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Rapid evolution of aphid pests in agricultural environments

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Aphids constitute a major group of crop pests that inflict serious damages to plants, both directly by ingesting phloem and indirectly as vectors of numerous diseases. In response to intense and repeated human-induced pressures, such as insecticide treatments, the use of resistant plants and biological agents, aphids have developed a series of evolutionary responses relying on adaptation and phenotypic plasticity. In this review, we highlight some remarkable evolutionary responses to anthropogenic pressures in agroecosystems and discuss the mechanisms underlying the ecological and evolutionary success of aphids. We outline the peculiar mode of reproduction, the polyphenism for biologically important traits and the diverse and flexible associations with microbial symbionts as key determinants of adaptive potential and pest status of aphids.

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Introduction

Deciphering the mechanisms underlying biological adaptations is not only a fundamental goal of evolutionary biology, it also has applied outcomes for controlling pest and invasive species and anticipating their *evolutionary responses* (see glossary) to global changes [1]. While experimental evolution can associate rapid (<hundreds of generations) phenotypic changes with extensive genomic responses to artificial selection [2,3], wild environments generally incur selective pressures that are less intense and more heterogeneous that those induced in the laboratory [4]. This contrast makes it difficult to predict evolutionary responses from simplified experiments. However, certain natural populations can undergo rapid phenotypic changes in response to environmental perturbations, induced by natural or anthropogenic events, and thus constitute ideal models to uncover the causes and genetic mechanisms (e.g. mutations, epigenetic modifications, or plasticity) underlying *adaptive evolution* [5–7]. Under such an evolutionary framework, aphids in agroecosystems are excellent models. As major insect crop pests, aphids are indeed exposed to intense human-induced pressures and in turn evolve rapid adaptive responses that have been the focus of recent research.

Agroecosystems as evolutionary laboratories for aphids

Among the c.a. 5000 known aphid species, about 450 thrive on cultivated plants and a hundred represent a major threat to agriculture worldwide [8], weakening crops by ingesting phloem sap and transmitting viral diseases [9,10••]. Agroecosystems expose these aphids to abrupt anthropogenic modifications of their environment, mainly through the succession of different crops modifying landscapes, and an array of pest management strategies. On the other hand, crop fields constitute widespread monotonous resources and simplified ecological networks with low diversity of aphid natural enemies, compared to wild habitats [11]. Aphids are perfectly armed against this combination of temporal instability and relative spatial uniformity [12,13], thanks notably to two key *polyphenic traits* allowing rapid phenotypic adjustment to environmental conditions. The first is *cyclical parthenogenesis*, which combines sexuality to generate new genotypic combinations, and parthenogenesis for rapid multiplication (see Figure 1, left for an illustration of the typical aphid life cycle and Figure 2 for different types of polyphenism). Parthenogenetic females (Figure 2b) are viviparous, hence highly prolific, and are produced under long-day conditions. This is why aphid outbreaks are frequently recorded in the growing season [14]. Males and oviparous sexual females are produced in the fall in response to long nights, and give birth to eggs resistant to winter frost. The second key polyphenic trait is the capacity, for the same genotype, to produce winged or wingless parthenogenetic females depending on crowding conditions or plant quality [15•]. Winged females (Figure 2c) are less fertile, but are able to disperse over long-distance, allowing aphids to colonize distant habitats and to limit local competition for resources, whereas wingless females (Figure 2b) allocate energy toward reproduction. In response to some environmental change,

Glossary
Evolutionary response: genetic shift leading to a change in phenotype in a population.
Adaptive evolution: an evolutionary response that is driven by natural selection.
Horizontal transfer: the movement of genetic material between organisms other than by the vertical transmission from parent to offspring.
Cyclical parthenogenesis: in aphids, regular alternation of clonal (apomictic) and sexual generations within a usually annual life-cycle. The ancestral reproductive mode of aphids.
Obligate parthenogenesis: permanent asexual all-female reproduction.
Phenotypic plasticity: the ability of a genotype to express different phenotypes under different environmental conditions.
Polyphenic trait/polyphenism: special case of phenotypic plasticity whereby a single genotype expresses clearly distinct (discrete) phenotypes in response to changes in environmental conditions.
Gene family: set of similar genes that have diversified by duplication.
Parasitoid: an insect that develops by feeding off another organism and eventually kills it.

up to 20 successive generations of parthenogenetic females will accelerate the spread of any advantageous allele, together with the genotype(s) (clones) carrying it. Winged forms allow clones to colonize the large uniform environments constituted by crop fields, on which genetic variability is less important [13]. Hereafter, we highlight four examples of rapid or ongoing evolutionary response of aphids to their agricultural habitats.

