential difference may occur in harsher  
324 bottom-up force conditions, *i.e.* that was not tested in the present study, *e.g.* stresses  
325 inducing more variations in aphid physiology. It may also indicate that *A. ervi*, being an  
326 intermediate generalist-specialist, may not be adapted to detect tedious differences in  
327 quality of hosts encountered. By contrast, the parasitoid behavior pattern, here detection  
328 rate, was modified when parasitizing the aphid *M. persicae* on LW plant. Host detection step  
329 by aphid parasitoid relies mostly on chemical cues on aphid cuticles (Hatano *et al.* 2008),  
330 *e.g.* glucosinate (Pope *et al.* 2008). Water stress-associated decrease of glucosinate  
331 induction in plants (Khan *et al.* 2011) may translate to a reduction of this compound in *M.*  
332 *persicae* cornicle secretion (Blande *et al.* 2008). Therefore, the decrease in *M. persicae*

333 detection by *A. ervi* females may be related to such reduction of glucosinolate in the aphid  
334 cornicle secretion.

### 335 **Parasitoid performance under bottom-up force**

336 *Aphidius ervi* showed reduced performance developing in high-quality hosts, *i.e.* *S. avenae*,  
337 *M. persicae*, and *M. euphorbiae* reared on plants suffering water stress (reduced mummy  
338 and adult numbers). It did not occur when developing in its natal host, *A. pisum*, on which  
339 the parasitoid performed well independently of the water stress applied to host plant  
340 (bean). Inadequate or imbalanced nutrients could play a role in significant mortality during  
341 the mummy stage of parasitoids (also evidence are scarce). Juvenile larval performance  
342 depends on host size and age at parasitism, which correlates with host nutritional quality in  
343 aphid parasitoids (Harvey *et al.* 1994; Sequeira and Mackauer 1992). In other insect families,  
344 poor host food quality increases parasitoid larval mortality (Brodeur and Boivin 2004;  
345 Jonasson 1994). Besides, low quality of egg and pupae as parasitoid hosts affected  
346 immature parasitoid survival (Panizzi *et al.* 2012) or supplement proteins enhance  
347 reproduction in an ectoparasitoid (Harvey *et al.* 2017) thus suggesting the role of host  
348 protein composition in successful parasitoid development.

349 Another possible mechanism underneath may be a decrease in density of the  
350 endosymbiont *Buchnera* in aphids feeding on low-quality plants. The venom the female  
351 parasitoid injects into its host while oviposition plays the role of aphid castration completed  
352 by tetracyte production, to redirect host nutrients to its larva; notably enhancing benefits  
353 from the metabolism of the obligate aphid symbiont *Buchnera* toward parasitoid needs  
354 (Pennacchio and Mancini 2012; Strand 2014). Moreover, there is evidence that parasitoid

355 could manipulate the abundance of the primary symbiont *Buchnera*, from the egg and larval  
356 stage (Martinez *et al.* 2014).

357 Parasitoid larval mortality may occur through sequestration of plant toxins via aphids  
358 (Mooney *et al.* 2012). However, plants could both induce or decrease their toxin production  
359 as a strategy to tolerate water stress. Plants then reallocate resources and increase their  
360 defense via secondary metabolism, resulting in aphid host less palatable for parasitoids  
361 (Mewis *et al.* 2012). Aphids may sequester specific toxins against their natural enemies  
362 (Goodey *et al.* 2015) also not always occurring, *e.g.* increase of plant toxins may negatively  
363 affect aphids without reaching parasitoids (Le Guigo *et al.* 2011). Among the plants used in  
364 the study, cabbage, milkweed, and potato belong to the families of *Brassicaceae*, *Asclepias*,  
365 and *Solanaceae*, respectively; all are well-known for their constitutive toxic compounds. The  
366 tissues of cabbage contain glucosinolates (sulfur derived compounds), *Solanaceae* contains  
367 glycosidic alkaloids (tomatine, solanine) and milkweeds contain cardenolides. However, the  
368 impact of water limitation on aphid performance on those plants is not similar. Different  
369 mechanisms might explain the results. For the *M. euphorbiae*-potato complex, the trichome  
370 increases and prohibit aphids from plant feeding, therefore the mortality of aphids on LW  
371 plants are relatively high (>60% under LW conditions vs. <20% under OW conditions).  
372 Decreased *M. persicae* performance on cabbage occurred owing to known reduced plant  
373 nutritional quality and increased glucosinate concentration which *M. persicae* tolerates only  
374 at low concentration (Ali and Agrawal 2012). By contrast, the performance of *A. nerii* on  
375 milkweed was not affected by water limitation, suggesting a tolerance to plant responses in  
376 this aphid. Besides, the status of the low-quality host of this species for *A. ervi* did not  
377 change to a better owing to bottom-up effect. There was a similar case for another low-

378 quality host for *A. ervi*: the aphid *R. padi* developing on wheat did not show increased  
379 suitability for *A. ervi* when developing on water stress plants. These occurred despite the  
380 apparent negative impact of bottom-up effect on the aphid itself; higher mortality occurred  
381 likely owing to increased wheat leaf rigidity (see LMA results).

382 Finally, impairment in host metabolism regulation by the parasitoid may explain also  
383 partially reduced the performance of *A. ervi* offspring when developing in hosts suffering  
384 water-stress bottom-up effect. Parasitoid female could manipulate host metabolism and  
385 adjust host nutritional balance to meet their larval dietary needs. The development,  
386 survival, and fitness of the parasitoid offspring depend on regulatory factors they inject into  
387 the host during oviposition including teratocytes, venoms, polydnviruses and virus-like  
388 particles (Harvey *et al.* 2013; Poirie *et al.* 2009). Such disturbance may have occurred in the  
389 case of *A. ervi* developing in *M. persicae* feeding on water stress plants as we observed  
390 mortality at larval and mummy stages.

391 It remains unclear why *A. ervi* was not affected when developing in *A. pisum*  
392 suffering water stress bottom-up effect. Various mechanisms may explain this result. First,  
393 bean plants are well tolerant to water stress thank their nitrogen fixation symbionts (Laranjo  
394 *et al.* 2014), which induce plant nitrogen fixation and trehalose under stress. These both  
395 compounds increase plant stress tolerance (Lunn *et al.* 2014). Second, photosynthesis rate  
396 of beans was maintained under water limitation conditions, the same as wheat and potato  
397 in our experiments. Differently, bean morphological palatability did not impact (like in  
398 wheat which increased leaf rigidity, or potato which produced more trichomes). Third, *A.*  
399 *pisum* was the natal host for *A. ervi*, and it may be more adapted to potential variations  
400 occurring in this particular host.

#### 401 **Pattern of correlation preference - performance**

402 The correlation between parasitoid preference and performance at optimal water condition  
403 proved that female *A. ervi* could detect low-quality hosts and avoid parasitizing those in  
404 some extent (in concordance with our previous results, Monticelli *et al.* 2018). However,  
405 when the aphid-plant systems were subjected to a bottom-up effect, water stress in our  
406 study, the preference-performance was weakened. The capacity of host evaluation of *A. ervi*  
407 may be disturbed when encountering hosts suffering suboptimal development conditions. It  
408 hinted that the assessment made by parasitoid females when facing hosts might be mostly  
409 based on fixed aphid species-related traits rather than characteristics potentially varying as  
410 a function of the aphid feeding status. We observed that there was no drastic change in *A.*  
411 *ervi* behavioral pattern when tested on aphids reared on LW plants; it hints that changes in  
412 *A. ervi* behaviors were minor, but the trend was strong enough to affect the overall female  
413 capacity of optimizing diet breath as done under the optimal water supply.

#### 414 **Bottom-up effects on aphids**

415 All aphids expressed in some extent tolerance to bottom-up impacts of water stress on  
416 plants, illustrated by their population stably maintained during several weeks in the  
417 laboratory on both treatments. However, their life history-traits were impacted at different  
418 levels. Among six aphid species, the performance of *A. nerii* and *A. pisum* were scarcely  
419 affected (it not) by water stress on plant hosts. Their ability to, well perform despite  
420 bottom-up effect may stem from two different mechanisms. *A. nerii* is a specialist of  
421 milkweed plants and Oleander trees. The host fidelity of *A. nerii* is likely linked to an  
422 optimized fitness on a given plant when compared to other host aphids that are for most of

423 them quite polyphagous (Harrison and Mondor 2011; Smith *et al.* 2008). The performance  
424 of *A. pisum* on water stress bean plants may result from the sound nutritional quality of  
425 their plant hosts under the suboptimal watering conditions. Among the five plants tested,  
426 only beans showed both LMA and photosynthesis not impacted by water stress. Such  
427 tolerance in beans results from the mutualist protection of plant symbionts, *i.e.*  
428 rhizobacteria and/or mycorrhizal fungi (Eldin and Moawad 1988; Nanjareddy *et al.* 2014). By  
429 contrast, the survival rate of *S. avenae*, *R. padi* on wheat and *M. euphorbiae* on potato was  
430 reduced under water stress. Both LW wheat and potato morphologically reduced aphid  
431 feeding, as wheat LMA significantly increased as well as the density of potato trichomes  
432 which entangled aphids (observed from our experiments).

433 The reduced performance of aphids on wheat, cabbage, and potato was highlighted by their  
434 increased generation time and decreased the intrinsic rate of development. We supposed  
435 the inadequate nutrients of plant hosts lengthened the aphid feeding time and reduced  
436 their fecundity as previously shown by other studies (Han *et al.* 2014; Price 1991; White  
437 1984; 2009).

#### 438 **Impact of water limitation on plants**

439 The assays used were successful in efficiently impacting key plant traits through water  
440 stress. Wheat under stress had higher LMA than OW plants. Leaf mass per area value (LMA,  
441  $\text{g.m}^{-2}$ ) is structural plant trait reflecting leaf thickness and/or leaf density. LMA relates to the  
442 plant metabolism (photosynthesis, respiratory rate), and plant vascular hydraulic transport  
443 system, as well as plant growth and decomposition (de la Riva *et al.* 2016). LMA is  
444 considered the trade-off between plant defenses, *e.g.* from herbivores, by the leaf rigidity

445 and the light prevention from photosynthesis and/or the plant resource allocation. Lower  
446 LMA enhances conductivity within the leaf, which may facilitate photosynthesis (Poorter *et*  
447 *al.* 2009). Impacted by water stress, folio cell walls are thicker. Therefore, LMA is a crucial  
448 trait to predict plant adaptation strategies and/or mortality pattern under unstable  
449 environments (Anderegg *et al.* 2016; Poorter *et al.* 2009). The change in leaf chemical  
450 composition mediated by LMA might reflect the difference in the vascular system. LMA in  
451 herbaceous plant correlates positively to leaf carbon concentration but negatively to leaf  
452 nitrogen concentration, organic acids and protein concentration (de la Riva *et al.* 2016;  
453 Poorter *et al.* 2009). As phloem- and xylem- feeders, insects rely on phloem available  
454 nutrients (free amino acids, sugars). Plant higher LMA associated with lower N content could  
455 decline aphid feeding efficiency and its quality as parasitoid host (Auclair 1963; Will *et al.*  
456 2013).

457 The plant water transport system is a vital function in plant life. In a simplified cycle, plants  
458 draw water from soil via root system, water then lost during plant transpiration in exchange  
459 for CO<sub>2</sub> uptake (Sack and Scoffoni 2012). Plant mortality paradigms state that plants die  
460 from either carbon starvation (carbon starvation hypothesis) or hydraulic failure (hydraulic  
461 hypothesis) (Barigah *et al.* 2013; McDowell 2011; McDowell *et al.* 2008; Sevanto *et al.* 2014).  
462 Parallely, plants might shift their regulation between strategies of reduction of respiration  
463 and/or carbon use efficiency to survive under water stress (Metcalf *et al.* 2010). Those  
464 accommodative behaviors in plants are classified into a spectrum of isohydric (remain leaf  
465 water potentials and reduce CO<sub>2</sub> uptake via the stomatal closure) and anisohydric  
466 categories (decline leaf water potential in optimizing CO<sub>2</sub> uptake) (Landsberg *et al.* 2017;  
467 Martinez-Vilalta *et al.* 2014). The stomatal closure as stress tolerance strategy consisted of

468 results described by (Flexas *et al.* 2013; Westoby *et al.* 2013), the strategy might benefit  
469 over leaf lifetimes. The trade-off reduction of respiration results in the decrease in  
470 photosynthesis and the deplete of carbon hydrate resources, which makes the plants more  
471 susceptible to herbivores (Landsberg *et al.* 2017).

#### 472 **Change in plant primary metabolism and its impacts on aphid feeding.**

473 During plant stress adaptation process, the plant quality as food resources for phloem  
474 suckers has been shown to be impacted. Physically, water scarcity results in phloem water  
475 shortage, or phloem viscosity increase and challenge aphid feeding (Landsberg *et al.* 2017).  
476 Chemically, plant nitrogen and phosphorus content reduce (He and Dijkstra 2014), carbon  
477 content (Reddy *et al.* 2004), increase ratio C: N which is an indicator for plant defensive  
478 compound concentration (Royer *et al.* 2013). Higher sugar concentration in phloem and  
479 weaken the immune defense of plants due to water scarcity might lead to aphid preference  
480 on stressed plants. But plant poor nutrient quality (plant stress hypothesis) lead to aphids  
481 smaller in size, lower in nutrient quality to bear parasitoid larvae. But the impacts depend as  
482 well on aphid foraging strategies, flush or senescence feeders (White 2009, White 2015). As  
483 there was no evidence of *A. pisum* and *S. avenae* belonging to senescence group (White  
484 2015), we assumed they belong to flush feeders group preferring young and soft leaves as  
485 the majority of insects (Price 1991). Under moderate constant water limitation, *A. pisum*  
486 performance at *the* population level was reduced but not at the early stage of plants  
487 (Mcvean 2001). However, no impact of water limitation is reported in *S. avenae* both at  
488 individual and population levels on wheat (Pons and Tatchell 1995). Therefore, the effects of  
489 abiotic stress on aphids are complex and simple measurements of aphid life history traits  
490 could not provide high predictive results regarding adaptive trend.

491 We demonstrated that the abiotic stress on plants could cascade to both second and third  
492 trophic levels, even though plants and herbivores may be tolerant of long-term water stress.  
493 In overall, water stress mediated by plant hosts had an indirect adverse effect on parasitoid  
494 survival and development on aphid hosts, but the impact magnitude depended on the  
495 aphid-plant complex. The interaction of plant tolerance strategies and aphid salivary protein  
496 profiles might result in different attenuation of aphid host quality. The parasitoid pre-imaginal  
497 adaptation could also occur in its adulthood fitness under severe constant water stress. To  
498 predict the diet breadth of parasitoids under constraint conditions, one should consider the  
499 biological nature and the host specificity of organisms in the micro-ecosystem as well as the  
500 stress profile, such as stress timing, frequency, duration, and intensity. For further research,  
501 the effects of moderate water stress or pulsed stress on the same tri-trophic complex  
502 should also be considered as plant reactions under different stress scenarios are proved to  
503 be very different, and it may cascade toward various outcomes in the wild.

