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Biological and genetic features of introduced aphid populations in agroecosystems

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In agroecosystems, introduced aphids that reproduce by obligate parthenogenesis (OP) show strong biased representation of a few genotypes (superclones), whereas species with cyclical parthenogenesis (CP) exhibit the opposite trend with many unique genotypes. We analyzed the biological and genetic features of 23 different aphid species introduced in different geographic areas and climates, finding putative superclones in about 60% of them. We have examined the proximal causes for aphid establishment and spread after their introduction, and found that OP, host availability, and phenotypic plasticity are among the main variables underpinning the ability of aphids to succeed in new geographic areas, which may explain the high potential for invasion in this group of pest insects.

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Introduction

Worldwide losses in crop yields due to insect pests are currently estimated at 15% and valued at US\$300 000 million a year [1]. Notably, this biotic threat is expected to increase as global warming progresses because (i) insect pests tend to succeed in warmer climates through feeding and increased reproduction [2], (ii) the abundance of natural enemies (i.e., pathogens, parasitoids and predators) will be negatively impacted, thus weakening the efficacy of biological control [3,4], and (iii) the occurrence of invasion events will become more likely through major changes in the distribution and dynamics of insect populations [5].

The establishment and spread of introduced species is often governed by the amount of genetic diversity in their populations [6]. The fate of some introduced insect herbivores, however, seems not to follow that rule [7]. For instance, the success of introduced pest populations of aphids (Hemiptera: Aphididae) seems to rely on their obligate parthenogenesis (OP) reproduction, the availability of their host plants, and the phenotypic plasticity that aphids can display [8,9]. Despite of the low genetic diversity detected in introduced aphid populations [10–12], they are distributed worldwide and have colonized several cultivated and wild hosts [10,13,14]. After reviewing the biological and genetic features reported for 23 invasive aphid species in the introduced versus their native ranges, we looked for common characteristics to explain how aphids can rapidly turn into serious pests for agriculture at a global scale.

Most introduced aphid populations reproduce by OP

The general reproductive mode of aphids is cyclical parthenogenesis (CP), in which one sexual generation alternates with several asexual ones all year round [15]. Intriguingly, this mechanism seems to actually operate in just a few (~3%) aphid species [16], exhibiting low to null genetic and genotypic diversities in some introduced populations. Thus, the low genetic diversity but wide invasiveness of some aphid species seems a paradox. Usually, introduced populations suffer from the deleterious effects of bottlenecks and genetic drift, which should limit the evolvability of populations [17]. However, introduced aphids share certain traits that facilitate their invasion. *First*, the predominant reproduction is OP of a few genotypes (i.e., those genotypes that after exposure to environmental conditions that induce sexuality remain asexual; [18]), thus allowing an exponential increase of their population sizes (Figure 1a). Our revision confirms that 12 out of 19 species described as CP in the native range are recurrently OP in the introduced range, displaying low genotypic diversities (G-1/N-1 ratios; see Table S1 in Supplementary material). This is typically the case of *Myzus persicae nicotianae*, *Rhopalosiphum padi* and *Sitobion avenae*, which are OP out of the palaearctic, and of *Aphis gossypii* which is OP out of the oriental region (Table S1; Figure 1a). Hence, OP enables genotypes with the highest fitness to rapidly increase by clonal amplification ('genetic inflation' *sensu* Loxdale *et al.* [19]), until the OP phenotype becomes predominant in introduced

2 Ecology

Glossary

Biological introductions: the introduction of living organisms from the native range to a novel environment where they were not present before; can be characterized by significant demographic and genetic instabilities

Population bottleneck: a dramatic reduction in population size due to stochastic events such as accidental introductions, which cause losses of genetic diversity by random drift.

Founder effect: biological subsampling of individuals in a new region (e.g., introduced populations) compared to the original population, causing significant reductions on the genetic diversity.

Genetic drift: the random sampling of alleles across generations that leads to allele frequency change, which has a larger effect in smaller populations.

Selection: evolutionary process by which some individuals have higher fitness and a greater probability of passing on their genes to the next generation.