Reproductive mode variation and global warming

In these simplified, monotonous ecosystems, the benefits of sexual reproduction may not always compensate for the demographic disadvantages incurred by winter egg diapause and male production. Interestingly, about a third of aphid species contain lineages that completely forgo sexual reproduction, which we refer to as *obligate parthenogenetic* (OP) lineages, together with typical cyclical parthenogenetic (CP) lineages [16] (Figure 1, left). OP lineages are essentially absent from cold-winter regions [14], since they consist of viviparous females that do not lay cold-hardy eggs. OP lineages dominate in many aphid species, in particular crop pests, wherever winter temperature allow their persistence [13,14,17] (and see Figueroa *et al.*, this issue). This the case for the pea aphid, *Acyrthosiphon pisum* whose OP lineages never produce sexual females due to a recessive allele, but instead produce asexual females all year long together with one generation of males in the fall [12,18]. OP males can therefore transmit this allele to other lineages, constantly producing new highly prolific OP genotypes that may be adapted to a range of local conditions [18]. Worryingly, OP lineages could see their geographical range increased by global warming, causing aphid outbreaks to occur earlier in the season. From 1974 to 2014, first flight records of aphids caught at suction traps in UK have advanced by one month [19]. Whether this response results from *phenotypic plasticity* or selection involving the rise of OP lineages deserves further attention.

Rapid emergence of insecticide resistance

Aphids have been regularly and intensively exposed to insecticides since the general use of pesticides in the late 1940s. This exposure has rapidly led to the emergence of multiple forms of resistance to the main classes of chemicals. So far, 14 aphid species have developed insecticide resistance [20], and most notably, the green peach aphid, *Myzus persicae*, is the champion of resistance mechanisms and a pest on many crops. In *M. persicae*, at least six types of resistance have been characterized. Two of them involve metabolic mechanisms: carboxylesterase overproduction providing resistance to organophosphates and carbamates and P450 overproduction conferring some resistance to neonicotinoids; four others rely on target-site mechanisms: a modified acetylcholinesterase conferring resistance to some carbamates, target-site resistance to pyrethroids, neonicotinoids, and organochlorines [10••,20]. Monitoring the spatio-temporal dynamics of insecticide resistance mechanisms in *M. persicae* over the last decades has revealed the labile efficacy of chemical products, which tends to be lost after approximately 15 years of use on average [10••]. It also highlights the rapid genetic changes operating in aphid populations to adapt to new toxic compounds and the rapid dissemination of resistance alleles over long distances [20]. However, insecticide resistance is frequently associated with costs, explaining why susceptible genotypes increase in frequency when insecticide pressure is relaxed [20]. Costs in overwintering survival and defensive behavior have been demonstrated in resistant clones of *M. persicae* [21,22].

Rapid adaptation to new host plants

It is assumed that most aphids are specialists to one or a few plant species [23], which constitute their exclusive resource and habitat. Therefore, changes in plant quality, defense and availability impose considerable selective pressure on aphid populations, and are major drivers of their evolution [23,24••]. These changes involve agroecosystems through the historical domestication of plant species, and the introduction of foreign crops and resistant cultivars.

Domestication of legume crops may have profoundly impacted the diversification of the pea aphid *A. pisum*. The pea aphid actually forms a complex of at least 15 sympatric biotypes, each specialized on one or a few legume species of the Fabaceae family [25]. A time-calibrated phylogeny of biotypes suggests that this complex rapidly diversified by acquiring new host plants some 10 000 years ago or less [26], constituting one of the fastest adaptive radiations on record. This timescale coincides with the domestication of certain legume species that pea aphid populations use as hosts. The availability of legume

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