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739

740 **LEGENDS**

741 Figure 1A, B, C. Plant height and plant nodes, respectively (N = 16–99) of 5 plants: bean,  
742 wheat, cabbage, milkweed and potato under optimal water (OW) versus limited water  
743 irrigation (LW, 30% of optimal watering volume). The treatment durations were from 3 to 6  
744 weeks for all plants. The asterisks indicate significant difference ( $p$  value < 0.05) between OW  
745 and LW plants (factorial ANOVA analysis). The bottom and the top part of the plots indicate  
746 the 25th and 75th percentile, respectively, the two whiskers the 10th and the 90th percentile,  
747 respectively, and the horizontal line within the box the median value.

748 Figure 2A, B, C: Leaf photosynthesis rate, transpiration rate, and stomatal conductance (95%  
749 confidence intervals of the means, N = 24–68) measured for bean, wheat, cabbage, milkweed  
750 and potato treated with optimal water input or limited water treatment (OW: optimal water;  
751 LW: limited water). The asterisks indicate significant difference ( $p$  value < 0.05) between OW  
752 and LW plants, using factorial ANOVA analysis. The bottom and the top part of the plots  
753 indicate the 25th and 75th percentile, respectively, the two whiskers the 10th and the 90th  
754 percentile, respectively, and the horizontal line within the box the median value.

755 Figure 3A, B, C: Survival ratio, generation time (D) and intrinsic rate of development ( $r_m$ ) of  
756 aphids feeding on optimal watered (OW) and limited watered (LW) plants (mean  $\pm$  SEM, N=  
757 18-39). The asterisks indicate significant difference ( $p$  value < 0.05) between aphids feeding  
758 on OW and LW plants, using Fisher's exact test for survival ratio and factorial ANOVA analysis  
759 for D and  $r_m$ .

760 Figure 4A, B, C. Preference and performance of *Aphidius ervi* while encountering six aphid  
761 host species: *Acyrtosiphon pisum*, *Sitobion avenae*, *Rhopalosiphum padi*, *Aphis nerii*, *Myzus*

762 *persicae*, and *Macrosiphum euphorbiae* under optimal water (OW) and low water (LW)  
763 supply, statistically analyzed using Fisher's exact test. Behavioral traits of *A. ervi* were  
764 measured from observation experiments and included: detection, acceptance and stinging  
765 rate. Physiological traits of *A. ervi* were measured from sequential dissection experiments and  
766 included: egg, larval, mummy and emerged adult survival ratio. Different letters show  
767 significant probability (significance code: 0 '\*\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05) to reject the null  
768 hypothesis of no difference between variables in favor to the alternative hypothesis.

769 **Table 1.** Effect of water stress on plant morphological traits and leaf gas exchange activities  
770 analyzed by factorial ANOVA test. The asterisks indicate critical probability threshold  
771 (significance code: 0 '\*\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05) that the observed data are inconsistent  
772 with the null hypothesis of no difference or no association between variables in case of  
773 covariance or correlation test, respectively. N/A means no information.

774 **Table 2.** Effect of water stress on aphid survival ratio, generation time (D) and intrinsic rate of  
775 development ( $r_m$ ) of aphids feeding on plants of optimal water (OW) and limited watered (LW)  
776 supply, analyzed using Fisher's exact test for survival ratio and factorial ANOVA analysis for D  
777 and  $r_m$ . The asterisks indicate critical probability threshold (significance code: 0 '\*\*\*\*' 0.001  
778 '\*\*' 0.01 '\*' 0.05) that the observed data are inconsistent with the null hypothesis of no  
779 difference or no association between variables in case of covariance or correlation test,  
780 respectively.

781 **Table 3.** Impacts of plant water limitation on the preference and performance of *Aphidius*  
782 *ervi* while encountering six aphid species: *Aphis nerii* on milkweed, *Myzus persicae* on  
783 cabbage, *Rhopalosiphum padi* on wheat, *Sitobion avenae* on wheat and *Acyrtosiphon pisum*

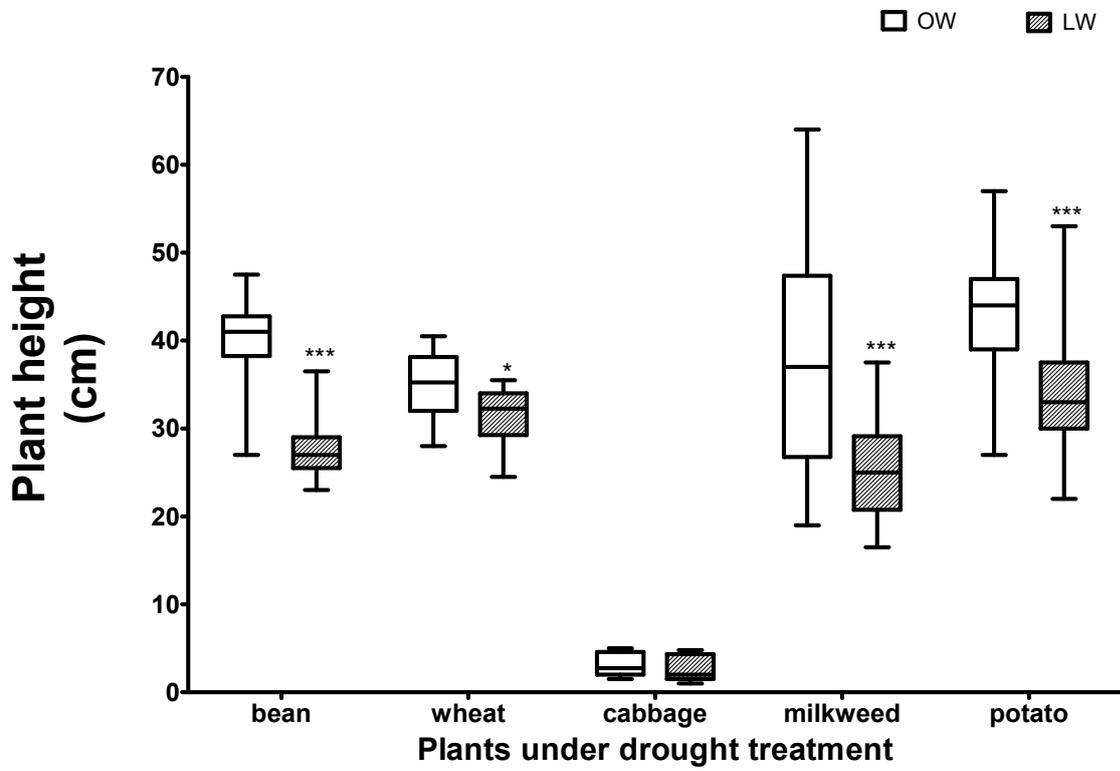
784 on beans and *Macrosiphum euphorbiae* on potato. Behavioral and suitable traits of *Aphidius*  
785 *ervi* on one species under LW and OW were compared using pairwise Fisher exact test. The  
786 asterisks indicate critical probability threshold that the observed data are inconsistent with  
787 the null hypothesis of no difference between variables ( $P$  value  $< P$  value  $< .05$ ).

788 **Table 4.** Comparison of behavioral stages or fitness gain during parasitoid parasitism; using  
789 multiple comparisons Fisher's exact tests with Bonferonni adjustment method. The asterisk  
790 means the probability of rejecting the null hypothesis below the threshold value (adjusted  $p$   
791 value  $< 0.0167$  in preference traits and  $p$  value  $< 0.0083$  in performance traits).

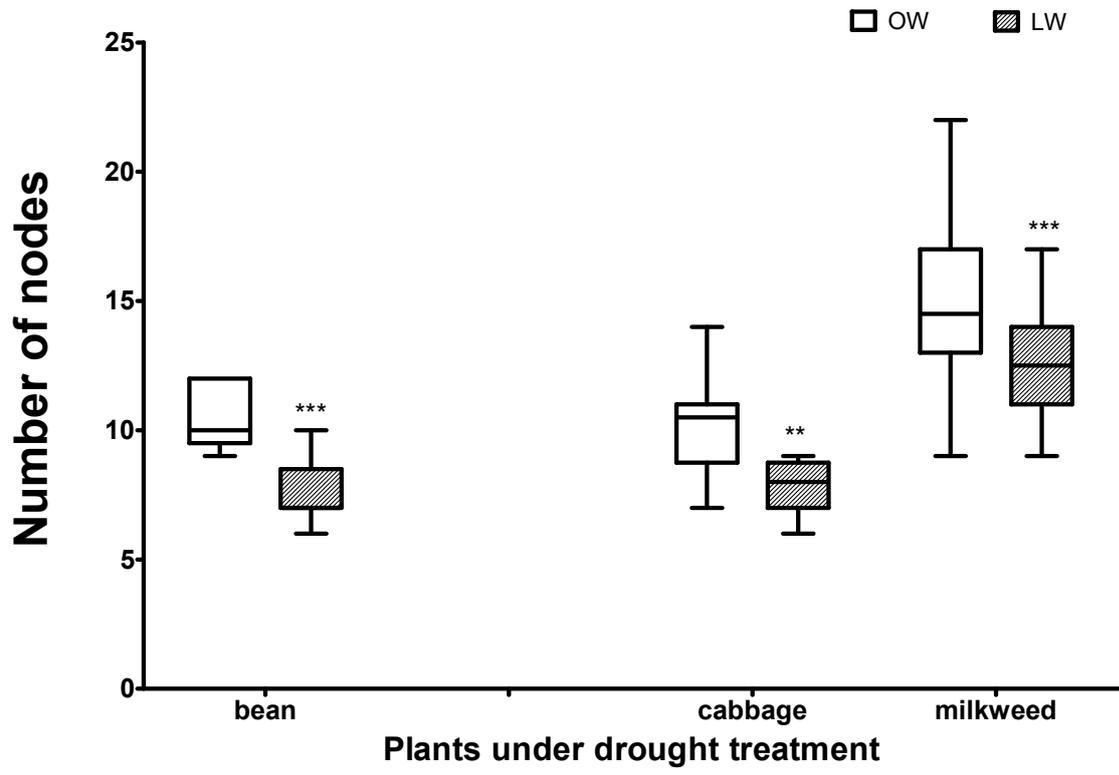
792 **Table 5.** The relationship between parasitoid preference for and performance on (logistic  
793 regression) a range of aphid hosts, *Aphis nerii* on milkweed, *Myzus persicae* on cabbage,  
794 *Rhopalosiphum padi* on wheat, *Sitobion avenae* on wheat and *Acyrtosiphon pisum* on beans  
795 and *Macrosiphum euphorbiae* on potato under optimal and limited water supply. The  
796 parasitoid preference represented by the successful sting rate from total behavioral  
797 observations, the parasitoid performance represented by the successful emergent rate from  
798 the follow-up of total stung aphids. The asterisks indicate critical probability threshold  
799 (significance code: 0 '\*\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05) that there is no association between  
800 variables in correlation test.

