Biological Control 199 (2024) 105656

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Editorial

Recent advances in characterizing trophic connections in biological control

ARTICLE INFO

Keywords:
Genetic bottleneck
High-throughput sequencing
Host location behaviour
Intraguild predation
Invasive arthropod species
Metabarcoding
Molecular gut-content analysis
Multitrophic interaction

ABSTRACT

This Special Issue presents articles that combine traditional approaches, novel experimental methods, and advanced techniques, to provide a more in-depth understanding of trophic interactions in biological control. Studies mainly cover behavioural and chemical ecology, molecular ecology using PCR, qPCR and high-throughput sequencing, population genetics, automated deep learning image analysis and photo trapping. Through laboratory and field investigations, articles provide novel insights into host/prey specificity of natural enemies, their multitrophic interactions, and how they behave in space and time. Ultimately, results may be useful for the development of management strategies that aim to improve biocontrol effectiveness against native and invasive herbivorous insects.

1. Introduction

Understanding whether a natural enemy can control a target pest is a critical component of biological control. This encompasses qualitative and quantitative characterisation of predator–prey, host-parasitoid, and pest-pathogen trophic interactions. Traditional methods have been instrumental in the past to evaluate natural enemy activity (reviewed by van Driesche and Hoddle, 2017), and continue to provide invaluable data. For example, using life table data and matrix models, Naranjo (2018) showed that the decline of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) in the western United States was mainly caused by native arthropod predators, rather than introduced exotic parasitoids. Through direct observations of predator foraging behaviour and the use of sticky traps, Hoddle et al., (2013) documented the successful control of *Novius* (*Rodolia*) *cardinalis* Mulsant (Coleoptera: Coccinellidae) on *Icerya purchasi* Maskell (Hemiptera: Monophlebidae) in the Galápagos Islands between 2009 and 2011. Furthermore, they demonstrated a high prey fidelity of the ladybird on *I. purchasi* and a negligible impact on non-target preys using field observations in walk-in cages (Hoddle et al., 2013). Other commonly used traditional methods include the use of exclusion cages, dummy prey, and sentinel prey and eggs (e.g., Tillman et al., 2020).

In recent years, molecular-based techniques and more advanced computational analyses have allowed precise identification and quantification of trophic relationships. For example, singleplex and multiplex PCR have been used to characterise hidden herbivore-parasitoid-predator interactions (Traugott and Symondson, 2008), and the disruption of parasitoid aphid control by intraguild predation by generalist predators (Traugott et al., 2012). DNA barcoding and, more recently, metabarcoding have both proved to be useful for exploring food-web networks before and after parasitoid emergence from the host (Miller et al., 2021). However, as these techniques have their own limitations and interpretation biases, complementary use with traditional approaches is recommended (Furlong et al., 2014; Miller et al., 2021). Using molecular detection of parasitoids in stink bug eggs and in-situ micro-computed tomography imaging of eggs, Konopka et al., (2020) described and quantified parasitoid development in suitable and unsuitable host eggs. Interestingly, their results confirmed previous egg dissection studies by Abram et al. (2014).

We are currently facing an increase in the biological control market (van Lenteren et al., 2018). In Europe, for example, invertebrate sales for biological control have increased by 65 % since 2019 (https://ibma-global.org/). This is mainly due to growing environmental and health concerns and the need to find alternative sustainable control solutions to face the decreasing availability of chemical pesticides because of tightened legislation (e.g., The EU's Farm to Fork strategy, which aims to reduce the use and risks of chemical pesticides by 50 % by 2030; Silva et al., 2022). In addition, the increased introduction and establishment of exotic herbivorous species implies the need to evaluate the efficacy of new biological control agents as well as those already available on the market (Hoddle et al., 2021).

