

## NEWS AND VIEWS

## PERSPECTIVE

**A closer look at the spatial architecture of aphid clones**

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Nearly 25 years ago, Ellstrand & Roose (1987) reviewed what was known at the time of the genetic structure of clonal plant species. What is the relationship between space and clonal fitness, they asked. What is the best way for a clone to grow within its ecological neighbourhood? The pot had been stirred 10 years previously by Janzen (1977), who pointed out how little we know about the population biology of clonal organisms like dandelions and aphids. He wondered whether, like good curries, outward appearances masked common ingredients. Because in no small part of the advent of molecular ecology, we know more about clonal life histories today, particularly in plants (van Dijk 2003; Vallejo-Marín *et al.* 2010). Surprisingly, studies of the spatial architecture of aphid clones have been comparably rare. In this issue of *Molecular Ecology*, Vantaux *et al.* characterize the fine-scale distribution of the black bean aphid (*Aphis fabae*) and in so doing, help to fill that gap. They describe a moderate degree of intermingling between aphid clones over a growing season—*A. fabae* clones are 'sticky', but only a bit. By mixing, clones directly compete with each other as well. The results of Vantaux *et al.* (2011) will help to integrate evolutionary patterns in aphids with the appropriate ecological scales out of which those patterns emerge.

*Keywords:* species interactions

Received 5 August 2011; revision received 2 September 2011; accepted 4 September 2011

Aphids and their relatives are small sap-feeding insects that parasitize plants. While most alternate between sexual and asexual generations, the bulk of reproduction over their life cycles is accomplished in the absence of males. Females beget daughters by apomictic parthenogenesis, who initiate reproduction even before they are born, packing generations like buckshot into explosive potentialities. Frustrating the plants they pursue or predators they evade, aphids can exhibit an array of specialized morphs,

designed for exploitation, hiding, dispersal and yes, even sex. If that were not enough, their clonal tendencies, leavened with sex, enable a response to selection that can result in rapid adaptation to and inundation of ecological niches. The result is often a population structure dominated by a small number of clonal lineages, accompanied by rapid turnover of genetic variation as rare clones replace common ones (Vorburger *et al.* 2003; Harrison & Mondor 2011; but see Loxdale *et al.* 2010).

For phytophagous insects like aphids, the name of the eco-evolutionary game is success within and between host plants across environmental gradients. How are aphid clones distributed across hosts at ecologically relevant spatial scales? If dispersal is limited and they do not acquire novel genetic variants, aphid clones are isogenic clumps. In some respects, might as well be you or me. Competition is dominated by kin and intraspecific interactions, and selection acts as it would between individuals. If mating occurs within the spatial neighbourhood, then there is the potential for inbreeding depression. But dispersal is one thing aphids do exceptionally well. When they do disperse broadly, a clone pours itself on its environment like water on rocks: Competition includes both intra- and interspecific components. When it occurs, sex may be prone to breaking-up favourable combinations of alleles. So which is it? How are aphid clones arranged across host plants? The truth is, we do not really know, despite the fact that how aphids move around could bear on everything from socio-biology to international affairs. (Sceptical? Try googling 'opium prices' and 'aphids').

Vantaux *et al.* (2011) used seven variable microsatellite loci to score the clonal composition of host-associated groups, sampled from a study plot and various gardens around Leuven, Belgium. Aphids can have byzantine life cycles, but most of the 4500 or so species are host-plant specialists at some taxonomic level. *Aphis fabae* is among the polyphagous exceptions and is a major pest (Fig. 1). Most *A. fabae* lineages alternate between one of three primary hosts (where sex occurs) and an array of approximately 200 secondary host species, where multiple asexual generations can occur. Some populations on different secondary hosts are genetically distinct. The authors studied two of these, one on the thistle *Cirsium arvense* (*A. fabae cirsiacanthoidis*), itself a clonally propagating weedy plant, and other on the broad bean *Vicia faba* (*A. fabae fabae*). Like many aphid species, *A. fabae* must negotiate a restive mutualism with ants, in this case, the black garden ant *Lasius niger*. At times, ants are benign benefactors, and collecting the honeydew, aphids produce as a by-product of their sap-feeding habit, in exchange for protection from predators, pathogens or other services. But for many aphid species, ants are fickle and move on to other liaisons when

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**Fig. 1** *Lasius niger* ant tending *Aphis fabae fabae* aphids on bean plant (*Vicia faba*). Photo credit: T. Wenseleers.

it suits them or even consume aphids altogether. Because the ability to recruit and appease ants may be a heritable property of aphid clones, the degree to which clones intermingle directly affects the balance of these complex cooperative/antagonistic interactions.