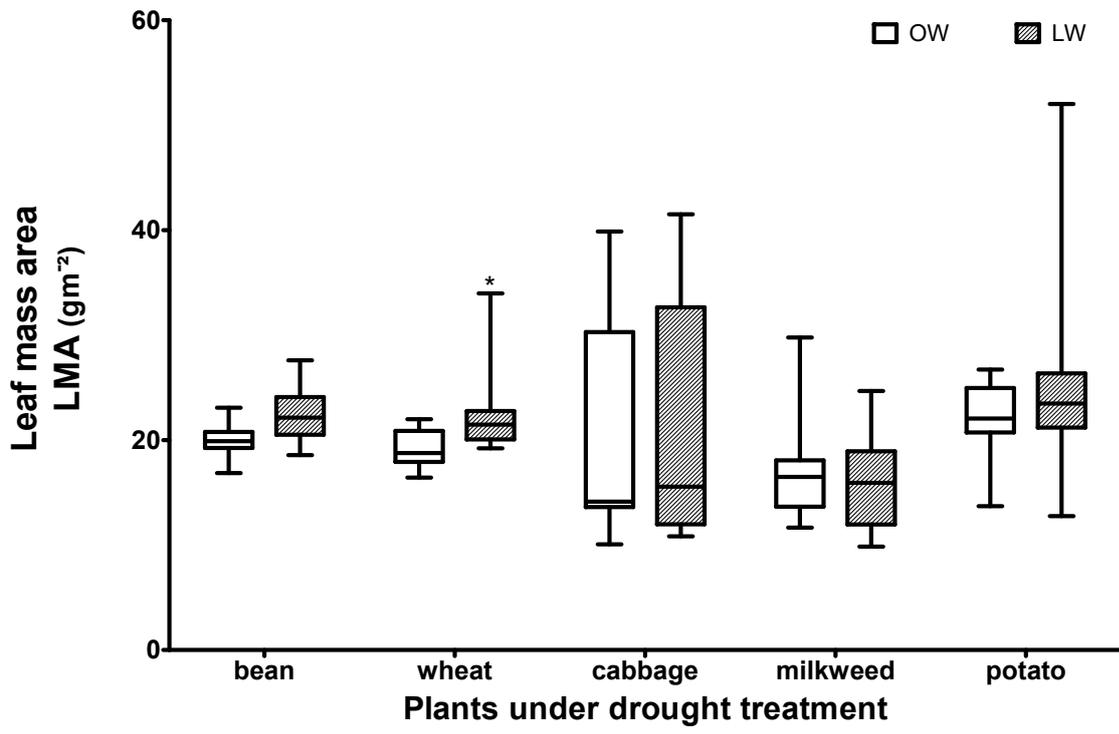
801 FIGURES AND TABLES

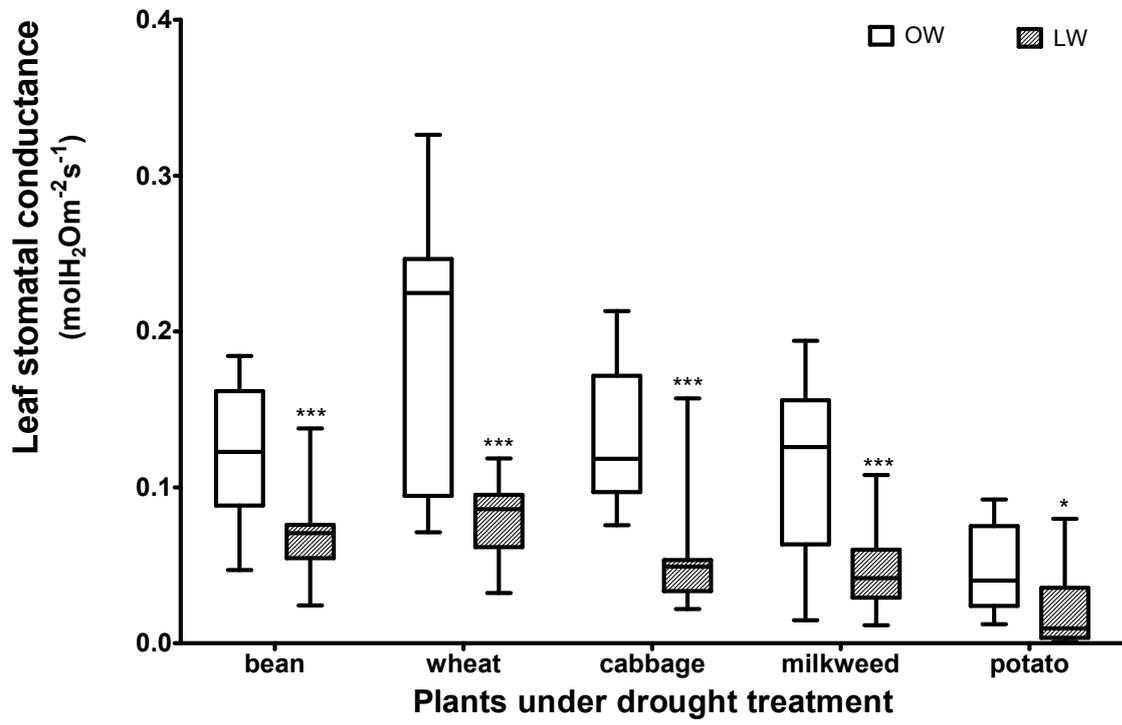
802 *Figure 1A*

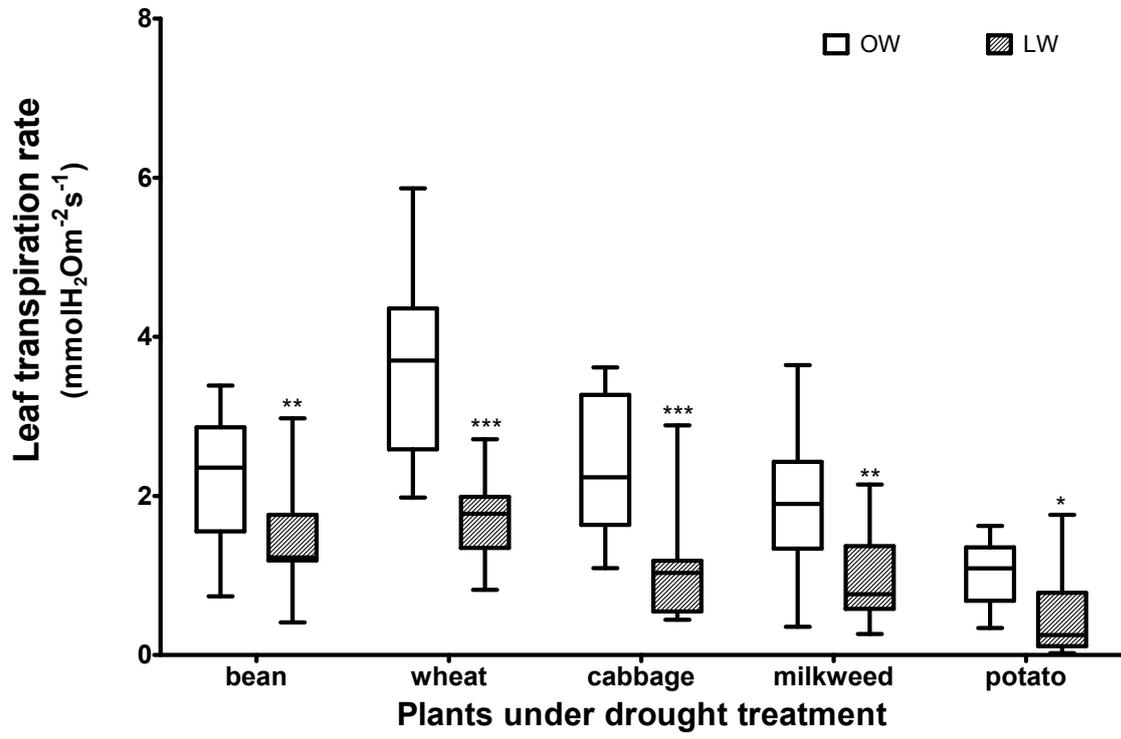


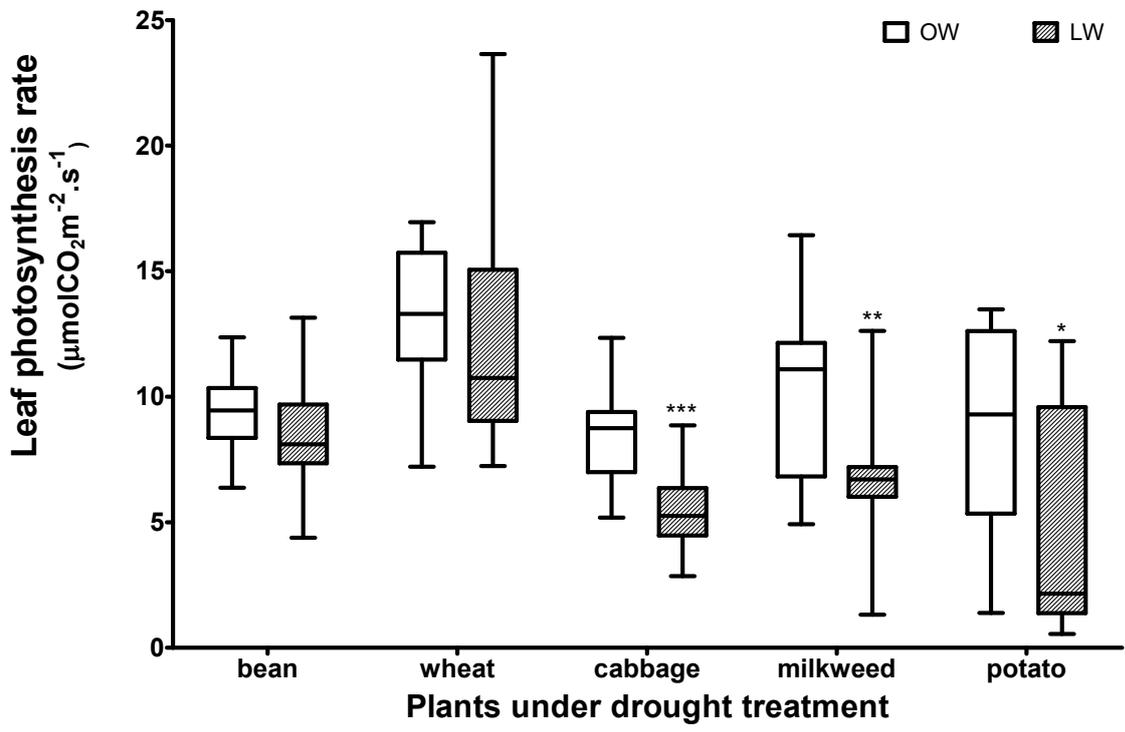
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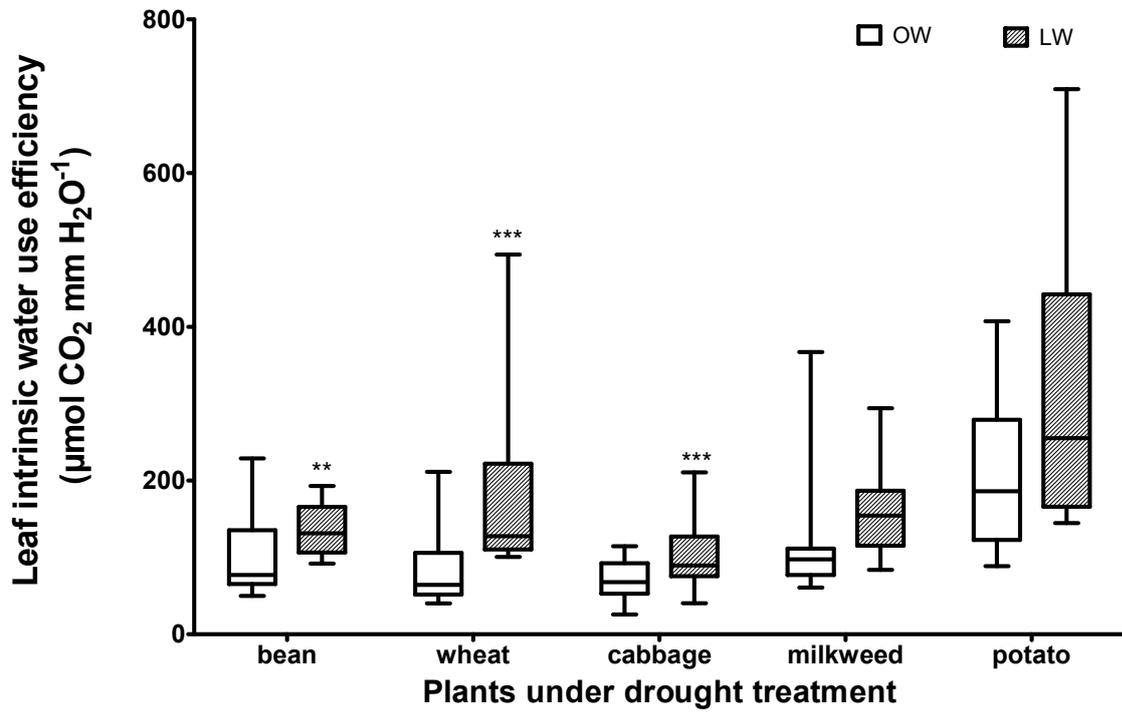