On the other hand, exotic natural enemies that have coevolved with invasive herbivores in their native range should be rapidly identified and evaluated for their host specificity and likelihood of establishment in the new area where they may be introduced for classical (importation) biological control (Messing and Brodeur, 2018; Hoddle et al., 2021). Typically, such evaluations include physiological host range bioassays of no-choice and choice tests conducted in quarantine laboratories (van Lenteren et al., 2006; Haye et al., 2020). Such protocols provide a first indication of prey/host range, but more complex evaluations have been advocated in pre-release risk assessment, for example by incorporating odour attractiveness mediated by the plants, or by considering the effect of parasitoid conditioning (van Driesche and Murray, 2004; Desurmont et al., 2014; Giunti et al., 2016; Rondoni et al.,

https://doi.org/10.1016/j.biocontrol.2024.105656
Received 1 November 2024; Accepted 6 November 2024

2022). Intrapopulation variability should also be considered, taking into account the specific strain of the natural enemy and its phenotypic plasticity (Leung et al., 2020; Sevarika et al., 2021; Chierici et al., 2023). Given the current restrictions on the import and release of exotic natural enemies into a new area (Barrett et al., 2021), the improvement of existing procedures for evaluating their effectiveness is strongly recommended.

The increased availability of advanced instrumentation in diagnostic laboratories, coupled with the associated reduction in cost per analysis, has opened new opportunities for the development of diagnostic protocols (Spadaro et al., 2020; Schmidt et al., 2021; Cuff et al., 2022). Rapid advances in deep learning image analysis have made it possible to automatically screen and identify pests and natural enemies under laboratory and field conditions (Høye et al., 2021). Not surprisingly, the introduction of new techniques and procedures can change the way biological control agents are viewed and evaluated. In addition, by providing information on seasonality and movements of natural enemies, results can be used to implement conservation biological control practices at farm, habitat and landscape level (Miller et al., 2021).

This is the first Special Issue dedicated to advances in characterizing trophic connections in the journal Biological Control. By bringing together novel research studies exploring advanced techniques and their applications in pest control, we aim to give greater visibility to this important topic.

2. Structure and content of the Special Issue

This Special Issue consists of 13 articles presenting original research. The papers mainly cover behavioural or chemical ecology (5 articles), molecular ecology using PCR, qPCR, or high-throughput sequencing (5), automated image analysis or photo trapping (2), and population genetics (1). Articles dealt with either predators (9) and parasitoids (4).

In addition to the case-specific research questions addressed in each paper, this Special Issue aims to make an important contribution to more general questions. For example, how can traditional DNA-based predation diagnostics be useful to assess trophic connections? What is the new contribution that high-throughput sequencing can make to the assessment of trophic interactions? How do natural enemy traits affect host-prey interactions? What factors influence the efficacy of biological control agents and how can exposure to pesticides affect the innate and conditioned behaviour of parasitoids? How do the availability of alternative preys and the occurrence of intraguild predation affect control by natural enemies?

The first group of papers deals with the evaluation of trophic interactions in behavioural and chemical ecology. The identification of an efficient and reliable candidate biological control agent is of paramount importance when focusing on biological invasions of important pests, such as fruit flies in Hawaii, or *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) and *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae) in Europe. Ramadan et al. (2023) investigated how previous parasitism by a suitable parasitoid can suppress the host's immune response, allowing a normally unsuitable parasitoid to develop into the host (kleptoparasitism). The authors reported that during biological control programmes of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) in Hawaii in the 1950s, over 30 parasitoid species were introduced, but only a few became established. Reasons for this may include inaccurate host range information, resulting in the indiscriminate introduction of inappropriate parasitoids, and the occurrence of unexpected interactions between introduced parasitoids (Wang et al., 2024). The solitary larval endoparasitoid *Psyttalia fletcheri* (Silvestri) (Hymenoptera: Braconidae) was able to find and oviposit on co-evolved (*Zeugodacus cucurbitae* Coquillett) and novel (*B. dorsalis*, *Bactrocera latifrons* Hendel, and *Ceratitis capitata* Wiedemann) hosts (all Diptera: Tephritidae). However, oviposition in *B. dorsalis* larvae was unsuccessful because eggs and first instars of the parasitoid were encapsulated. However, when larvae of this unsuitable host were parasitised first by its most effective parasitoid (*Diachasmimorpha longicaudata* Ashmead; Hymenoptera: Braconidae) and next by *P. fletcheri*, the latter was able to complete development. The authors conclude that when kleptoparasitism occurs in the field, records based solely on parasitoid emergence from field-collected hosts may lead to misleading interpretations of host range.