The authors found that for both races, about half of the groups were monoclonal and the other half were mixtures of just a handful (2–4) clones. There was no lack of variation at their study plots overall: For *A. fabae cirsiacanthoi-*

*dis*, they detected more than 50 clones among the 432 individuals they sampled across 31 plants. Most were found on only a single host plant, and there was no evidence that clones on nearby plants were especially related, nor were there widespread multilocus genotypes. While there was evidence of differentiation between clones within host plants, there was a tendency for polyclonal colonies to become more diverse over time. Altogether, these patterns indicate that the clonal composition of *A. fabae* groups at any given time is dynamic and ultimately is influenced not only by dispersal and birth/death processes occurring at the level of host plants but also by processes occurring at more inclusive spatial scales as well (see also Loxdale *et al.* 2010, 2011). Accordingly, the authors found that clonal diversity was not correlated with any of the ecological parameters they measured at their sites, including colony size or the presence or absence of predators or mutualistic ants. This latter result is an interesting contrast with the results of a study by Yao & Akimoto (2009). Yao & Akimoto (2009) found that clonal diversity is reduced in the colonies of a nonhost alternating (autoecious) aphid species with a less capricious ant mutualist, implying that ants enforce a sort of monoculture on their aphid herd. To what extent does ant mutualism shape general features of the spatial genetic structure and dispersal strategies of aphids or vice versa? How do these patterns vary with aphid life histories?

It may seem a long way from aphids on plants in Leuven to general patterns in nature. But it is impossible to not be impressed by the similarity in problems faced by clonal organisms. In clonal plants, ramets can exhibit stereotypical growth forms bookended by high-vs.-low aggregative strategies ('phalanx' and 'guerrilla' strategies; Charpentier 2002). The tillers and stolons of plants represent structures that directly connect the evolution of clonal architecture to issues ranging from how plant populations

**Table 1** A sample of studies in which the clonal composition of aphid groups at small spatial scales has been assayed with molecular markers, with a coarse approximation of inferred diversity for comparison purposes (*low* = most groups monoclonal; *medium* = many mixed groups with multiple clones; *high* = nearly as many genotypes as individuals). Life cycle is coded as: *host alternation—reproductive mode—host range* (*host alternation*: no = 0, yes = 1; *typical reproductive mode*: asexual = 0, cyclic parthenogenesis or mixed modes = 1 (simplified); *host range*: narrow = 0, broad = 1)

Species	Markers	Inferred group diversity	Life cycle*	Study
<i>Aphis fabae</i>	DNA fingerprint	Low	1-1-1	MacKenzie 1996
<i>Pemphigus spyrothecae</i>	Microsats	Low	0-1-0	Johnson <i>et al.</i> 2002
<i>Sitobion fragariae</i>	Allozymes	Medium	1-1-1	Loxdale & Brookes 1990
<i>Sitobion avenae</i>	DNA fingerprint	Medium	0-1-1	de Barro <i>et al.</i> 1994
<i>Sitobion miscanthi</i>	Microsats & DNA seq	Medium	0-0-1	Wilson <i>et al.</i> 1999
<i>S. avenae</i>	Microsats	Medium	0-1-1	Haack <i>et al.</i> 2000
<i>Pemphigus</i> spp.	Microsats	Medium	1-1-1	Abbot 2009
<i>M. tanacetaria</i>	Microsats	Medium	0-1-0	Loxdale <i>et al.</i> 2011
<i>A. fabae</i>	Microsats	Medium	1-1-1	Vantaux <i>et al.</i> 2011
<i>Schizaphis graminum</i>	DNA fingerprint	High	0-1-0	Shufron <i>et al.</i> 1991
<i>Macrosiphoniella tanacetaria</i>	Microsats	High	0-1-0	Massonnet & Weisser 2004
<i>Tuberculatus quercicola</i>	Microsat	High	0-1-0	Yao & Akimoto 2009
<i>Dysaphis plantaginea</i>	Microsats	High	1-1-0	Guillemaud <i>et al.</i> 2011

\*Generalized life cycles, summarized from Blackman & Eastop 2006.

are regulated to how mating systems evolve. Aphids may not have stolons, but as Vantaux *et al.* (2011) and others have demonstrated, as we look more closely, we find intriguing parallels: Despite the enormous variation in aphid life cycles and host affiliations, the spatial distributions of clones often do fall somewhere in the intermingled middle (Table 1). These clonal arrangements are probably not haphazard, bear on patterns of population genetic variation, population regulation and ultimately, the evolution of aphid life cycles. Given what we have learned in recent years about the interactions between aphids and their microbial antagonists and mutualists, and the degree to which aphid genotypes vary in these interactions (Bieri *et al.* 2009; Oliver *et al.* 2010), it seems likely that the spatial strategies of aphids affect microbial interactions in interesting and mostly unexplored ways. Anyway, it is worth pointing out to graduate students just starting out that if clonality seems to be nature's answer to problems posed by the environment, then what exactly those problems are is as relevant today as when they were first identified (Jackson *et al.* 1985). The results of Vantaux *et al.* (2011) suggest that having a close look at what is going on with insects like aphids at small spatial scales, particularly in natural populations, might reveal new problems to think about.

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doi: 10.1111/j.1365-294X.2011.05300.x