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Diversity, population structure, and individual behaviour of parasitoids as seen using molecular markers

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Parasitoids have long been models for host–parasite interactions, and are important in biological control. Neutral molecular markers have become increasingly accessible tools, revealing previously unknown parasitoid diversity. Thus, insect communities are now seen as more speciose. They have also been found to be more complex, based on trophic links detected using bits of parasitoid DNA in hosts, and host DNA in adult parasitoids. At the population level molecular markers are used to determine the influence of factors such as host dynamics on parasitoid population structure. Finally, at the individual level, they are used to identify movement of individuals. Overall molecular markers greatly increase the value of parasitoid samples collected, for both basic and applied research, at all levels of study.

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Introduction

The tools of molecular biology have developed rapidly over the past decade, and infiltrated into most aspects of biological research. Neutral genetic markers are short, sometimes repetitive, DNA sequences that can be used to classify individuals as part of a group, or to distinguish among groups, or among individuals based on differences in sequence data. In this brief review I will summarize the current use of neutral genetic markers in studies of parasitoid diversity and community structure, population structure, and individual behaviour and movement (Figure 1). I will then discuss how genetic markers are used at each of these ecological levels in biological control.

Parasitoid diversity and community structure

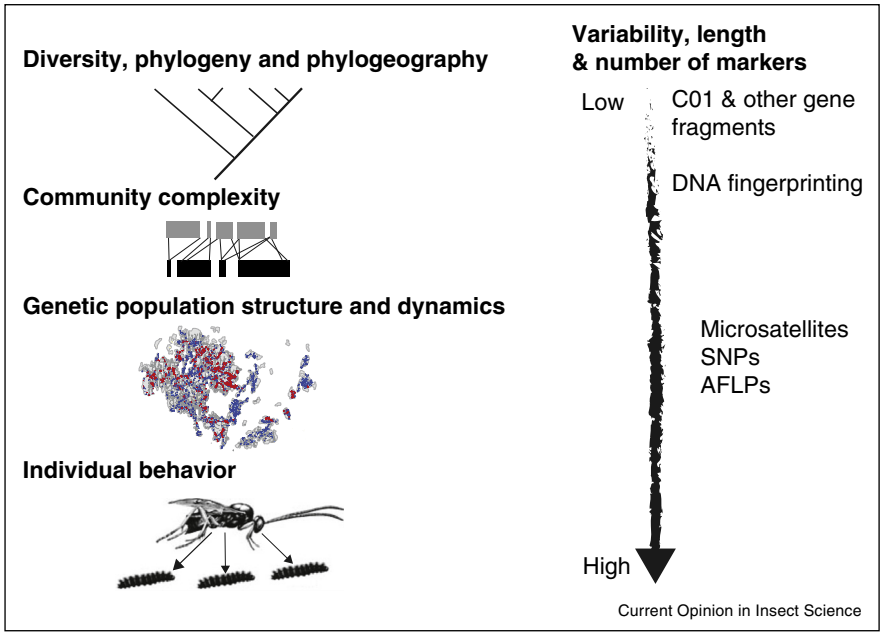
Diversity

Detailed studies of taxonomic groups of parasitoids, using traditional morphology based taxonomy in combination with molecular markers show increased diversity, and the formation of cryptic species groups rooted in long-known single named species [1,2]. In some case these are interpreted in a phylogeographic context in order to understand the ecological or evolutionary context of species geographic and host ranges [3–8]. More recently molecular markers, mostly DNA barcoding, are being used even without morphological study, to elucidate the diversity of parasitoid species, resolve parasitoid phylogeny, and build host–parasitoid food webs. The barcoding approach to quantifying parasitoid diversity started with work based in Costa Rica by Janzen *et al.* [9,10]. That and later studies show very high diversity of parasitoids, with high host specialization in the tropics (e.g. [11,12••,13]). The same techniques have now been used in temperate and even subarctic systems, where less dramatic increases in species diversity have been found [14,15]. The greater increase in diversity in the tropics can be attributed both to there being less previous knowledge of the taxonomy of parasitoids to begin with in the tropics [13], as well as the general trend of high tropical diversity due to resource specialization of species [16].