Gonthier et al. (2024) conducted host specificity tests on two parasitoids, *Necremnus tutae* Ribes & Bernardo (Hymenoptera: Eulophidae) and *Dolichogenidea gelechiidivoris* Marsh (Hymenoptera: Braconidae), candidates for biocontrol of *T. absoluta* in the Mediterranean area. They combined no-choice and laboratory tests using sentinel plants in and around a greenhouse. This approach proved useful in characterising the ability of the parasitoids to locate the target species at a distance, as well as its response to four non-target species of European leaf miners. The study provided evidence for oligophagy of *D. gelechiidivoris* and polyphagy of *N. tutae* in the study area. The high host specificity and attractiveness of *D. gelechiidivoris* towards *T. absoluta* and the closely related species *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) make this parasitoid an ideal candidate for classical biological control or for augmentation in areas where it is already present. In contrast, the polyphagous nature of *N. tutae* poses a potential risk to non-target species. The study suggests that countries interested in classical biological control should prioritise *D. gelechiidivoris* and conduct host specificity testing, focusing on leafminers of the family Gelechiidae. More generally, the inclusion of long-range attraction bioassays in host specificity tests would provide more realistic information on the ability of the parasitoid to effectively locate non-target organisms at distance.

The importance of specific and reliable infochemical communication in a plant-pest-parasitoid complex was investigated by Leo et al. (2024). They elucidated how pepper plant and insect volatiles specifically mediate the attraction of a pteromalid parasitoid, *Jaliscoa hunter* (Crawford) (Hymenoptera: Pteromalidae), to immature stages of the pepper weevil, *Anthonomus eugenii* Cano (Coleoptera: Curculionidae). This economically important pest is difficult to control on cultivated pepper crops in North America. The authors compared the chemical volatiles emitted by pepper plants infested by the pepper weevil to uninfested plants. Using a Y-tube olfactometer, they observed a parasitoid preference for infested plants. Interestingly, this attraction to volatiles associated with its main host was maintained even when the parasitoid was reared on an alternative host.

Rondoni et al., (2024) provided first evidence on the effects of neonicotinoid pesticides on learning behaviour and memory retention in hymenopteran egg parasitoids. Open and closed arena bioassays were conducted to investigate the innate and learned foraging behaviour of *Trissolcus japonicus* (Ashmed) (Hymenoptera: Scelionidae), an exotic parasitoid used in biological control programmes against the invasive *H. halys*. They hypothesised that a low concentration (causing 20 % parasitoid mortality) of a commonly used neonicotinoid insecticide (acetamiprid) would alter the behaviour and learning ability of the parasitoid to exploit chemical traces left by reproductive females of either the main host, *H. halys*, or an alternative host, the predatory stink bug *Arma custos* (F.) (Hemiptera: Pentatomidae). Parasitoids pre-exposed to neonicotinoids showed changes in foraging behaviour, with increased time spent in the host-contaminated area and altered kinetics of walking behaviour. Interestingly, neonicotinoid exposure did not affect the learning ability of female parasitoids 1 h after oviposition experience, but prolonged memory retention. As acetamiprid is widely used to control *H. halys* outbreaks in the EU, the results may be useful for a better understanding of the factors that may limit the establishment of the parasitoid in areas where it is being introduced.

Royer et al., (2024) investigated whether intraspecific variation in predator aggressiveness and the availability of an extraguild prey affect intraguild predation. Using two artificially selected genetic lines of the generalist predator, *Nabis americoferus* Carayon (Hemiptera: Nabidae), one "aggressive" and one "docile" line, they tested intraguild predation towards *Orius insidiosus* Say (Hemiptera: Anthocoridae) in presence and absence of the extraguild prey, *Lygus lineolaris* Palisot de Beauvois (Hemiptera: Miridae). They found that the aggressive line of *N. americoferus* exhibited higher attack rate and intraguild predation upon the intraguild prey compared to a less aggressive line, even in the presence of the extraguild prey. Furthermore, the docile line of *N. americoferus* was more likely to adapt its behaviour to environmental conditions, as the intensity of intraguild predation increased in the presence of the extraguild prey. Whether this difference in foraging behaviour is likely to be relevant under open field conditions remains to be investigated.

A second group of papers used molecular techniques to assess predator–prey interactions under field conditions, to validate a method for estimating relative predation rates using quantitative molecular gut content data, or to assess population dynamics of introduced natural enemies.