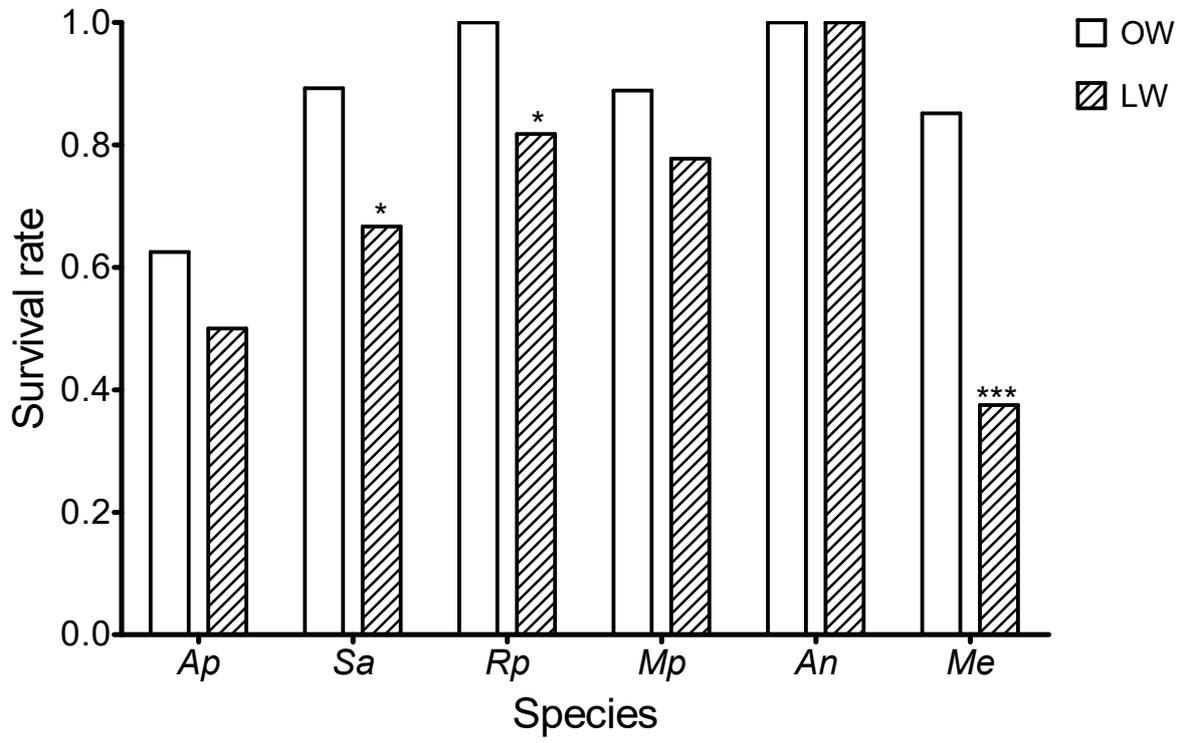


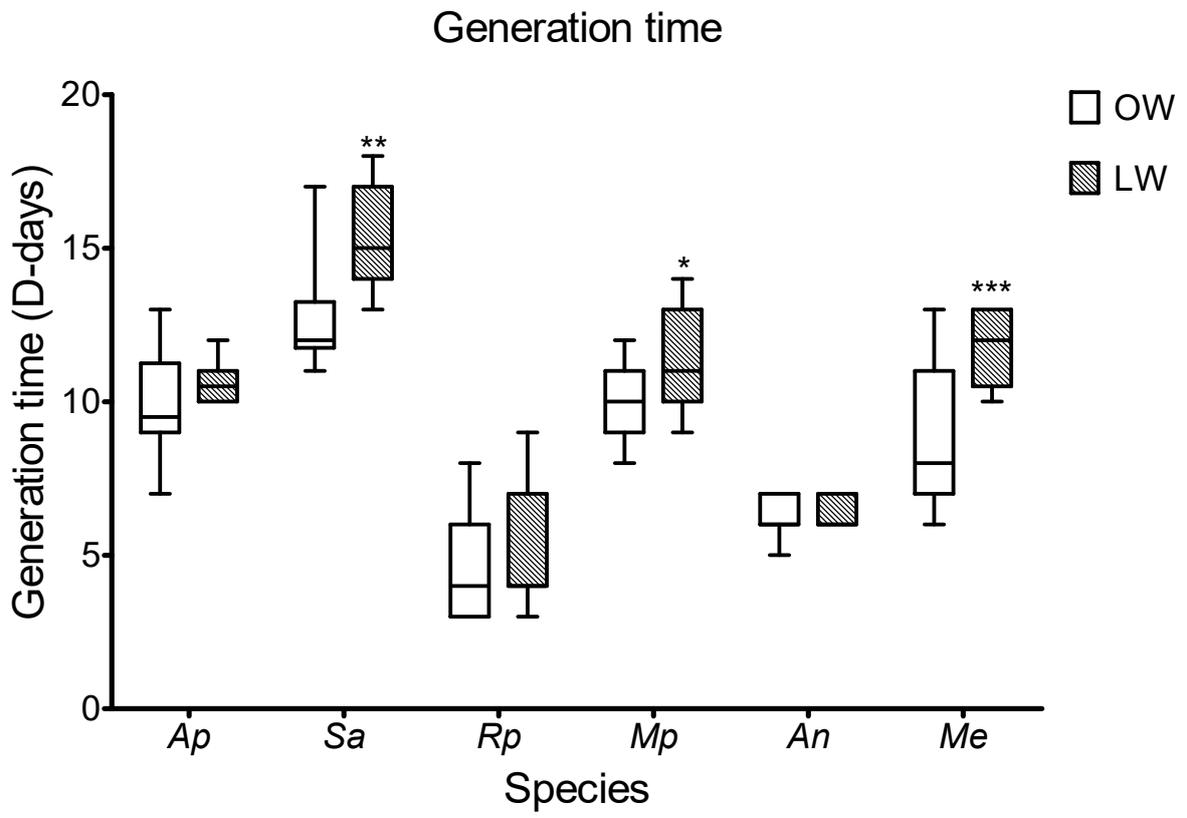


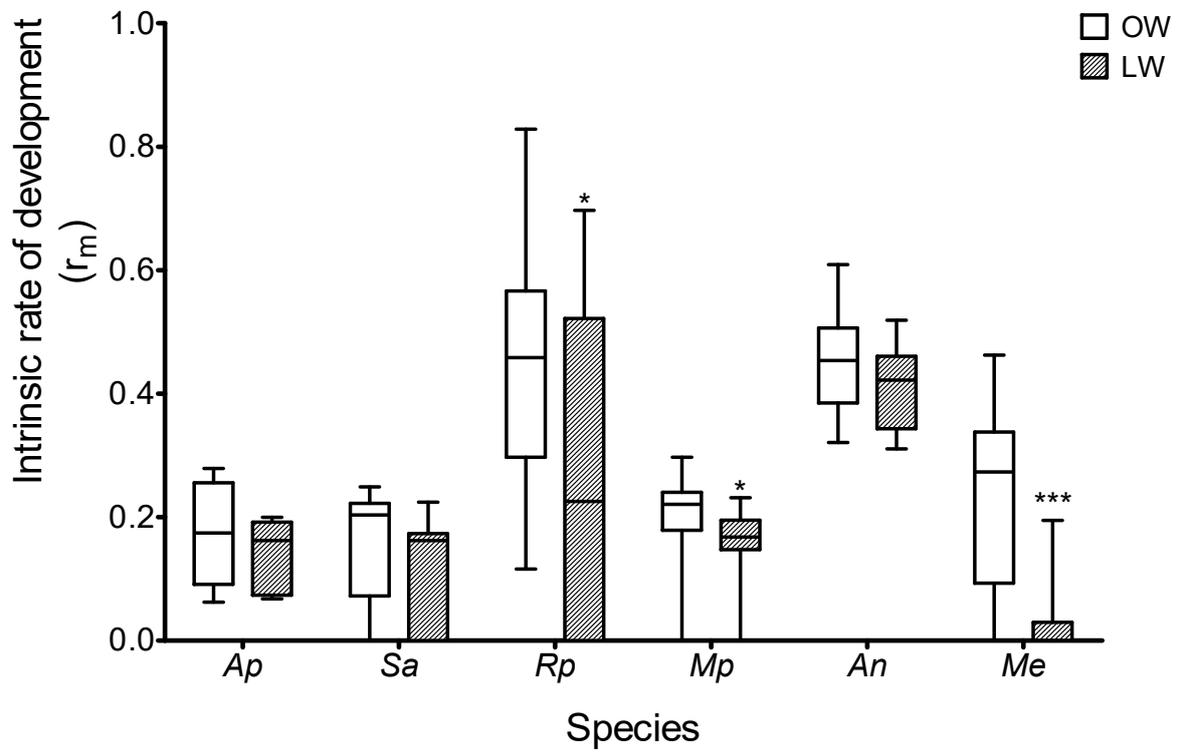


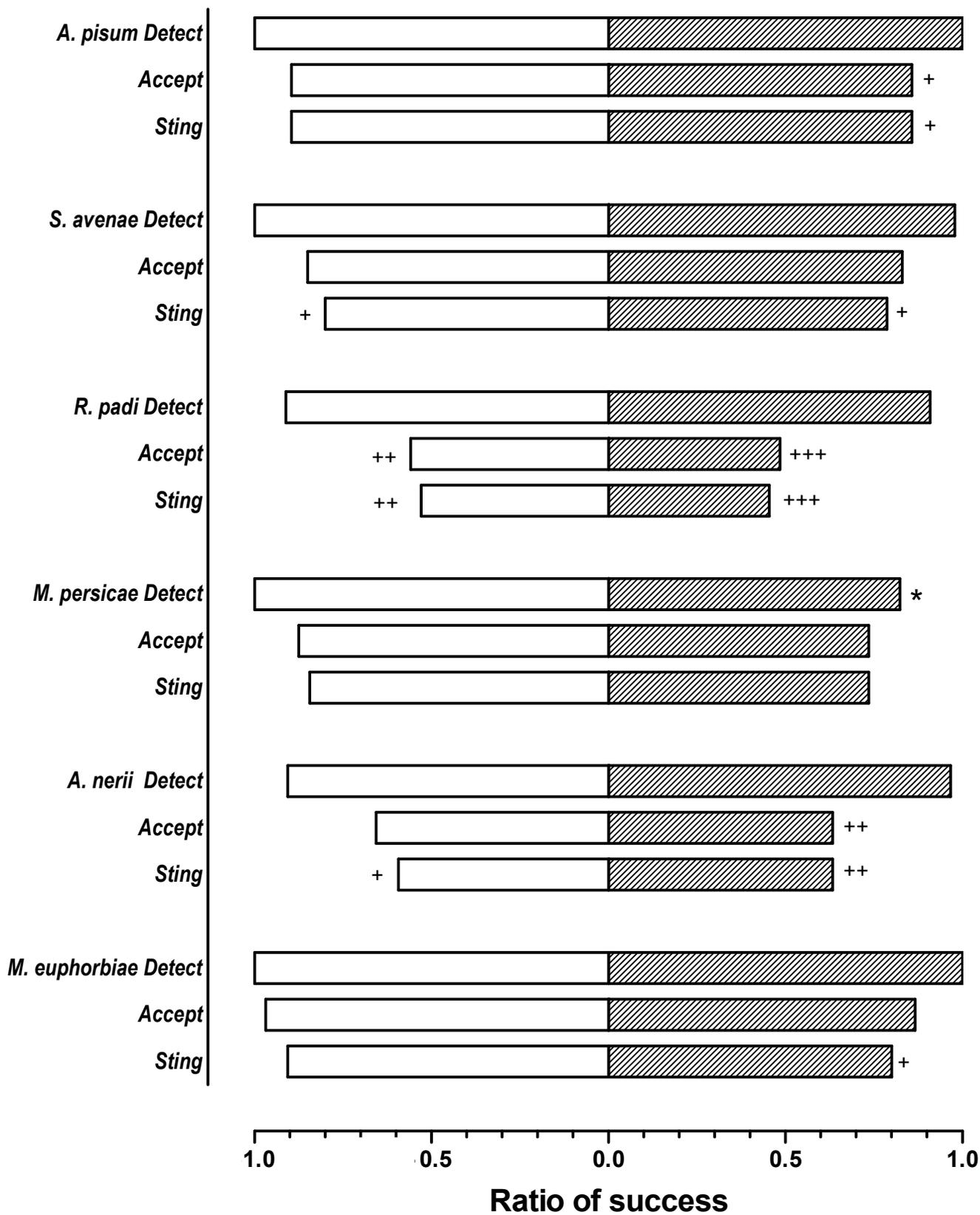


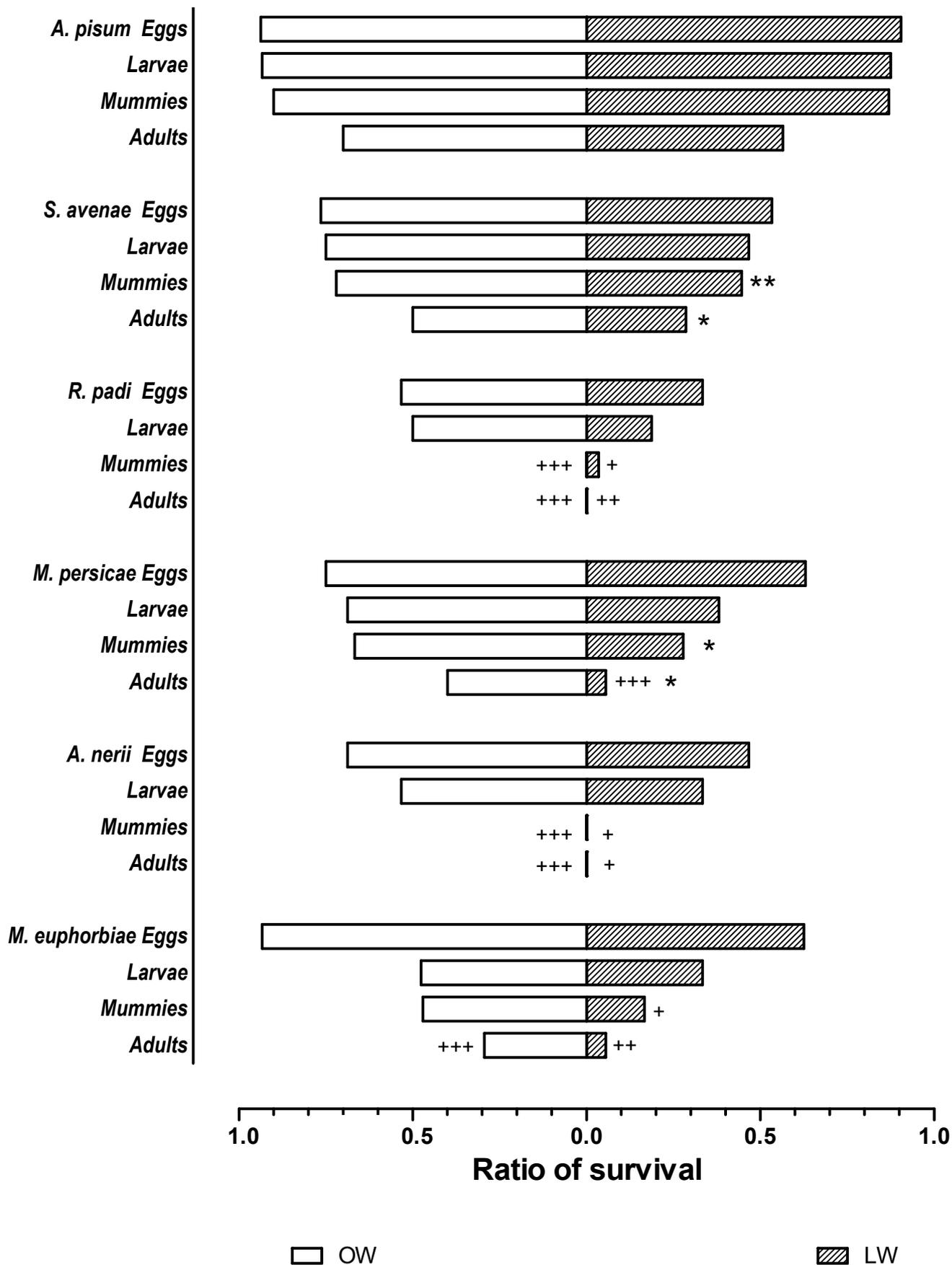












Effect of water stress	Water stress duration (week-old)	Bean	Wheat	Cabbage	Milkweed	Potato
		3-5	3-5	3-10	3-11	3 – 7
Plant height (H)	<i>p</i> value	<b>&lt; 0.001 ***</b>	<b>0.023 *</b>	0.621	<b>&lt; 0.001 ***</b>	<b>&lt; 0.001 ***</b>
	<i>F</i>	<b><math>F_{1,30} = 34.28</math></b>	<b><math>F_{1,26} = 5.81</math></b>	$F_{1,16} = 0.254$	<b><math>F_{1,127} = 42.21</math></b>	<b><math>F_{1,99} = 50.89</math></b>
Number of nodes (N)	<i>p</i> value	<b>&lt; 0.001 ***</b>	N/A	<b>0.008 **</b>	<b>&lt; 0.001 ***</b>	N/A
	<i>F</i>	<b><math>F_{1,16} = 26.51</math></b>		<b><math>F_{1,16} = 9.262</math></b>	<b><math>F_{1,127} = 19.06</math></b>	
Leaf mass area (LMA)	<i>p</i> value	0.825	<b>0.013 *</b>	0.548	0.638	0.232
	<i>F</i>	$F_{1,54} = 0.05$	<b><math>F_{1,23} = 7.20</math></b>	$F_{1,52} = 0.366$	$F_{1,29} = 0.226$	$F_{1,27} = 1.494$
Photosynthesis	<i>p</i> value	0.125	0.605	<b>&lt; 0.001 ***</b>	<b>0.002 **</b>	<b>0.012 *</b>
	<i>F</i>	$F_{1,30} = 2.487$	$F_{1,24} = 0.275$	<b><math>F_{1,68} = 17.23</math></b>	<b><math>F_{1,29} = 11.7</math></b>	<b><math>F_{1,27} = 7.293</math></b>
Conductance	<i>p</i> value	<b>&lt; 0.001 ***</b>	<b>&lt; 0.001 ***</b>	<b>&lt; 0.001 ***</b>	<b>&lt; 0.001 ***</b>	<b>0.018 *</b>
	<i>F</i>	<b><math>F_{1,30} = 15.47</math></b>	<b><math>F_{1,24} = 21.38</math></b>	<b><math>F_{1,52} = 34.06</math></b>	<b><math>F_{1,29} = 17.88</math></b>	<b><math>F_{1,27} = 6.323</math></b>
Transpiration	<i>p</i> value	<b>0.00292 **</b>	<b>&lt; 0.001 ***</b>	<b>&lt; 0.001 ***</b>	<b>&lt; 0.001 ***</b>	<b>0.0103 *</b>
	<i>F</i>	<b><math>F_{1,30} = 10.5</math></b>	<b><math>F_{1,24} = 27.52</math></b>	<b><math>F_{1,52} = 24.11</math></b>	<b><math>F_{1,29} = 15.31</math></b>	<b><math>F_{1,27} = 7.617</math></b>
Intrinsic water use efficiency (W <sub>UE</sub> )	<i>p</i> value	<b>0.005 **</b>	<b>&lt; 0.001 ***</b>	<b>0.0001 ***</b>	0.059	0.060
	<i>F</i>	<b><math>F_{1,30} = 9.16</math></b>	<b><math>F_{1,24} = 27.52</math></b>	<b><math>F_{1,68} = 16.19</math></b>	$F_{1,29} = 3.88$	$F_{1,27} = 3.868$

Main effect of water stress		<i>Acyrtosiph on pisum</i>	<i>Sitobion avenae</i>	<i>Rhopalosiphu m padi</i>	<i>Myzus persicae</i>	<i>Aphis nerii</i>	<i>Macrosiphum euphorbiae</i>
Generation time (factorial ANOVA)	<i>p</i> value	0.251	<b>0.004 **</b>	0.19	<b>0.026 *</b>	0.575	<b>&lt; 0.001 ***</b>
	<i>F</i>	$F_{1,18} = 1.41$	$F_{1,19} = 11$	$F_{1,39} = 1.77$	$F_{1,28} = 5.56$	$F_{1,29} = 0.32$	$F_{1,30} = 17.92$
Intrinsic rate of development ( $r_m$ ) (factorial ANOVA)	<i>p</i> value	0.4	0.320	<b>0.010 *</b>	<b>0.047 *</b>	0.134	<b>&lt; 0.001 ***</b>
	<i>F</i>	$F_{1,18} = 0.75$	$F_{1,26} = 1.02$	$F_{1,43} = 7.16$	$F_{1,30} = 4.29$	$F_{1,29} = 2.381$	$F_{1,49} = 33.41$
Survival rate (Fisher's exact test)	<i>p</i> value	0.45	<b>0.041 *</b>	<b>0.013 *</b>	451	1	<b>&lt; 0.001 ***</b>