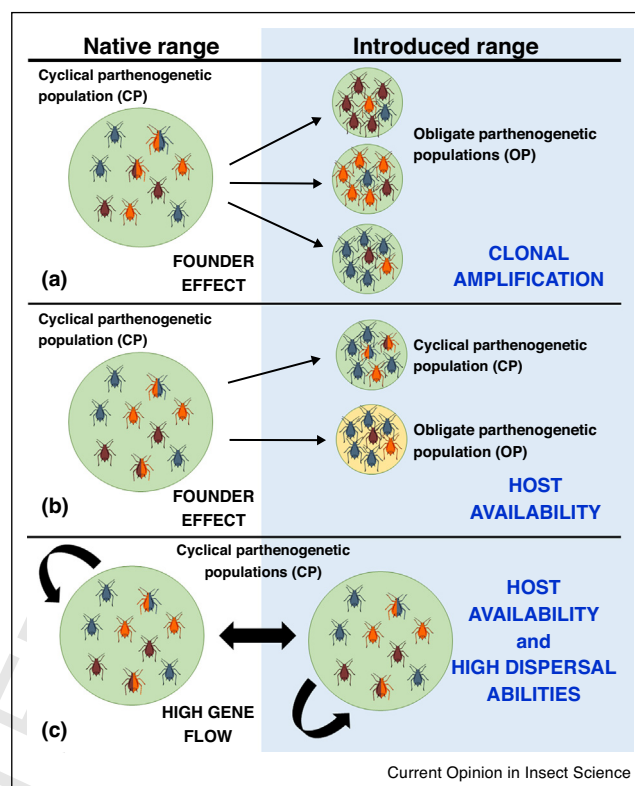
Clonal selection: over-representation of some clones (multilocus genotypes or MLGs) caused by selection (e.g., some lifecycle morphs in aphids are better adapted to particular climates), which may give rise to variable clonal composition among local populations.

Gene flow: the movement of alleles among populations caused by the migration and interbreeding of individuals; high rates of gene flow reduce genetic differentiation among populations.

Adaptation: a trait displayed by an organism that increase its fitness (reproduction and survival), and which has evolved by selection.

Preadaptation: a neutral (non-adaptive) trait that may turn adaptive when individuals face new environmental conditions (e.g., different agricultural practices).

Figure 1



populations [20,21*,22–24,25*]. Thus, the initial founder effect is exacerbated due to substantial genetic drift, as genetic inflation increases this drift by selecting a single or few clonal genotypes (Figure 1a). But the other 11 aphid species do not change from their ancestral reproduction mode (7 and 4 species maintain CP or OP, respectively, depending on the availability of their primary host; Figure 1b,c). *Second*, OP aphids can still gain genetic variation through mutations, chromosomal rearrangements and rare events of interspecific hybridizations, all mechanisms that can increase the phenotypic variation on which selection can operate [15,26]. *Third*, OP aphids can display phenotypic plasticity that increases the opportunity of aphids to invade new environments, which include the expression of detoxifying enzymes at low energy cost [27–30], thus leaving more energy budgeted for parthenogenetic reproduction and production of winged morphs [31,32].

Introduced aphid populations are dominated by a few OP genotypes

The presence of few widespread and high frequency genotypes has been reported for several introduced pest aphids worldwide [33], their populations characterized by low genetic and genotypic diversities (G-1/N-1 ranged from 0 to 0.026; see Table S1 in Supplementary material). The idea of natural selection favouring certain OP genotypes is not new [34], but previous hypotheses predict that the most common genotypes should be generalists. The wide distribution and ecological success of asexual

Biological and genetic features displayed by introduced aphids in agroecosystems. The figure shows how different reproduction modes influence the invasion process from the native to the introduced ranges. **(a)** Invasion from a cyclical parthenogenetic population (CP) to areas where aphids reproduce by obligate parthenogenesis (OP). **(b)** Invasion from CP to either CP or OP, which depends on the availability of the primary host where aphids mate. **(c)** Invasion from CP to CP where the amount of gene flow prevent the structuring of populations.

invaders was first explained by HG Baker [35], who coined the general-purpose genotype concept to refer those weeds displaying generalism, a concept later used by M. Lynch to explain the environmental tolerance of asexual lineages in animals [34]. But Vorburger *et al.* [36] found no support to this hypothesis in aphids, showing OP as a strategy conferring differential fitness across distinct host plants and temperatures ranges. In addition, Vorburger *et al.* [37] called OP genotypes found at high frequency and wide distribution as ‘superclones’. The success of superclones in the introduced range may result from preadaptations in clonal lineages, or neutral mutations that become favourable in the introduced environment (e.g., chemically defended hosts, managing practices) [38,39]. Because asexual lineages can rapidly accumulate mutations, OP genotypes can rapidly evolve closely related clonal lineages and persist in agroecosystems [19*,26]. Alternatively, superclones rapidly proliferate if they arrive in an agroecosystem (Figure 1a), which even if located in different biogeographic regions, can

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