Golan et al, (2023) used molecular gut content analysis to identify which native predators have the best potential to control an invasive crucifer pest, the yellowmargined leaf beetle, *Microtheca ochroloma* Stahl (Coleoptera: Chrysomelidae) in the Southeastern US. Over two years, arthropods were surveyed on a range of susceptible *Brassica* cultivars and a shortlist of commonly associated predators was developed. Molecular gut content analysis using species-specific primers for *M. ochroloma* identified key predator links and suggested a density-dependent tracking response for the ladybird *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae). Ground beetles also showed a density-dependent tracking response. Evidence of common generalist predators exploiting the invasive herbivore provides targets for habitat management for conservation biological control.

Branco Leote et al., (2024) investigated intraguild predation among soil-dwelling beetles in cereal fields in Tirol (Austria). Multiplex PCR was used to detect main and alternative prey from the regurgitates of soil-dwelling predators (Carabidae, Staphylinidae, and Araneae), manipulating the presence of alternative prey by applying organic fertiliser (manure). They found that a reduction in pest dispersal between tillers within fields correlated with lower intraguild predation, while pest density remained unchanged between treatments, making the net effect on biological control unclear. They hypothesized that a change in predator behaviour, allowing predators to exert more pressure on pests, could be the main mechanism behind the link between reduced intraguild predation and reduced pest dispersal. Conversely, the lack of effect on pest density may be due to other effects, such as fertilisation, resulting in increased pest and plant growth, counteracting any increase in predation pressure. Given the large number of predators screened (over 6000), the analysis of regurgitates from live individuals prevented significant biodiversity losses that would otherwise have been necessary in the case of gut dissection.

Batuecas et al. (2024) used high-throughput multi-primer metabarcoding to analyse heteropteran and coccinellid predator taxa collected in peach orchards and alfalfa agroecosystems in the Ebro Basin (Spain) and to map trophic interactions towards arthropods and plants. The methodology adopted was valuable in demonstrating the omnivorous role of four heteropteran predator taxa, *Adelphocoris lineolatus* Goeze, *Lygus* sp. (both Hemiptera: Miridae), *Nysius* sp. (Hemiptera: Lygaeidae), and *Nabis* sp. (Hemiptera: Nabidae) and three coccinellid species, *Coccinella septempunctata* L., *Hippodamia variegata* Goeze, and *Stethorus punctillum* Weise (all Coleoptera: Coccinellidae). The analysis of trophic interactions was also helpful in elucidating the movement of these predators between neighbouring habitats. The consumption of non-crop plants suggests that the surrounding vegetation may play an important role in maintaining the predators in the habitat when their common prey is scarce.

Using molecular gut content analysis with PCR and landscape habitat diversity analysis, Kheirodin et al. (2024) tested several ecological theories in cotton-dominated landscapes in Georgia, US. Their results suggest that some semi-natural habitats (i.e., forests and wetlands) increase the abundance of predators, ultimately leading to greater pest control in cotton fields ("natural enemy hypothesis"). Partial support for the "resource concentration hypothesis" was found, with whiteflies being more abundant in landscapes with more cotton (preferred host) and vegetables, and aphid abundance being negatively correlated with whitefly abundance. Overall, landscape configuration played an important role in explaining pest and natural enemy abundance, with smaller field sizes promoting biocontrol and diluting host crop area. Taken together, the results of this study could provide the basis for conservation biological control strategies.

Andow and Paula, (2024) addressed the problem of estimating predation rates from molecular gut content data. They described how gut content data from qPCR, quantitative ELISA, metabarcoding and unassembled shotgun reads (Lazaro) can be used to estimate relative *per capita* predation rates among ants (Hymenoptera: Formicidae) or by ladybird beetles (Coleoptera: Coccinellidae) upon aphids (Hemiptera: Aphididae). Their method was used to estimate the relative per capita predation rate in laboratory feeding trials and field experiments (Brazil), and was found to be a rapid way to assess how predator–prey interactions change over space and time.

Sethuraman and Obrycki (2024) used demographic population genomics techniques as a complementary aspect of understanding trophic interactions in biological control. They presented examples of three species of predatory ladybirds (*C. septempunctata*, *Harmonia axyridis* Pallas and *Hippodamia convergens* Guérin-Méneville; all Coleoptera: Coccinellidae) and the solitary braconid parasitoid *Dinocampus coccinellae* (Hymenoptera: Braconidae), which attacks over 50 species of predatory ladybirds. The genetic studies and simulations presented indicated a bottleneck in North American *H. axyridis* populations about 40 years ago, soon after its discovery in the US. In addition, a bottleneck in populations of the native species, *H. convergens*, was indicated about 24 years ago. Interestingly, populations of *C. septempunctata* did not show a bottleneck, as this species was estimated to be growing exponentially in the populations sampled in the US.