<i>p</i> value (Fisher's exac test)	Preference			Performance				
	Detect	Accept	Sting	Eggs	Larvae	Mummies	Adults	Female
<b>Optimal water vs. limited water supply</b>								
<i>Acyrtosiphon pisum</i>	1	0.7593	0.7593	1	1	1	0.5282	1
<i>Sitobion avenae</i>	1	1	1	0.2662	0.1489	<b>0.0058**</b>	<b>0.0289*</b>	0.4477
<i>Rhopalosiphum padi</i>	1	0.6278	0.6278	0.4621	0.1351	1	1	1
<i>Myzus persicae</i>	<b>0.0248*</b>	0.2183	0.3708	0.5293	0.0991	<b>0.0383*</b>	<b>0.03*</b>	0.2857
<i>Aphis nerii</i>	0.6132	1	0.7986	0.2852	0.4621	1	1	1
<i>Macrosiphum euphorbiae</i>	1	0.1887	0.294	0.0829	0.5006	0.075	0.0877	1

34 Table 4.

Life-history traits	<i>p</i> value	An30	An100	Mp30	Mp100	Rpi30	Rp100	Sa30	Sa100	Ap30	Ap100	Me30	Me100
Preference	D vs. A	<b>0.0025*</b>	0.0319	0.5597	0.1132	<b>0.0003*</b>	<b>0.002**</b>	0.0304	0.0255	<b>0.0124*</b>	0.056	0.1124	1
		*				**							
	D vs. S	<b>0.0025*</b>	<b>0.0081*</b>	0.5597	0.0528	<b>0.0001*</b>	<b>0.0009*</b>	<b>0.0076*</b>	<b>0.0053*</b>	<b>0.0124*</b>	0.056	<b>0.0237*</b>	0.2381
		*				**	*						
Performance	E vs. L	0.7104	0.4725	0.1449	0.7225	0.4331	1	1	1	1	1	0.1556	0.005
	E vs. M	<b>0.0063*</b>	<b>0.0001*</b>	0.0331	0.7118	<b>0.013*</b>	<b>0***</b>	0.5742	1	1	1	<b>0.0122*</b>	0.0073
			**										
	E vs. Ad	<b>0.0063*</b>	<b>0.0001*</b>	<b>0.0001*</b>	0.0796	<b>0.0028*</b>	<b>0***</b>	0.122	0.0884	0.0174	0.1041	<b>0.0006*</b>	<b>0.0003*</b>
			**	**		*						*	**

35

836 *Table 5*

<b>Water supply</b>	<b>Df</b>	<b>Deviance residuals</b>	<b><i>p</i> values</b>	<b>R<sup>2</sup></b>
<b>Optimal water</b>	4	0.113	0.0018**	0.71
<b>Limited water</b>	4	0.140	0.071	0.45

837

838 **Supplementary data**

839 *Table 6: The difference between female ratio and emergence ratio of parasitoids testing on aphid species-treatment combinations in compare to*  
 840 *host natal on optimal treatment; using multiple comparisons Fisher's exact tests. The asterisk means the probability of rejecting the null*  
 841 *hypothesis below the threshold value (adjusted p value < .00455)*

$\chi^2$	An30	An100	M.p30	Mp70	Rp30	Rp100	Sa30	Sa100	Ap30	Me30	Me100
	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.	vs.
	Ap100	Ap100	Ap100	Ap100	Ap100	Ap100	Ap100	Ap100	Ap100	Ap100	Ap100
<b>Emergence ratio</b>	0.00002* **	0.00002* **	0.00005* **	0.0966	0***	0***	0.00271* 0.18374	0.5282	0.00005* **	0.02171	
<b>Female ratio</b>	0.00055* *	0.00055* *	0.00017* *	0.30636	0.00001* **	0.00001* **	0.02497	0.28505	0.54669	0.00141* 0.03967	

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843 Table 7: Impacts of water stress on parasitoid offsprings parasitized six aphid species feeding on plants received under optimal water (OW) versus  
 844 limited water irrigation (LW, 30% of optimal watering volume? N = 7–21). The asterisks indicate significant difference (p value < 0.05) between  
 845 parasitoids on aphids feeding OW and LW plants (factorial ANOVA analysis).

Main effect of water stress on parasitoid offspring	<i>Aphidius ervi</i> on <i>Acyrtosiphon</i>					
	<i>pisum</i>		<i>A. ervi</i> on <i>Sitobion avenae</i>		<i>A. ervi</i> on <i>Myzus persicae</i>	
	p value	$F_{1,21}$	p value	$F_{1,15}$	p value	$F_{1,7}$
<b>Tibia length</b>	0.0599	3.954	0.0557	0.303	<b>0.00017***</b>	52.56
<b>Glycogen content</b>	0.417	0.687	0.058	4.213	<b>0.0327*</b>	7.054
<b>Fructose content</b>	<b>0.0131*</b>	7.349	0.169	2.093	0.0688	4.615
<b>Sucrose content</b>	0.0608	3.927	<b>0.00304**</b>	12.45	<b>0.0319*</b>	7.139
<b>Total sugar content</b>	0.120	2.628	<b>0.0292*</b>	5.816	0.0732	0.128

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<b>Aphid classification</b>	<b>Sub-guild trophic: Senesce nce (Se) vs. flush feeder (Fl)</b>	<b>Plant host special ity: special ist (Sp) vs. genera list (Ge)</b>	<b>Reference</b>
<i>Myzus persicae</i>	Se	Ge	Simpson 2012,
<i>Brevicoryne brassicae</i>	Fl	Sp	van Emden and Harrington 2007
<i>Schizaphis graminum</i>	Se	Sp	Sandstrom <i>et al.</i> 2000
<i>Rhopalosiphum padi</i>	Se	Sp	White 2015
<i>Sitobion avenae</i>	Fl	Sp	White 2015
<i>Acyrtosiphon pisum</i>	Fl	Sp	van Emden and Harrington 2007
<i>Aphis nerii</i>	Fl	Sp	Agrawal 2011, Hall and Ehler (1980)
<i>Macrosiphum euphorbiae</i>	Fl	Ge	<a href="http://www.cabi.org/isc/data-sheet/32154">http://www.cabi.org/isc/data-sheet/32154</a>

**ANNEXES CHAPTER 5**

Figure 36. Distribution of studies on bottom-up effects of abiotic stress

by subjects and year (A), parasitoid species (B) and types of stress (C) (data from )

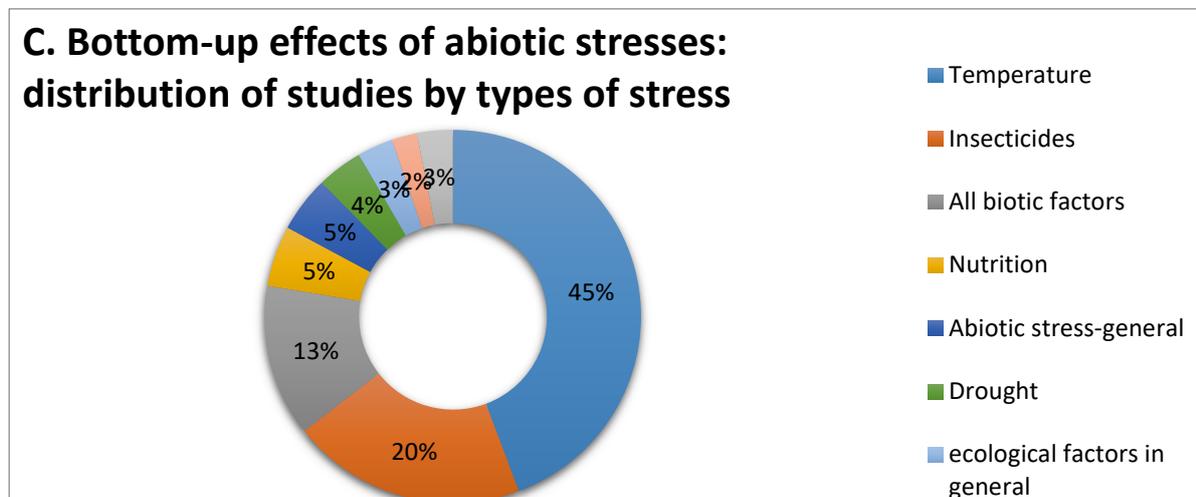
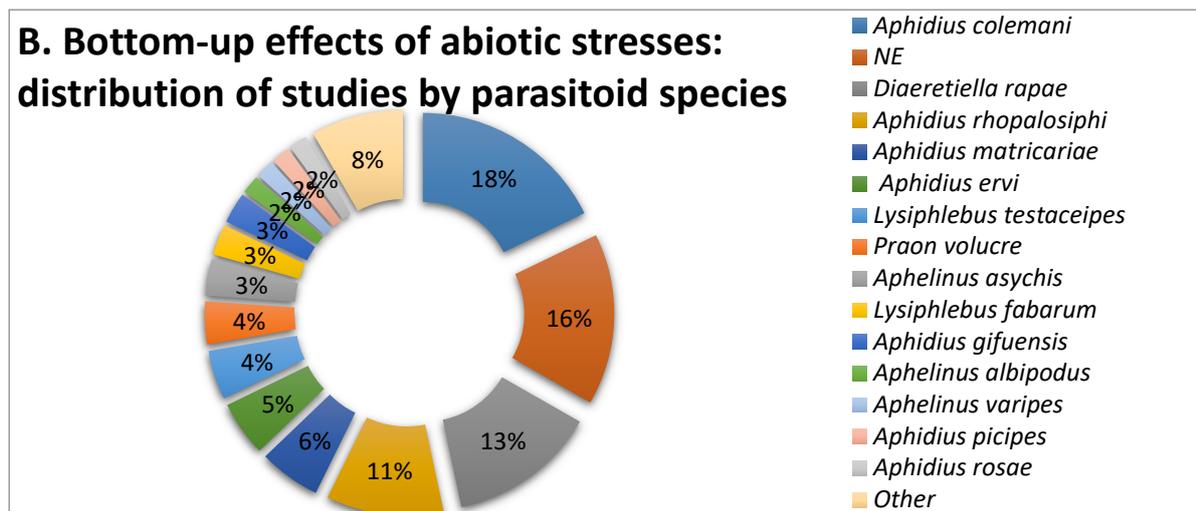
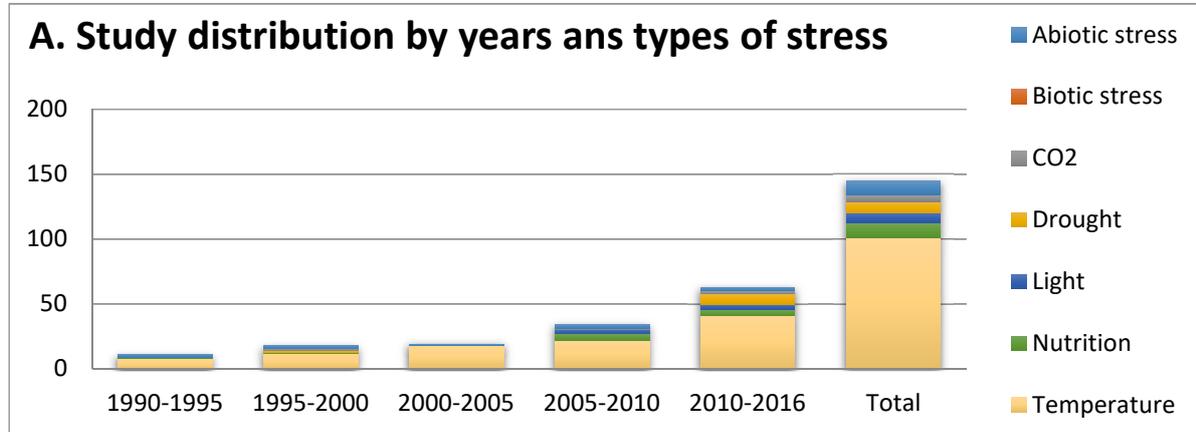


Table 5. Articles on the subject: ‘Impacts of abiotic stress on the tritrophic plant-aphid-parasitoid system’. Results were found from the database of Web of Science (c). Codes of stress type: all ecological = A+B; T: thermal (cold/hot); CO2 = C; Abiotic = A; cid : toxins/pesticides; B: biotic. Codes of experimental scales: laboratory: L; Greenhouse: G; Field: F; Observation in the field: O. NE = parasitoids in general.s

CODE	STRESS	YEAR	SCALE	PARASITOID SPECIES	ARTICLES
1	T	2015		<i>Aphidius matricariae</i>	Al Antary et al. (2015)
2	T	2015	M	NE	Amarasekare (2015)
3	T	2008		<i>Aphidius picipes</i>	Amice et al. (2008)
4	D	2012	O	<i>Diaeretiella rapae</i>	Amini et al. (2012)
5	T	2013		<i>Aphidius rhopalosiphi</i>	Andrade et al. (2013)
6	T	2016		<i>Aphidius rhopalosiphi</i>	Andrade et al. (2016)
7	N	2015		<i>Aphidius colemani</i>	Aqueel et al. (2015)
8	N	2015		<i>Aphidius rhopalosiphi</i>	Aqueel et al. (2015)
9	D	2013	L	<i>Aphidius ervi</i>	Aslam et al. (2013)
10	B	2005		<i>Aphidius ervi</i>	Azzouz et al. (2005)
11	T	2011		<i>Aphidius matricariae</i>	Bannerman et al. (2011)
12	T	2014	M	NE	Bannerman and Roitberg (2014)
13	T	2014		<i>Diaeretiella rapae</i>	Basheer et al. (2014)
14	T	2006		<i>Aphidius ervi</i>	Bensadia et al. (2006)
15	T	1998		<i>Aphidius matricariae</i>	Bezemer et al. (1998)
16	C	1998	L	<i>Aphidius matricariae</i>	Bezemer et al. (1998)
17	B	2000		<i>Aphidius ervi</i>	Birkett et al. (2000)
18	T	1998		<i>Lysiphlebia mirzai</i>	Biswas and Singh (1998)
19	B	2003		NE	Hunter (2003)
20	T	2006		<i>Aphidius rhopalosiphi</i>	Bourdais et al. (2006)
21	T	2012		<i>Aphidius rhopalosiphi</i>	Bourdais et al. (2012)
22	T	1997		<i>Aphelinus perpallidus</i>	Bueno and Van Cleave (1997)
23	T	2011		<i>Aphelinus asychis</i>	Byeon et al. (2011)

