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Taxonomy and Biological Control: New Challenges in an Old Relationship

Eduardo Mitio Shimbori¹ · Ranyse Barbosa Querino² · Valmir Antonio Costa³ · Roberto Antonio Zucchi¹

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Abstract

Biological control and taxonomy are continuously developing fields with remarkable impacts on society. At least 80 years of literature have documented this relationship, which remains essentially the same in its mutualistic nature, as well as in its major challenges. From the perspective of Brazilian taxonomists, we discuss the impacts of important scientific and social developments that directly affect research in these areas, posing new challenges for this lasting relationship. The increasing restrictions and concerns regarding the international transit of organisms require improvements in research related to risk assessment for exotic biological control agents and also stimulate prospecting within the native biota. In our view, this is a positive situation that can foster a closer relationship between taxonomists and applied entomologists, as well as local surveys and taxonomic studies that are necessary before new programs and agents can be implemented. We discuss the essential role of molecular biology in this context, as an iconic example of the synergy between applied sciences and natural history. As our society comes to need safer and more sustainable solutions for food security and the biodiversity crisis, scientific progress will build upon this integration, where biological control and taxonomy play an essential role.

Keywords Applied entomology \cdot Databases \cdot Molecular taxonomy \cdot Parasitoids \cdot Biocontrol legislation \cdot Species delimitation

Edited by Élison Fabrício Bezerra Lima	
	Eduardo Mitio Shimbori shimbori@gmail.com
	Ranyse Barbosa Querino ranyse.silva@embrapa.br
	Valmir Antonio Costa valmir.costa@sp.gov.br
	Roberto Antonio Zucchi razucchi@usp.br
1	Departamento de Entomologia e Acarologia, Escola Superior de Agricultura "Luiz de Queiroz" (ESALQ), Universidade de São Paulo (USP), São Paulo, Piracicaba, Brazil
2	Empresa Brasileira de Pesquisa Agropecuária, Embrapa Cerrados, Planaltina, Distrito Federal, Brazil
3	Centro Avançado de Pesquisa e Desenvolvimento em Sanidade Agropecuária, Instituto Biológico, São Paulo, Campinas, Brazil

Perspectives and overview

Since the early days of biological control as a scientific field, its close relationship with taxonomy has remained essentially unchanged. One field has fostered the development of the other, leading to advances in the recognition of species and knowledge of their biology, behavior, and evolutionary and ecological relationships. The study of natural enemies of pests, such as parasitoids, has benefited from this integration, even though much work remains to be done. Recent examples show that even in critical situations, whether from an economic or conservation perspective, highly important groups for biological control programs still lack adequate taxonomic support. Thus, the knowledge, investments, and actions taken may not only be completely lost but also generate negative results (Bortolus 2008). The same problems and possible solutions raised by authors in the past remain relevant today, as unexplored problems and possibilities.

The science of taxonomy has biological diversity as its object of study, describing and classifying organisms using the comparison of characters between distinct evolutionary entities, or taxa (i.e., base units of taxonomy including species and higher-level groups such as genus and family) as a method (Amorim 1997). Taxonomic work extends beyond species description and identification in that it often includes collections and surveys, maintenance of biological collections and museums, composition of catalogs and databases, and phylogenetic studies, which can provide important information about evolutionary aspects such as geographic distribution and host relationships. It is a hypothesis-driven science, in which taxa are proposed and tested in a complex routine. Therefore, a new species description involves the generation of a new hypothesis represented by a name, which in turn is governed by nomenclature rules (Thiele and Yeates 2002; Lipscomb et al. 2003; Wheeler 2004; Thomson et al. 2018). For the purposes of the present discussion, we consider three levels of taxonomic studies: alpha (species level, their discovery and description), beta (supraspecific level, phylogenetic relationships and classification), and gamma (infraspecific level and speciation processes) (Mayr 1958). We use the terms "taxonomy" and "systematics" interchangeably, as we see no advantage in divorcing these terms (Wheeler 2007) or a logical difference between them (see Hennig 1999).

Biological control, in turn, is a branch of applied ecology, which derives most of its theoretical basis from population ecology and demography in a consumer-resource dynamic (Murdoch et al. 2003). The results are usually integrated into environmental management practices, aiming to reduce undesirable populations which may be agricultural or forest pests, urban pests, or invasive species in natural areas. Over the years, several books and articles have provided more general explanations about the applicable terminology, such as DeBach and Rosen (1991), Van Driesche and Bellows (1996), Eilenberg et al. (2001), and Parra et al. (2002; 2021). Biological control programs may have positive impacts on food security and the quality of agricultural products or the recovery of natural areas, but may also lead to population reductions and even extinction of native species. These potential outcomes place great responsibility on researchers and practitioners, which increases the need for taxonomic and ecological studies of the species involved (Van Driesche et al. 2016).