Host–parasitoid communities

DNA barcoding is also used to determine the structure and complexity of trophically structured communities. Recent reviews by Smith *et al.* [17] and Hrček and Godfray [18•] point out that as the cost of using molecular tools decreases and they become more convenient, host–parasitoid food webs are built with increasingly accurate species diversity, and patterns of trophic linkage. Quantification of species diversity in parasitoid communities has again been exemplified by studies of tropical host–parasitoid communities [9,19], but detailed food webs have also been constructed in temperate [14] and even in high arctic [15] host–parasitoid communities. Though it is still resource and time consuming to sample sufficiently to make a quantitative food web, molecular methods increase the value of these efforts greatly because much more can be learned from each sample if they are associated with molecular markers. For instance, trophic linkages can be identified using molecular methods to detect parasitoids, or the remains of parasitoids in sampled hosts [19]. Using this method Condon *et al.* [12••] found high host specificity in the 18 parasitoid species using 14 *Blepharoneura* fly species on Cucurbit flowers in Peru.

Figure 1



Schematic drawing of the scales of parasitoid research and types of neutral molecular markers used.

However, analysis of parasitoid tissue in host pupae revealed that many of the parasitoid species actually attacked multiple fly species, but failed to develop in most of them. This study brings to light the role of hosts in determining the apparent specificity of parasitoids. It also demonstrates the risk of overestimating host range of parasitoids by analysing parasitoid samples detected in hosts but not reared from them.

Just as parasitoid remains can be found in hosts, remnants of hosts can also be found in adult parasitoids. Species-specific genetic markers can be used identify parasitoid–host links [19,20•,21••] just as they have been used to identify predator–prey trophic structure [22]. In a recent study of the community associated with high arctic Diptera and Lepidoptera, Wirta *et al.* [21••] detected host remains in parasitoids as well as in the guts of spider and bird predators. With this they showed qualitatively the breadth and overlap of parasitism and predation by higher trophic level species, making the relative role of parasitoids in the community apparent.

Genetic population structure

Genetic markers are used for studying populations of parasitoids as well. Since the data of interest are variation within a species rather than among species, more variable markers than those used for DNA barcoding are needed. These have mostly been DNA-microsatellite markers, and more recently also SNPs [23]. PCR techniques such as AFLPs have also been used [24,25]. Over the past decade the use of these tools for studying population genetics of parasitoids has blossomed, as it has in the study of other taxa. Traditional population genetics measures, such as heterozygosity, population differentiation (F_{st}), effective population size (N_e) and isolation by distance are used to quantify the genetic variability in a population, degree of inbreeding, and its history, such as evidence of founder effects [26]. Researchers go on to quantify how populations are genetically structured, often using multi-locus genotype clustering techniques [27]. Samples taken over a geographic area are used to determine limitations of gene flow due to many factors, such as geography [28], climate [29,30], host species [31–35] and host plant [35–39].

Because parasitoids have a close relationship with their hosts, the host population dynamics and distribution in the landscape impose structure and dynamics on the parasitoid [40]. The genetic structure of some parasitoid species matches that of the host suggesting that the parasitoid population is tracking that of the host. Nyabuga *et al.* [41•] showed that the parasitoid *Lysiphlebus hirticornis* had lower population genetic structure than that of its host aphid. This is expected because aphids are mostly wingless and reproduce clonally for generations on a single host plant, while the parasitoid reproduces sexually and is winged. Nonetheless, Nyabuga *et al.* [41•] argued that the genetic structure of the parasitoid is driven by the small-scale distribution of the host, because both contained structure at the scale of host subpopulation, though the host structure was of higher magnitude.