24	T	2013		<i>Lysiphlebus fabarum</i>	Cayetano and Vorburger (2013)
25	T	2013		<i>Aphidius picipes</i>	Chen <i>et al.</i> (2007)
26	T	2007	L	<i>Aphidius ervi</i>	Christiansen-Weniger and Hardie (1999)
27	C	1999	L	<i>Aphidius colemani</i>	Colinet and Hance (2009)
28	A+B	2009		<i>Aphidius colemani</i>	Colinet and Hance (2010)
29	T	2010		<i>Aphidius ervi</i>	Colinet and Hance (2010)
30	T	2010		<i>Aphidius matricariae</i>	Colinet and Hance (2010)
31	T	2010		<i>Ephedrus cerasicola</i>	Colinet and Hance (2010)
32	T	2010		<i>Praon volucre</i>	Colinet and Hance (2010)
33	T	2006		<i>Aphidius colemani</i>	Colinet <i>et al.</i> (2006)
34	T	2010		<i>Praon volucre</i>	Colinet <i>et al.</i> (2010)
35	T	2010		<i>Praon volucre</i>	De Conti <i>et al.</i> (2011)
36	T	2011		<i>Lysiphlebia japonica</i>	Deng and Tsai (1998)
37	T	1998		<i>Aphidius colemani</i>	Prado <i>et al.</i> (2015)
38	T	2015	G	<i>Aphidius avenae</i>	Dong <i>et al.</i> (2013)
39	A+B	2013		<i>Aphidius rosae</i>	Fink and Volkl (1995)
40	A+B	1995	L	<i>Aphidius ervi</i>	Flores-Mejia <i>et al.</i> (2016)
41	T	2010		<i>Aphidius ervi</i>	Garratt <i>et al.</i> (2010b)
42	A	2010		NE	Garratt <i>et al.</i> (2010a)
43	T	2015	M	<i>Diaeretiella rapae</i>	Gebauer <i>et al.</i> (2015)
44	N	2005	M	<i>Diaeretiella rapae</i>	Geiger <i>et al.</i> (2005)
45	N	2012		<i>Aphelinus abdominalis</i>	Gillespie <i>et al.</i> (2012)
46	A	2012		<i>Aphidius matricariae</i>	Gillespie <i>et al.</i> (2012)
47	T	2009		<i>Aphidius ervi</i>	Guay <i>et al.</i> (2009)
48	T	1991	L	<i>Aphidius colemani</i>	Guenaoui (1991)
49	T	1990		<i>Diaeretiella rapae</i>	Hayakawa <i>et al.</i> (1990)
50	A	2009		<i>Aphidius rhopalosiphi</i>	Hempel <i>et al.</i> (2009)
51	T	2012		<i>Aphidius ervi</i>	Henri <i>et al.</i> (2012)
52	T	1998	O	<i>Aphelinus abdominalis</i>	Honek <i>et al.</i> (1998)
53	B	2011	L	<i>Lysiphlebus testaceipes</i>	Hughes <i>et al.</i> (2011)

54	A	2013		<i>Aphidius ervi</i>	Ismaeil <i>et al.</i> (2013)
55	D	2013		<i>Aphidius ervi</i>	Ismaeil <i>et al.</i> (2013)
56	T	2015		<i>Aphidius colemani</i>	Jerbi-Elayed <i>et al.</i> (2015)
57	T	2015		<i>Aphidius matricariae</i>	Jerbi-Elayed <i>et al.</i> (2015)
58	T	2011		<i>Aphidius ervi</i>	Johnson <i>et al.</i> (2011)
59	T	2008	L	<i>Lysiphlebus testaceipes</i>	Jones <i>et al.</i> (2008)
60	T	2007		<i>Lysiphlebus testaceipes</i>	Jones <i>et al.</i> (2007)
61	D	2009		<i>Aphidius colemani</i>	Karatolos and Hatcher (2009)
62	T	2013		<i>Diaeretiella rapae</i>	Klaiber <i>et al.</i> (2013)
63	T	1997	L	<i>Aphidius ervi</i>	Krespi <i>et al.</i> (1997)
64	B	2001	O	<i>Aphidius ervi</i>	Lagos <i>et al.</i> (2001)
65	C	2004		<i>Aphidius ervi</i>	Langer <i>et al.</i> (2004)
66	A	2004		<i>Aphidius rhopalosiphi</i>	Langer <i>et al.</i> (2004)
67	T	2004		<i>Praon gallicum</i>	Langer <i>et al.</i> (2004)
68	T	2004		<i>Praon volucre</i>	Langer <i>et al.</i> (2004)
69	T	2000		<i>Aphidius ervi</i>	Langer and Hance (2000)
70	T	2000		<i>Aphidius rhopalosiphi</i>	Langer and Hance (2000)
71	T	2013		NE	Lavandero and Tylianakis (2013)
72	T	2012	M	<i>Diaeretiella rapae</i>	Le Guigo <i>et al.</i> (2012)
73	T	2014		<i>Aphidius rhopalosiphi</i>	Le Lann <i>et al.</i> (2014)
74	A	1998		<i>Aphelinus albipodus</i>	Lee and Elliott (1998)
75	B	2004		<i>Aphidius rhopalosiphi</i>	Legrand <i>et al.</i> (2004)
76	T	2005		<i>Aphidius rhopalosiphi</i>	Levie <i>et al.</i> (2005)
77	T	2004		<i>Aphidius transcaspicus</i>	Li and Mills (2004)
78	T	2013		<i>Praon volucre</i>	Lins <i>et al.</i> (2013)
79	T	2002		<i>Lysiphlebia mirzai</i>	Liu and Tsai (2002)
80	T	2000		<i>Aphidius nigripes</i>	Marchand and McNeil (2000)
81	T	1997	L	<i>Aphelinus asychis</i>	Mason and Hopper (1997)
82	T	2015		<i>Aphidius colemani</i>	Mauck <i>et al.</i> (2015)
83	C	2014		<i>Aphidius ervi</i>	Meisner <i>et al.</i> (2014)

84	T	1997		<i>Aphelinus asychis</i>	Mesquita <i>et al.</i> (1997)
85	B	1994		<i>Aphidius matricariae</i>	Miller and Gerth (1994)
86	T	2016		<i>Aphidius ervi</i>	Moiroux <i>et al.</i> (2016)
87	B	2015		<i>Aphidius ervi</i>	Moiroux <i>et al.</i> (2015)
88	T	2004		<i>Aphidius colemani</i>	Moraes <i>et al.</i> (2004)
89	T	2002	L	<i>Aphelinus albipodus</i>	Nowierski and Fitzgerald (2002)
90	T	2002		<i>Aphelinus asychis</i>	Nowierski and Fitzgerald (2002)
91	cid	2002		<i>Diaeretiella rapae</i>	Nowierski and Fitzgerald (2002)
92	T	2006		<i>Aphidius gifuensis</i>	Ohta and Ohtaishi (2006)
93	T	1998		<i>Lysiphlebia mirzai</i>	Pandey and Singh (1998)
94	T	2012		<i>Lysiphlebia mirzai</i>	Pope <i>et al.</i> (2012)
95	T	2013		<i>Aphidius colemani</i>	Prado and Frank (2013)
96	T	2000		<i>Aphelinus varipes</i>	Prinsloo and Plessis (2000)
97	N	2000		<i>Aphidius rhopalosiphi</i>	Rigaux <i>et al.</i> (2000)
98	B	2004		<i>Lysiphlebus testaceipes</i>	Rodrigues <i>et al.</i> (2004)
99	T	2002		<i>Aphelinus varipes</i>	Rohne (2002)
100	T	2013		<i>Diaeretiella rapae</i>	Romo and Tylianakis (2013)
101	T	2013	L	<i>Diaeretiella rapae</i>	Romo and Tylianakis (2013)
102	T	2013	L	<i>Diaeretiella rapae</i>	Romo and Tylianakis (2013)
103	D	2010	L	<i>Aphidius avenae</i>	Roux <i>et al.</i> (2010)
104	T	2014		<i>Aphidius colemani</i>	Saleh <i>et al.</i> (2014)
105	D	2007		<i>Aphidius colemani</i>	Sampaio <i>et al.</i> (2007)
106	T	2005		<i>Aphidius colemani</i>	Sampaio <i>et al.</i> (2005)
107	T	2015		<i>Aphidius ervi</i>	Sanders <i>et al.</i> (2015)
108	T	2015	G	<i>Aphidius megourae</i>	Sanders <i>et al.</i> (2015)
109	T	2015	G	<i>Lysiphlebus fabarum</i>	Sanders <i>et al.</i> (2015)
110	L	2010	G	<i>Aphidius colemani</i>	Schadler <i>et al.</i> (2010)
111	L	2008		<i>Aphelinus asychis</i>	Schirmer <i>et al.</i> (2008)
112	L	2011	L	NE	Schmidt <i>et al.</i> (2011)

113	B	2001		<i>Aphidius ervi</i>	Schworer and Volkl (2001)
114	A	1992	L	<i>Aphidius ervi</i>	Sequeira and Mackauer (1992)
115	N	2004		<i>Lysiphlebus testaceipes</i>	Shufran <i>et al.</i> (2004)
116	A	2015		<i>Praon volucre</i>	Silva <i>et al.</i> (2015)
117	N	1996		<i>Ephedrus californicus</i>	Stadler and Mackauer (1996)
118	T	2011		<i>Lysiphlebia japonica</i>	Sun <i>et al.</i> (2011)
119	T	1995	L	<i>Aphelinus gossypii</i>	Tang and Yokomi (1995)
120	N	1995		<i>Aphelinus spiraecolae</i>	Tang and Yokomi (1995)
121	C	1995		<i>Lysiphlebus testaceipes</i>	Tang and Yokomi (1995)
122	T	2013		<i>Aphidius colemani</i>	Tariq <i>et al.</i> (2013)
123	T	2013	L	<i>Diaeretiella rapae</i>	Tariq <i>et al.</i> (2013)
124	T	2012	L	<i>Diaeretiella rapae</i>	Tazerouni <i>et al.</i> (2012)
125	D	2010		<i>Diaeretiella rapae</i>	Ahuja <i>et al.</i> (2010)
126	.	1993		<i>Aphidius colemani</i>	Vansteenis (1993)
127	T	1994		<i>Lysiphlebus testaceipes</i>	Vansteenis (1994)
128	B	2016		<i>Aphelinus asychis</i>	Wanget <i>et al.</i> (2016)
129	T	2016		<i>Aphelinus albipodus</i>	Wang <i>et al.</i> (2016)
130	T	2004		<i>Lysiphlebus testaceipes</i>	Weathersbee <i>et al.</i> (2004)
131	T	1997		<i>Aphidius rosae</i>	Weisser <i>et al.</i> (1997)
132	T	2006	M	<i>Aphidius colemani</i>	Chiel <i>et al.</i> (2006)
133	T	2006	L	<i>Eretmocerus mundus</i>	Chiel <i>et al.</i> (2006)
134	A	2011	L	<i>Aphidius colemani</i>	Wu <i>et al.</i> (2011)
135	L	2013		<i>Aphelinus varipes</i>	Yashima and Murai (2013)
136	L	2006		<i>Aphidius colemani</i>	Zamani <i>et al.</i> (2006)
137	T	2006		<i>Aphidius matricariae</i>	Zamani <i>et al.</i> (2006)
138	T	2013		<i>Aphidius ervi</i>	Babikova <i>et al.</i> (2013)
139	T	1998		NE	Bottrell <i>et al.</i> (1998)
140	T	2009		NE	Boutard-Hunt <i>et al.</i> (2009)
141	B	2010		NE	Chen <i>et al.</i> (2010)
142	T	2006		<i>Aphidius colemani</i>	Colinet <i>et al.</i> (2006)

143	B	2007		<i>Aphidius colemani</i>	Colinet <i>et al.</i> (2007a)
144	B	2007		<i>Aphidius colemani</i>	Colinet <i>et al.</i> (2007b)
145	B	2011		NE	Denis <i>et al.</i> (2011)
146	N	2007	M	NE	Doukas and Payne (2007)
147	T	1995	G	<i>Aphidius rosae</i>	Fink and Volkl (1995)
148	T	2009	L	<i>Aphidius ervi</i>	Härri <i>et al.</i> (2009)
149	T	2008		<i>Aphidius ervi</i>	Härri <i>et al.</i> (2008a)
150	T	2008		<i>Aphidius ervi</i>	Härri <i>et al.</i> (2008b)
151	L	2012		<i>Aphidius ervi</i>	Ismail <i>et al.</i> (2012)
152	A	2012		NE	Kos <i>et al.</i> (2012)
153	B	2007		NE	Krauss <i>et al.</i> (2007)
154	B	2011		<i>Aphidius rhopalosiphi</i>	Le Lann <i>et al.</i> (2011)
155	B	2011		<i>Aphidius avenae</i>	Le Lann <i>et al.</i> (2011)
156	T	2014		<i>Aphidius ervi</i>	Legarrea <i>et al.</i> (2014)
157	N	2009	G	<i>Aphidius ervi</i>	McClure and McNeil (2009)
158	N	2010	L	<i>Aphidius ervi</i>	Mitchell <i>et al.</i> (2010)
159	T	2013		NE	Moreira and Mooney (2013)
160	T	2009		<i>Diaeretiella rapae</i>	Newton <i>et al.</i> (2009)
161	L	2006		NE	Ode (2006)
162	A	2014		<i>Aphidius gifuensis</i>	Pan <i>et al.</i> (2014)
163	B	2010		NE	Petermann <i>et al.</i> (2010b)
164	B	2010		NE	Petermann <i>et al.</i> (2010a)
165	B	2013		<i>Diaeretiella rapae</i>	Pineda <i>et al.</i> (2013)
166	B	1980		NE	Price <i>et al.</i> (1980)
167	B	2011		<i>Aphelinid spp.</i>	Shipp <i>et al.</i> (2011)
168	B	2009		NE	Staley <i>et al.</i> (2009)
169	B	2010		<i>Aphidius ervi</i>	Tompkins <i>et al.</i> (2010)
170	D	2010	L	NE	Zytynska <i>et al.</i> (2010)
171	T	2009	M	<i>Aphidius matricariae</i>	Das (2009)
172	N	2009	O	<i>Aphidius uzbekistanicus</i>	Das (2009)
173	B	2009	O	<i>Diaereteilla rapae</i>	Das (2009)

174	D	2009	O	<i>Kashmiria aphidis</i>	Das (2009)
175	B	2003	O	<i>Lysiphlebus japonicus</i>	Kaneko (2003)
176	A+B	2004		<i>Diaeretiella rapae</i>	Acheampong and Stark (2004)
177	A+B	2003	L	NE	Bieri (2003)
178	A+B	1993		<i>Aphidius rhopalosiphi</i>	Borgemeister <i>et al.</i> (1993)
179	A+B	1996		<i>Aphelinus mali</i>	Cohen <i>et al.</i> (1996)
180	B	2004		NE	Collier and Van Steenwyk (2004)
181	cid	2007		NE	Desneux, <i>et al.</i> (2007)
182	cid	2005		<i>Diaeretiella rapae</i>	Desneux <i>et al.</i> (2005)
183	cid	2004		<i>Aphidius ervi</i>	Desneux <i>et al.</i> (2004a)
184	cid	2004		<i>Aphidius ervi</i>	Desneux <i>et al.</i> (2004b)
185	cid	2004		<i>Aphidius matricariae</i>	Desneux <i>et al.</i> (2004a)
186	cid	2011		<i>Diaeretiella rapae</i>	Foster <i>et al.</i> (2011)
187	cid	2003		<i>Aphidius colemani</i>	Foster <i>et al.</i> (2003)
188	cid	2007		<i>Aphidius colemani</i>	Foster <i>et al.</i> (2007)
189	cid	2012		<i>Aphelinus certus</i>	Frewin <i>et al.</i> (2012)
190	cid	2016		<i>Aphidius colemani</i>	Garantonakis <i>et al.</i> (2016)
191	cid	1995		<i>Praon volucre</i>	Giller <i>et al.</i> (1995)
192	cid	1999		<i>Aphidius rhopalosiphi</i>	Jansen (1999)
193	cid	2011		<i>Aphidius ervi</i>	Joseph <i>et al.</i> (2011)
194	cid	1998		<i>Diaeretiella rapae</i>	Kakakhel <i>et al.</i> (1998)
195	cid	2003		<i>Lysiphlebus japonicus</i>	Kaneko (2003)
196	cid	2015		NE	Kaser and Heimpel (2015)
197	cid	2004	M	<i>Aphidius gifuensis</i>	Kobori and Amano (2004)
198	cid	2003		<i>Aphidius ervi</i>	Kramarz and Stark (2003)
199	cid	2003		<i>Aphidius colemani</i>	Langhof <i>et al.</i> (2003)
200	cid	1999		NE	Longley (1999)
201	cid	1994		<i>Diaeretiella rapae</i>	Longley <i>et al.</i> (1994)
202	cid	1996		<i>Aphidius rhopalosiphi</i>	Longley and Jepson (1996a)
203	cid	1996		<i>Aphidius rhopalosiphi</i>	Longley and Jepson (1996b)