The different methods of biological control (see Eilenberg et al. 2001, for a discussion of terminology applied to biological control strategies) vary in their potential effects on the environment and the economics of the productive sector. For example, *classical* biological control aims at establishing populations of a biological control agent and its subsequent dispersal in the new environment. This approach can produce irreversible results, through both target control and non-target effects (Howarth 1991). It is not directed at mass production and marketing of the agent, but benefits producers in a broad and general way (e.g., Neuenschwander 2001) and can help to mitigate the environmental impacts of invasive species (Van Driesche et al. 2016). Applied biological control, including inundation¹ and inoculation, depends on mass rearing and release of agents, and therefore on methods to produce and apply the product (i.e., the agent); a review of the state of this area was published by van Lenteren (2012). In most cases, the establishment of the agent after release is not a target attribute of this approach, and its impact, positive or negative, tends to be transient (Boivin et al. 2006). Finally, conservation biological control depends exclusively on native fauna and tends to generate additional benefits, with an increase in local biodiversity (Barbosa 1998). This method is also referred to as "ecological engineering" (Gurr et al. 2004) and is based on habitat manipulation, aiming to provide resources for natural enemies to improve natural control in agroecosystems (Altieri and Letourneau 1982).

In all these cases, knowledge and correct determination of the species involved is a fundamental step. In addition, because there can be significant biological differences between populations of a species, biological control often requires gamma-level taxonomic studies, that is, what has been referred to as biosystematics (Schlinger and Doutt 1964; Gordh 1977). Many advances in this area were also responses to the demands of biological control programs, including proposals in integrative taxonomy (for example, Dayrat 2005; Schlick-Steiner et al. 2010; Beltrà et al. 2015; Gokhman 2018). Taxonomically important research studies involving species concepts, cryptic species, and hybridization (for example, Goldson et al. 2003; Hopper et al. 2006; Bickford et al. 2007; Yara et al. 2010; Derocles et al. 2016) have been stimulated thanks to their relevance to biological control.

From Clausen (1942) to Zucchi (2021), a vast literature extending over at least eight decades has discussed the intricacies and the intimate mutualistic relationship between taxonomic and biological control research (Clausen 1942; Sabrosky 1955; DeBach 1960; Schlinger and Doutt 1964; Compere 1969; Rosen and DeBach 1973; Delucchi et al. 1976; Gordh 1977; Knutson 1981; Rosen 1986; Moraes 1987; Danks 1988; Hanson 1993; Heraty 1998, 2004, 2009; Schauff and LaSalle 1998; Gordh and Beardsley 1999; Huber et al. 2002, 2021; Zucchi 2002, 2021; González-Hernández and López-Arrollo 2007; Bin et al. 2012; Andersen and Wagner 2016). Despite the exhaustive discussion of this topic, which undeniably denotes its importance, the desirable cooperation

¹ The term "augmentation" biological control is widely used in the literature, mostly referring to inundation biological control, as defined by Eilenberg et al. (2001). Here, we use the term "applied" biological control to refer to both inoculation and inundation biological control, even though most of the examples used in applied biological control are for inundation.

between the fields of taxonomy and biological control still occurs only in particular cases. To some degree, the rhetorical question raised by Sabrosky (1955) regarding taxonomic knowledge of an agent still seems to echo in practice: "What difference does it make, if control is achieved?" This is a valid question, since the entities in question, whether insect pests or biological control agents, have characteristics that allow them to be distinguished as important pests or efficient agents, regardless of the names assigned to them. In the taxonomist's search for natural groups or for a more appropriate philosophical concept of species, the name could not be a more artificial aspect. Could this realization cause a rupture between the two fields of knowledge? For most authors who have discussed the topic, scientific communication justifies the importance of taxonomy. However, the distinction between real entities and abstract concepts of species and populations must be explicit, allowing unambiguous understanding by the researchers involved. To this end, some situations may require an infraspecific nomenclatural system (Kim and McPheron 1993).

Even in the best possible scenario, an identification may still be flawed and the name assigned to a particular entity may not be the most accurate, or the species concept not appropriate, or even the samples used may originate from mixed populations that differ in their biology. History shows that all these problems, among many others, have already occurred, which highlights the need for careful, in-depth studies of both taxonomic and ecological aspects, as flawed identifications can lead to large economic losses, lack of confidence in biological control, and environmental impacts (e.g., Louda et al. 2003; Bin et al. 2012). Perhaps the most important point is understanding that taxonomic issues will occasionally occur, as taxonomic concepts are neither universal nor stable (Minelli 2020), and that some actions, such as introduction of agents into new areas, are irreversible. For both problems, there are best practices that must be followed by both taxonomists and applied entomologists, and can increase efficiency and safety and, consequently, confidence in biological control as a management practice, through closer interaction between these two fields of research.