Finally, two papers explored deep learning image analysis and automatic detection of natural enemies. Mouratidis et al. (2023) developed a method to assess egg predation by zoophytophagous piercing-sucking predators using deep learning image analysis. The developed algorithm, YOLOv5, provided high accuracy in detecting predated *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. When compared to two human observers performing the task of counting predated eggs under a stereomicroscope under standard laboratory conditions, the detection algorithm made significantly fewer errors and achieved higher accuracy. A case study is also presented comparing the predation activity of the generalist predators *Orius laevigatus* (Fieber), *Orius majusculus* (Reuter), *Orius minutus* (Linnaeus) (all Hemiptera: Anthocoridae), *Nesidiocoris tenuis* (Reuter), *Macrolophus pygmaeus* (Rambur) and *Dicyphus errans* (Wolff) (all Hemiptera: Miridae).

Seimandi-Corda et al. (2024) used camera traps to detect the predators of two oilseed rape herbivores, the pollen beetle (*Brassicogethes aeneus* Fabricius; Coleoptera: Nitidulidae) and the brassica pod midge (*Dasineura brassicae* Winnertz; Diptera: Cecidomyiidae) occurring in the UK. In addition, they tested the hypothesis that the timing of predator activity coincides with the presence of pest larvae on the ground. By combining the use of camera traps, pitfall traps and sentinel prey over two years, the data showed that beetle larvae, rather than adults, were responsible for most of the predation events. Interestingly, they showed that the traditional method of using pitfall traps failed to detect the presence of large numbers of beetle larvae, ultimately underestimating the importance of particular predator species. Finally, predators were most active when pest dropping behaviour from the plant was more intense. Providing information on two important spring pests of oilseed rape in Europe could ultimately help practitioners to develop sustainable management practices aimed at maintaining effective predator stages.

The papers collected in this Special Issue provide some examples of how experimental protocols and new techniques can offer a more in-depth understanding of trophic interactions in biological control. Better pre-release risk assessment of a candidate biological control should consider infochemical communication between all members of the tritrophic systems under evaluation (Gonthier et al., 2024), the effect of kleptoparasitism (Ramadan et al., 2023), or anthropogenic causes (e.g., pesticide applications) that could eventually limit natural enemy establishment (Rondoni et al., 2024). Interestingly, the method proposed by Andow and Paula, (2024), based on quantitative gut-content data, allows the per capita quantification of the amount of food ingested by a single predator. The papers based on field surveys of arthropods provided support for better targeting management strategies aiming at improving the biocontrol activities of local natural enemies (Golan et al., 2023; Batuecas et al., 2024; Branco Leote et al., 2024; Kheirodin et al., 2024; Seimandi-Corda et al., 2024).

All aspects in this Special Issue represent advances in their respective fields. Next research can specifically address the potential impact of climate change, and investigate whether the magnitude of the observed patterns and behaviours apply at environmental conditions other than the optimal rearing temperatures and humidity imposed by the climatic chambers. Automatic detection of herbivores and predators has increased in recent years, and a next step would be to incorporate it into decision support systems. Finally, the development and validation of DNA-based protocols for evaluating multitrophic interactions of natural enemies would help to understand agroecosystem functioning, optimistically leading to better conservation biological control practices.

CRediT authorship contribution statement

Gabriele Rondoni: Conceptualization, Writing – original draft, Writing – review & editing. **Jana Collatz:** Conceptualization, Writing – review & editing. **Mattias Jonsson:** Conceptualization, Writing – review & editing. **Oskar Rennstam Rubbmark:** Conceptualization, Writing – review & editing. **Eric W. Riddick:** Conceptualization, Writing – review & editing. **Jason M. Schmidt:** Conceptualization, Writing – review & editing. **Jacques Brodeur:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Antonio Biondi, the overseeing editor of this Special Issue, for his guidance and encouragement and for facilitating a smooth editorial process. We thank all the contributors for their commitment to providing high quality papers and all the reviewers for their comments and recommendations on the manuscripts. Support was provided by the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 101026399.

Data availability

No data was used for the research described in the article.

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