<b>204</b>	cid	1997	<i>Aphidius ervi</i>	Longley and Jepson (1997)
<b>205</b>	cid	1997	NE	Longley <i>et al.</i> (1997)
<b>206</b>	cid	2016	<i>Lysiphlebus fabarum</i>	Mardani <i>et al.</i> (2016)
<b>207</b>	cid	1996	NE	Oakley <i>et al.</i> (1996)
<b>208</b>	cid	2015	<i>Aphidius gifuensis</i>	Ohta and Takeda (2015)
<b>209</b>	cid	2012	<i>Aphidius ervi</i>	Pennacchio <i>et al.</i> (2012)
<b>210</b>	cid	2013	<i>Diaeretiella rapae</i>	Rimaz and Valizadegan (2013)
<b>211</b>	cid	2011	<i>Lysiphlebus fabarum</i>	Sabahi <i>et al.</i> (2011)
<b>212</b>	cid	2012	<i>Lysiphlebus confusus</i>	Satar <i>et al.</i> (2012)
<b>213</b>	cid	2000	<i>Aphidius colemani</i>	Shipp <i>et al.</i> (2000)
<b>214</b>	cid	1995	<i>Aphidius ervi</i>	Stark <i>et al.</i> (1995)
<b>215</b>	cid	2002	<i>Diaeretiella rapae</i>	Umoru and Powell (2002)
<b>216</b>	cid	1996	<i>Diaeretiella rapae</i>	Umoru <i>et al.</i> (1996)
<b>217</b>	cid	2009	<i>Diaeretiella rapae</i>	Wu <i>et al.</i> (2009)
<b>218</b>	cid	1995	<i>Aphidius ervi</i>	Giller <i>et al.</i> (1995)
<b>219</b>	cid	1995	<i>Aphidius picipes</i>	Giller <i>et al.</i> (1995)
<b>220</b>	cid	1995	<i>Aphidius rhopalosiphi</i>	Giller <i>et al.</i> (1995)
<b>221</b>	cid	2004	NE	Cowgill <i>et al.</i> (2004)

Table 6. Lists of study using *Aphidius ervi* as biological models. The data were found with keyword “*Aphidius ervi*” in either titles, abstracts or keywords from the database of Web of Science®.

Subjects	Characteristics	References
<b>Aphid defenses from natural enemies</b>	Immunity-based	Gwynn <i>et al.</i> 2005; Poirie and Coustau 2011
	Symbiont-dependent	Donald <i>et al.</i> 2016; Ferrari <i>et al.</i> 2004; Lukasik <i>et al.</i> 2015; Nyabuga <i>et al.</i> 2010; Sanders <i>et al.</i> 2016; Smith <i>et al.</i> 2015; Vorburger 2017; Zepeda-Paulo, F. <i>et al.</i> 2017; Bilodeau <i>et al.</i> 2013; Cloutier and Douglas 2003; Heyworth and Ferrari 2015; Lukasik <i>et al.</i> 2013; McLean, A. H. C. and Godfray 2014; 2015; Nyabuga <i>et al.</i> 2010; Oliver <i>et al.</i> 2008; Oliver <i>et al.</i> 2009; Oliver <i>et al.</i> 2005; 2006; Oliver <i>et al.</i> 2012; Oliver <i>et al.</i> 2003;
	Behaviors	Gillespie and Acheampong 2012; Sloggett and Weisser 2002; 2004;
	Multi-modal	Gerardo <i>et al.</i> 2010; Lagos <i>et al.</i> 2001; Martinez <i>et al.</i> 2016; Martinez <i>et al.</i> 2017;
	Impacts of environmental stress	Guay <i>et al.</i> 2009
<b>Parasitoid offense /counterdefenses</b>	Aphid resistance genome/proteome	Hansen <i>et al.</i> 2012; Nguyen <i>et al.</i> 2008;
	Host manipulation by venom injection	Colinet, D. <i>et al.</i> 2014; Le Ralec <i>et al.</i> 2011; Digilio <i>et al.</i> 2000; Digilio <i>et al.</i> 1998; Falabella <i>et al.</i> 2005; Falabella <i>et al.</i> 2007; Falabella <i>et al.</i> 2009; Falabella <i>et al.</i> 2000; Thi <i>et al.</i> 2013;
	Host regulation: aphid phenotype and behavior	Christiansen-Weniger and Hardie 2000; Demmon <i>et al.</i> 2004; Guerra <i>et al.</i> 1998; Chow and Mackauer 1999 ; Khudr <i>et al.</i> 2013; Martinez <i>et al.</i> 2014b; Pennacchio <i>et al.</i> 1995; Rahbe <i>et al.</i> 2004; Rahbe <i>et al.</i> 2002 ; Villagra <i>et al.</i> 2002; Walton <i>et al.</i> 2011;
<b>Parasitoid behavioral and physiological traits</b>	Adaptation	Hufbauer 2001; Dion <i>et al.</i> 2011; Le Ralec <i>et al.</i> 2010; Henry <i>et al.</i> 2006;
	Host location and recognition	<i>Volatile cues</i> : Battaglia <i>et al.</i> 1993; Battaglia <i>et al.</i> 1995; Dewhirst <i>et al.</i> 2008; Du <i>et al.</i> 1996; Du <i>et al.</i> 1998; Guerrieri <i>et al.</i> 1993; 1997; Heuskin <i>et al.</i> 2012; Pareja <i>et al.</i> 2009; Poppy <i>et al.</i> 1997; Powell <i>et al.</i> 1998; Stilmant <i>et al.</i> 1994; Wickremasinghe and Vanemden 1992; Bruce, T.J. <i>et al.</i> 2002; Bruce, T.J.A. <i>et al.</i> 2008; Glinwood <i>et al.</i> 1999a; Glinwood <i>et al.</i> 1999b; Weinbrenner and Volkl 2002; <i>Visual cues</i> : Michaud and Mackauer 1994; Powell <i>et al.</i> 1998

		<i>Physical cues</i> : Battaglia, D. <i>et al.</i> 1995; Battaglia, Donatella <i>et al.</i> 2000; Nakashima and Akashi 2005
	Host acceptance	Michaud and Mackauer 1994; Poppy <i>et al.</i> 1997 ; Guerrieri <i>et al.</i> 1997; Henry <i>et al.</i> 2009; Langley <i>et al.</i> 2006; Schworer and Volkl 2001; Larocca <i>et al.</i> 2007; Pennacchio <i>et al.</i> 1994
	<b>Reproductive strategy</b>	Bueno <i>et al.</i> 1993; He <i>et al.</i> 2004; Schworer and Volkl 2001; Henry <i>et al.</i> 2005; Olson <i>et al.</i> 2000;
	Learning: innate <i>i.e.</i> Premature or acquired	Chow and Mackauer 1992; Du <i>et al.</i> 1997; Guerrieri <i>et al.</i> 1997; Gutierrez-Ibanez <i>et al.</i> 2007; Langley <i>et al.</i> 2006; Takemoto <i>et al.</i> 2009; 2012; Lanteigne <i>et al.</i> 2015; Villagra <i>et al.</i> 2007;
	Mating	Battaglia <i>et al.</i> 2002; He and Wang 2008; McClure and McNeil 2009; McClure <i>et al.</i> 2007; Villagra <i>et al.</i> 2005; 2008; Nyabuga <i>et al.</i> 2012; Villagra <i>et al.</i> 2011; Villagra <i>et al.</i> 2008;
	Sex ratio	Mackauer and Lardner 1995;
	Oviposition behavior: multi and super parasitism	Bai 1991; Bai and Mackauer 1991; 1992; Chua <i>et al.</i> 1990; Donald <i>et al.</i> 2016; Mcbrien and Mackauer 1990; 1991; Micha <i>et al.</i> 1992; Sidney <i>et al.</i> 2010a; Bai 1991; Bai and Mackauer 1991; 1992; Mcbrien and Mackauer 1991; Micha <i>et al.</i> 1992;
	Adult parasitoid physiological traits	Christiansen-Weniger and Hardie 1997; He and Wang 2006; He <i>et al.</i> 2004; Grbic and Strand 1998; Malina <i>et al.</i> 2010;
	Immature parasitoid traits	He <i>et al.</i> 2011; Henry <i>et al.</i> 2009; Poppy <i>et al.</i> 1997; Sequeira and Mackauer 1992a
<b>Impacts of hosts</b>	Host developmental stages: age, body size	Clarke <i>et al.</i> 2017; Colinet, H. <i>et al.</i> 2005; Sequeira and Mackauer 1992b; 1994; Sidney <i>et al.</i> 2010b; He <i>et al.</i> 2011; Mackauer 1996; Trotta <i>et al.</i> 2014;
	Host genotypes intra and inter-specific variation	Gagic, Vesna <i>et al.</i> 2016; Ferrari <i>et al.</i> 2001; Li <i>et al.</i> 2002; Martinez <i>et al.</i> 2014a; Michaud 1996; Sidney <i>et al.</i> 2010;
	Host pathogens	Ban <i>et al.</i> 2008; Baverstock <i>et al.</i> 2005
	Host density	Ives and Settle 1996; van Veen <i>et al.</i> 2005;
	Host phenotype	Losey <i>et al.</i> 1997;
	Host cues	Nakashima <i>et al.</i> 2016;
<b>Impacts of plants</b>	Plant symbionts	Bennett <i>et al.</i> 2016; Calvo and Fereres 2011; Harri <i>et al.</i> 2009; Battaglia, D. <i>et al.</i> 2013;
	Plant pathogens	Calvo and Fereres 2011; Christiansen-Weniger <i>et al.</i> 1998; Hodge <i>et al.</i> 2011a; Hodge and Powell 2008

	Semiochemical compounds	Rodriguez <i>et al.</i> 2002; Sasso <i>et al.</i> 2007; Sasso <i>et al.</i> 2009; Guerrieri <i>et al.</i> 1999; Powell and Wright 1991; Takemoto, H. and Takabayashi 2012; Takemoto, Hiroyuki and Takabayashi 2015; Wickremasinghe and Vanemden 1992;
	Plant defensive compounds	Hodge <i>et al.</i> 2011b; Dewhurst <i>et al.</i> 2012; Matthes <i>et al.</i> 2010;
	Resistance to aphid	Lanteigne <i>et al.</i> 2014
	Plant morphology	Chang <i>et al.</i> 2004;
	Plant genotype	Hufbauer and Via 1999;
<b>Impacts of abiotic factors in the ecosystem</b>	Temperature	Christiansen-Weniger and Hardie 1999; Flores-Mejia <i>et al.</i> 2016; Ismail <i>et al.</i> 2013; Meisner <i>et al.</i> 2014; Moiroux <i>et al.</i> 2016; Sigsgaard 2000; Bensadia <i>et al.</i> 2006; Langer and Hance 2000; Stacey and Fellowes 2002;
	Seasons	Guerrieri <i>et al.</i> 1993; Sequeira and Mackauer 1993
	Fertilizers	Garratt <i>et al.</i> 2010
	Light	Goff and Nault 1984; Legarrea <i>et al.</i> 2014
	<b>Water availability</b>	Aslam <i>et al.</i> 2013; Johnson <i>et al.</i> 2011;
	Disturbed systems	Rauwald and Ives 2001
	<b>Ecological specialization</b>	Host switching/fidelity
Specialism / generalism		Derocles <i>et al.</i> 2016; Zepeda-Paulo, F.A. <i>et al.</i> 2013
Habitat specialization		Stilmant <i>et al.</i> 2008
<b>Ecological interaction</b>	Inter-guild competition	George <i>et al.</i> 2013; Le Lann <i>et al.</i> 2011;
	Intra-guild competition	Bribosia <i>et al.</i> 1995; McLean and Godfray 2016; Almohamad and Hance 2014; Baverstock <i>et al.</i> 2009; Nakashima and Senoo 2003; Schellhorn <i>et al.</i> 2002; Taylor <i>et al.</i> 1998; Frago and Godfray 2014; Snyder and Ives 2003; Kraft <i>et al.</i> 2017; McLean, A. H. C. <i>et al.</i> 2017
	Apparent	Frago 2016; Fan <i>et al.</i> 2010; McLean, A. H. C. and Godfray 2017; Meisner <i>et al.</i> 2007; Morris <i>et al.</i> 2001; Pope <i>et al.</i> 2002;
	Larval stage	Sidney <i>et al.</i> 2010a
	Parasitoid natural enemies: hyperparasitoid	Muller and Godfray 1998; Raworth <i>et al.</i> 2008; Schooler <i>et al.</i> 1996; Araj <i>et al.</i> 2009; McMenemy <i>et al.</i> 2009; Noma <i>et al.</i> 2005; Schooler <i>et al.</i> 2011; Volkl and Sullivan 2000;