With the recent developments in these fields, increased specialization seems to be the trend. In the past, scientists such as David Rosen and Paul DeBach were able to conduct research in both taxonomy and biological control. Today, they would probably encounter more difficulty in conducting studies in both areas. How this change may affect this collaborative relationship is not yet clear. This opinion paper aims to explore aspects of the relationship between insect taxonomy, especially parasitoids, and biological control, that affect the development of these areas and their mutualistic relationship.

Taxonomy in the context of biological control

Three fundamental aspects of biological control increase the importance of taxonomy. First, control agents are species (or a lineage within a species), and therefore need to be studied taxonomically: species must be discovered/ delimited, described, and named within a classification based on their phylogenetic (=evolutionary) relationships, and this process must ensure accurate identification of the species in the future. Second, it is not uncommon for biological control agents to be more specific than chemical agents, making correct identification of the target even more crucial to success. A third, emerging factor is the association between the pest and the natural enemy. Identification and observations of these associations are not infrequently subject to errors that cause numerous problems in biological control programs (Danks 1988; Bin et al. 2012).

Taxonomy of insects, especially natural enemies of pests, has certain aspects that should be considered for a better understanding of the relationship to biological control: (i) there is an immense diversity of insects (mostly unknown) and species delimitation is often, if not always, a complex task; (ii) biological control requires a fine delimitation of species, and sometimes infraspecific refinement of strains or populations within a species, which has led taxonomists to push the boundaries of *alpha* and gamma levels; (iii) taxonomists are aware of the need for identification tools for use by applied entomologists, and the development of such tools may increase identification accuracy and expand the use of biological control agents, even in the most complex groups; (iv) the amount of information on species of economic importance is, as expected, much larger than on other species with no direct/ obvious importance to humans, and so are the cumulative errors in identification, especially in host-parasitoid associations; (v) molecular markers are rapidly increasing in importance in taxonomy, and research should also focus on curating public databases; however, in many cases, published information is impossible to confirm due to a lack of voucher specimens (Packer et al. 2018).

The diversity of insects is the highest among living beings, although about 80% of species remain to be described (Stork 2018). Hymenopteran parasitoids, which are arguably the most important group of macroorganisms in biological control, are an excellent example of the scale of this knowledge gap. According to Forbes et al. (2018), the number of unknown species of parasitoid wasps must be around twice that of the order Coleoptera, currently the group with the largest number of described species. These numbers are based on estimates, such as that of Hawkins and Lawton (1987), that a typical phytophagous species is attacked by 5–10 species of parasitoids. Besides the evident lack of taxonomic studies, this immense diversity may be partly masked by the high frequency of cryptic species and minute size of these organisms (Gokhman 2018), exacerbating the complexity of species delimitation and identification. In addition, many environments have been scarcely studied, which makes it difficult to estimate the true diversity of this group of wasps (Grissell 1999; Sharkey and Fernández 2006; Forbes et al. 2018; Stork 2018).

Despite this deficit in knowledge, economically important groups are relatively well studied, such as the chalcidoids (Hymenoptera) Trichogramma Westwood (e.g., Pinto 1999; Borghuis et al. 2004; Zucchi et al. 2010; Parra and Coelho 2019; Querino and Zucchi 2019), Encarsia Foerster (e.g., Heraty and Polaszek 2000; Manzari et al. 2002; Gebiola et al. 2016a, 2016b), and Gonatocerus Nees (de León et al. 2004, 2006; Vickerman et al. 2004; Triapitsyn 2006; Triapitsyn et al. 2010; Huber 2015). These taxonomic studies have clarified the identity of the species, often based exclusively on morphological characters, regardless of the minute body size of these wasps. Likewise, geographic distributions are better known for species of economic importance. For Braconidae (Hymenoptera), for instance, the two species with the most records in Brazil (Yu et al. 2016), Doryctobracon areolatus (Szépligeti) and Opius bellus Gahan, are both important in the control of several tephritid fruit flies (Marinho et al. 2018).

Well-studied groups tend to have relatively more synonyms, as taxonomists may have different concepts or may fail to effectively communicate these concepts (Gaston and Mound 1993). A negative effect of focusing on species of economic importance is reflected in the large number of synonyms. For example, the species of aphids with the most synonyms listed in the catalog by Remaudière and Remaudière (1997) are widespread polyphagous agricultural pests, including Aphis gossypii Glover, Aphis fabae Scopoli, Aulacorthum solani (Kaltenbach), Brachycaudus helichrysi (Kaltenbach), and Myzus persicae (Sulzer), with more than 30 and up to 47 junior synonyms (Miller and Foottit 2009). Besides polyphagy, morphological variations on different hosts, and difficulties in communication among researchers, including access to type material (Hunter 1901; Ilharco and van Harten 1987), economic interest is largely responsible for these high numbers. These long lists of synonyms may obscure species identification, due to the concatenation of all associated ecological records and other aspects, or hide relevant intraspecific variation that can only be revealed by an integrative approach, as done for B. helichrysi for example (Piffaretti et al. 2012).