	Parasitoid natural enemies: predators	Meisner <i>et al.</i> 2011; Nakashima <i>et al.</i> 2004; Nakashima <i>et al.</i> 2006;
<b>Population dynamic</b>	Bottom-up regulation	Desneux and Ramirez-Romero 2009; Petermann <i>et al.</i> 2010a; Powell and Wright 1991; Schadler <i>et al.</i> 2010
	Top-down regulation	Feng <i>et al.</i> 1991; Nakashima <i>et al.</i> 2016; Sanders <i>et al.</i> 2016; Hufbauer 2002; Ingerslew and Finke 2017; Kavallieratos <i>et al.</i> 2004; Mitchell <i>et al.</i> 2010; Northfield <i>et al.</i> 2012;
	Field observation	Bosque-Perez <i>et al.</i> 2002; Gruber <i>et al.</i> 1994; Senoo <i>et al.</i> 2002; Zuparko and Dahlsten 1993; Al Dobai <i>et al.</i> 1999; Baudino <i>et al.</i> 2007; Desneux <i>et al.</i> 2006b; Feng, M.C. <i>et al.</i> 1993; Feng, M.G. <i>et al.</i> 1991; 1992; Tomanovic <i>et al.</i> 2009; Gruber <i>et al.</i> 1994; Havelka <i>et al.</i> 2012; Kos <i>et al.</i> 2012; Lumbierres <i>et al.</i> 2007; Nebreda <i>et al.</i> 2005; Pons <i>et al.</i> 2011; Pons and Sary 2003; Rakhshani <i>et al.</i> 2008; Sary and Havelka 1991; Tomanovic <i>et al.</i> 2008; Wickremasinghe and Vanemden 1992;
<b>Molecular and biochemical mechanisms</b>	Host-dependent transcriptome	Ballesteros <i>et al.</i> 2017; Clarke <i>et al.</i> 2017
	Parasitoid genome	Gilchrist 1996; Sequeira and Mackauer 1992c; Varricchio <i>et al.</i> 1995;
	Molecular identification	Trybush <i>et al.</i> 2006; Derocles <i>et al.</i> 2012; Gadallah <i>et al.</i> 2017;
	Nutrient absorption of larvae / metabolism	Fiandra <i>et al.</i> 2010; Caccia <i>et al.</i> 2007; Caccia <i>et al.</i> 2012; Caccia <i>et al.</i> 2005; de Eguileor <i>et al.</i> 2001; Giordana <i>et al.</i> 2003; Grossi <i>et al.</i> 2016; Sabri <i>et al.</i> 2011; Eguileor <i>et al.</i> 2001
<b>Intra-specific variation</b>	Physiological traits	Takada and Tada 2000 by geography
	Morphological traits	Nemec and Sary 1983a; b; Sary 1983; Villegas <i>et al.</i> 2017; by geographical variation; by host species
	Genetic diversity/gene flow	Emelianov <i>et al.</i> 2011; Henry 2008; Henry <i>et al.</i> 2010; Henter 1995; Henter and Via 1995; Nemec and Sary 1985; Sequeira and Mackauer 1992c; Zepeda-Paulo, F. <i>et al.</i> 2015; Daza-Bustamante <i>et al.</i> 2004; Ferrari and Godfray 2006; Hufbauer <i>et al.</i> 2004; Hufbauer <i>et al.</i> 2001;
	Behavioral traits	Daza-Bustamante <i>et al.</i> 2002; Ives <i>et al.</i> 1999;
<b>Biological control</b>	Cold storage	Colinet and Hance 2010; Ismail <i>et al.</i> 2014; Ismail <i>et al.</i> 2012; Ismail <i>et al.</i> 2010; Frère <i>et al.</i> 2011;
	Introduction	Gavkare <i>et al.</i> 2014; Hufbauer 2002; Milne 1986; Sary 1993; Brewer <i>et al.</i> 2005; Cameron <i>et al.</i> 2013; Milne 1999; Sterk and Meesters 1997;

	Genetic management	Hopper <i>et al.</i> 1993; Zepeda-Paulo, F. <i>et al.</i> 2016
	Mix assemblage	Enkegaard <i>et al.</i> 2013; Rocca and Messelink 2017; Snyder and Ives 2001; Cardinale <i>et al.</i> 2003;
	Side-effect of insecticides	Araya <i>et al.</i> 2010; Hogervorst <i>et al.</i> 2009; Kramarz and Stark 2003; Azzouz <i>et al.</i> 2005; De Zutter <i>et al.</i> 2016; Desneux <i>et al.</i> 2006a; Desneux <i>et al.</i> 2004a; Desneux <i>et al.</i> 2004b; Joseph <i>et al.</i> 2011; Stark <i>et al.</i> 1995;
	Side-effect of Bt-based compound	Cowgill <i>et al.</i> 2004; Digilio <i>et al.</i> 2012
<b>Nutritional ecology</b>	Sugar sources	Araj <i>et al.</i> 2008; Araj <i>et al.</i> 2011; Azzouz <i>et al.</i> 2004; Lenaerts <i>et al.</i> 2016; Vollhardt <i>et al.</i> 2010; Wade and Wratten 2007; Hayashi and Nakashima 2014; Hogervorst <i>et al.</i> 2007;
	Artificial diet	Couty <i>et al.</i> 2001; Larocca <i>et al.</i> 2005;
	Diet for immature parasitoid	Pennacchio <i>et al.</i> 1999;

## GENERAL DISCUSSION

The use of biological control agents: BCA that are natural enemies of agricultural pests requires a deep understanding of their ecological specialization. BCA preference and performance on specific hosts/preys determine their pest suppression efficacy. Their host fidelity predicts their ability to switch from one targeted host to another non-targeted species. Their diet breadth predicts the ability to implement and maintain their presence in a new environment. These parameters depend on the BCA host specificity, which is furthermore influenced by ecological forces.

Aphid parasitoids, one common BCA were the model in this study. Their larvae develop inside the aphid host of which the adults emerge. The host bodies, then, represent both food resource and environment for larva parasitoid development. The host choice of female adults is the dead-or-living matter for the larvae. On encountering a host, the female adult should decide to lay eggs or not, and the sex ratio of their offspring. It seems that parasitoid mothers know what is best for their descendants and their species as a whole. Understanding factors leading to such preference is therefore essential. The parasitoid strategies of specialization could focus on plant or aphid resources because both aphid and plant host quality could impact parasitoid performance. Some parasitoids, for instance, specialize in phylogenetically closed aphids. Others could specialize on plant species regardless of aphid phylogeny.

This study focused on the factors modulating the host specificity of aphid parasitoids within the plant-aphid-parasitoid tri-trophic system in the laboratory. These factors are both biotic and abiotic, *i.e.* plant-, aphid- and parasitoid traits as well as environmental stress, more especially soil water limitation. The first goal was to assess the fundamental host specificity of three parasitoids by the host range testing method on 14 aphid species. Also, their degree of host specificity was evaluated with the host specificity index and the relationship preference-performance. The discrimination between parasitoid specialists and generalists vaguely mentioned in literature has been clarified on a subtle scale in this study. The second goal was to assess the impact of water limitation on the fundamental host specificity of one parasitoid, *i.e.* on their preference and performance and their optimal foraging pattern.

First of all, we showed that our three parasitoids have different fundamental host specificity. One parasitoid (*A. ervi*) is an intermediate specialist and mainly parasitizes aphids from the Macrosiphini tribe. The others, *D. rapae*, and *A. abdominalis* are generalists and parasitize a phylogenetically broad range of aphid hosts. Their behaviors differed: *A. ervi* showed a preference for hosts on which they performed well, but *D. rapae* and *A. abdominalis* did not. The preference-performance correlation relates to a lower host range for *A. ervi* and a smaller host specificity index. In other words, specialist parasitoids are more selective in host choice if they specialize in a few hosts and is called the optimal foraging pattern. As the three parasitoids are often considered host generalists in literature, the host specificity index and the optimal foraging strategy are efficient ways to classify specialist/generalist species on a fine scale.

This study on host specificity confirms the general statement that *A. ervi* is an intermediate specialist, not sufficiently proved in previous literature, of the Macrosiphini tribe. However, among Macrosiphini, *A. ervi* was unable to parasitize *M. dirhordum*, either because it is protected by its bacterial symbiont *Hamiltonella defensa* or because the *A. ervi* strain in this study did not genetically adapt to *M. dirhordum*. Biotic or biogeographical factors might be able to modulate the host range. The difference between the parasitoid field host range and the fundamental host range implies the impact of environmental and geographical factors to parasitoid specialization. Future research should focus on the calculation of field host specificity index for a wide range of BCA, as in the Skoracka and Kuczyński study (2012). Moreover, the host specificity index would provide a broader and deeper view on the potential phylogenetic signal of parasitoid species on their host specificity (Derocles *et al.* 2016) as the phylogenetic relationship may correlate to similar traits in host species (Guénard *et al.* 2013). Furthermore, we could study the characteristics of intermediate specialist/generalists, for example, whether the correlation preference-performance only exists for intermediate specialist/generalist but not for extreme specialists or generalists?

Secondly, water limitation was proved to affect parasitoid efficiency, specifically *A. ervi*. Both their preference and performance on aphid hosts were adversely impacted, however asymmetrically. In most cases, *A. ervi* preference on aphid hosts was not significantly reduced except the detection rate when they encountered the aphid *M. persicae*. However, their

performance on good or suboptimal quality hosts decreased considerably. These asymmetrical modifications in life-history traits of *A. ervi* led to the loss of the correlation preference-performance. Differently speaking, their host selection efficiency was impacted; parasitoids mother no longer knew which best hosts for their offspring were. For further study, we should test *A. ervi* behavior in choice-conditions to see if learning could improve their capacity of evaluating low-quality hosts.

This study also showed a diversity of responses to water stress at both trophic levels, plant, and aphid, resulting in different impacts on the third trophic level, parasitoid. Plants react differently to water regimes. For example, optimal water supply for cabbages was 70% field capacity while it was 100% for all the other plants. The 100% soils saturated volume cause stress symptom on cabbages similar to water limitation (consistent with Khan *et al.* 2010). Interestingly, parasitoid performance was more efficient on 70% cabbages (chapter 5, article 3) compare to 100% (chapter 4, article 1), strengthening the preference-performance correlation under optimal environmental conditions. Water limitation might also influence plant physical and/or chemical defenses. In this study, aphid survival rate significantly decreased in water-stressed wheat with harden structure (increased LMA) and Glas *et al.* (2012) shown a negative impact on aphid of the increased of trichome density in potato.

The resistance of aphid *A. pisum* to the bottom-up effect of water stress and *A. ervi* performance on such aphids are interesting. Why could not the bottom-up impact reach the top-level like in the other plant-aphid combinations? One hypothesis suggests a positive effect of the symbiosis between Rhizobium and fava beans that buffer the bottom-up effect at higher trophic levels. Also, whether the advantage of natal hosts on *A. ervi* could buffer impacts of plant water stress? What happens if *A. ervi* are reared on a different host species but not *A. pisum*? For further study, one could test *A. ervi* on natal host *S. avenae* and compare their performance on *S. avenae* and *A. pisum* under similar water limitation.

In parasitoids, the mortality at egg stage is caused by host immune defenses or symbionts, at larva stage by plant toxins sequestered by aphids and at the nymphal stage by low nutritional quality (Desneux *et al.* 2009a). Regardless of insecticidal compounds of plant hosts or host quality, *A. ervi* mortality happened mostly from the nymphal stage but not earlier. *A. ervi* late mortality inside aphid hosts probably because they have a placenta-like structure of eggs with

a thick cellular wall, which helps the egg to second instar larva to drive the nutrients efficiently (Sabri *et al.* 2011). This structure is unique to *A. ervi* until now (Martinez *et al.* 2016) and probably confer resistance to *A. ervi* larva even when they develop on aphid hosts feeding on toxic plant hosts like *A. nerii*. It could be interesting to test the hypothesis on other parasitoids to see their pattern of mortality inside aphid hosts. Nitrogen-deprived compounds in aphids might have high impacts on the parasitoid larval development

Diet breadth of both aphids and parasitoids seems to affect their efficiency of host exploiting, as predicted by the “trade-off host range breadth – host use efficiency” model (Straub *et al.* 2011). *Myzus persicae*, an extreme generalist aphid, was severely suffered from water stress as well as parasitoid parasitizing them. The trade-off model could be investigated further at aphids, that is to say, whether more specialist aphids could resist better under bottom-up impacts of water stress. One could equally examine other parasitoids share the same hosts with *A. ervi* but have different diet breadth like *Aphidius rhopalosiphi*, a so-called specialist on wheat aphids, or *Aphelinus abdominalis*, a generalist, to compare the magnitude of bottom-up impacts.

### **Implication in biological control and ecology**

Overall, this evidence of the bottom-up effect of soil water limitation on parasitoid host specificity raises a concern for parasitoids as BCA. Both plants and aphids can tolerate a moderate, long-term water limitation, even though their performance were negatively impacted. Aphid populations could be maintained on water stress plants for several weeks without extinction in this study. However, the parasitoid mortality on aphid hosts significantly increased, such as from 60% under optimal water supply to 94.5% under water limitation on *M. persicae* hosts. Therefore, the top trophic level with high degree of food specialization like parasitoids might suffer more than the lower trophic levels. Further studies should be done to confirm this statement, for example investigating parasitoid population dynamic on aphid hosts feeding on water-stressed plants.

In case of confirmed negative bottom-up impacts of abiotic factors on parasitoids, should one release these BCA under abiotic constraints? That could be an economic loss. In the field application, practitioners could increase parasitoid host selection effectiveness by methods

like (1) previous learning, such as exposing them to low-quality hosts before or by inducing volatile plant compounds to locate hosts; (2) application of a mix of natural enemies, *e.g.* specialist BCA on shared host aphids; (3) use of banker plant-aphid combination that are resistant to abiotic stress to support BCA. The responses of organisms from their morphology to metabolism and proteome profiles are very different for each kind of water stress or stress combination, *e.g.* the intensity, duration, and timing (Huberty and Denno 2004; White 2009; Price 1991). It could be interesting to test all kinds of water limitation regimes or combined abiotic stress, *e.g.* water limitation and fertilizer supply on similar tri-trophic systems to optimize water regimes.

### **Prospects for risk and efficiency assessments of BCA**

From this study, we highlighted the importance of parasitoid capacity of adaptation under field conditions, especially on current climate change era. This capacity is called parasitoid plasticity. We also emphasized the necessity of both efficiency and risk assessments of BCA, where parasitoid specificity could predict parasitoid plasticity. We shared the same view with Heimpel (2017) of raising acceptable risk levels of non-targeted species for BCA. Zero-risk parasitoids could fail in the field in considering the trade-off between specialist and generalist, specificity and plasticity. Firstly, the more specialist parasitoids could result in the less productive BCA on the disturbed environment. Secondly, risk assessment in laboratory conditions could result in overestimating the ecological risks of the BCA and pretermite good BCA. Thirdly, invasive species are continuously introduced into new areas following human activities; the ecological risks are nonetheless unavoidable. The requirement of non-risk BCA could delay the process of new BCA approval and BC practices in general. However, this shifting paradigm requires cautious improvement of risk and efficiency the assessment. Notably, we suggested several ideas of specificity and plasticity evaluations as following. Methods of host specificity evaluation could be broadened to find correlation among parasitoid traits in combining with different indexes. For example, we could study the set of criteria of host specificity index and correlation performance-host phylogeny, or the set of host specificity index and ovigeny index. Concerning parasitoid plasticity, it should be considered multidimensional concept similar to specificity. The degree of plasticity could be different to each dimension. Parasitoid behavioral plasticity could be understood as the low

choosiness towards aphid hosts. Determinants of generalist behaviors in parasitoids could be innate, such as parasitoid time, energy and egg constraints; or through interactions like host deprivation/availability, competition. Determinants of parasitoid physiological plasticity could underly in their venom compositions. Therefore a comparison of venom compositions of parasitoids reared on different hosts over several generations could be interesting. The study of parasitoid plasticity to disturbed conditions should play vital roles in BCA efficiency assessments. Determinants of stress tolerance at both aphid and parasitoid levels should be highlighted. In aphids, this information serves to understand aphid prevalence, in parasitoids to choose relevant BCA. These determinants could be surprisingly similar in both parasitoids and aphids, *e.g.* multi-dimensional specificity could impact plasticity: generalist vs. extreme specialist parasitoid, time-limited vs. egg-limited, habitat vs. host. The types of stressors such as nutrients or soil salinity could determine the defensive and adaptive strategies of all trophic levels. The frequency, intensity, and duration of stressors: pulsed vs. continuous, high vs. medium, long-term vs. short-term could drive the outcomes of plasticity.

This study of factors modulating the host specificity of aphid parasitoids not only suggest the significant roles of abiotic constraints on BCA but also contributing to more extensive ecological understanding and theory on parasitoid host specialization.

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