The same is true for parasitoids (see the example of the *Peristenus pallipes* complex in the section "Recent

examples"); and for associations, the issue reaches another level of complexity. Noves (1994) reviewed the reliability of host-parasitoid association data and demonstrated that most records, including many for wellknown species such as Cotesia glomerata (L.) (Hymenoptera, Braconidae) and its hosts, or Plutella xylostella (L.) (Lepidoptera, Plutellidae) and its natural enemies, were in fact incorrect. For a parasitoid widely used in biological control such as Lysiphlebus testaceipes (Cresson) (Hymenoptera, Braconidae), with many known synonyms (21) and dozens of recorded hosts, including A. gossypii and A. fabae (Yu et al. 2016), it is highly probable that a significant portion of reported associations are observation errors (Bin et al. 2012). One of the most important issues in biological control that arises from the existence of polyphagy as well as large numbers of cryptic species and synonyms was examined by Derocles et al. (2016) in the article "Are generalist Aphidiinae (Hym. Braconidae) mostly cryptic species complexes?" The frequency of such cases in economically important species makes catalogs even more important, especially catalogs for natural enemies that include their host associations, such as those for Ichneumonoidea (Yu et al. 2016) and Chalcidoidea (Noyes 2019).

One final issue involving taxonomy and economically important species (i.e., pests and their natural enemies) is their higher likelihood of crossing natural barriers and colonize areas outside their original distribution aided by human action. This poses a challenge for taxonomists, especially when the species in question belongs to a group (e.g., a genus) with a cosmopolitan distribution and an inadequately documented introduction history. Species might be described for the first time from individuals that formed populations outside their native range, as in the case of the Chinese mealybug Ceroplastes sinensis Del Guercio (Hemiptera, Coccidae), an important citrus pest with worldwide distribution, eventually discovered to be native to Argentina (Qin et al. 1994). Similarly, the important orchid pest Contarinia maculipennis Felt (Diptera, Cecidomyiidae) was first described in Hawai'i but later found to be native to Southeast Asia (Gagné 1995; Uechi et al. 2003). For cosmopolitan species such as Pachycrepoideus vindemmiae (Rondani) (Hymenoptera, Pteromalidae), the center of origin and how they spread across the planet remain unknown (Shimbori et al. 2020). Obviously, such situations may hinder any search for biological control agents within the native range of the target pest. Furthermore, the recent profound changes in international transit of species through human actions, including the intentional introduction of biological control agents, require even greater collaboration among taxonomists, applied entomologists, and regulators, as discussed below.

Changes in biological control, the role of regulations, and impacts on taxonomy

The advent of stronger restrictions on the introduction of exotic biological control agents around the world has changed the biological control landscape (Heimpel and Cock 2018). On one hand, we have a drastic drop in new introductions and therefore in the number of new classical biological control programs. On the other hand, we now have an incentive to search for native organisms that can be used in other methods of biological control (Cock et al. 2010). This process has important consequences for the relationships between biological control and taxonomy.

Classical biological control

With the widespread concern that biological control agents introduced outside their native range could negatively impact non-target populations, there has also been a shift in focus from classical biological control to other methods. Initial discussions on the relationships between taxonomy and biological control (e.g., Clausen 1942; Sabrosky 1955; DeBach 1960) took place at a time when classical biological control was the predominant approach, and less consideration was given to other methods. Currently, classical biological control faces numerous obstacles and has ceded its prominence to applied and, to a lesser extent, conservation biological control.

Two articles by Francis Howarth (1983; 1991) and the Convention on Biological Diversity (CBD 1992) are important milestones, as they reflect increasing awareness of the risks of classical biological control and the negative effects of invasive species on global biodiversity. Classical biological control is by definition an intentional introduction of an exotic agent that can establish in a new area and regulate populations of pest species in the long term (Eilenberg et al. 2001). The change in perception regarding the introduction of exotic species (Heimpel and Cock 2018) is associated with a drastic reduction in the number of new introductions from the 1980s onward, as demonstrated by Cock et al. (2016), as well as greater specificity of the agents introduced (Van Driesche and Hoddle 2016). In response to concerns raised, Food and Agriculture Organization (FAO) of the United Nations published the Code of Conduct for the Import and Release of Exotic Biological Control Agents (ISPM3) (FAO 1996), which led to significant advances in regulations, especially in developing countries (Kairo et al. 2003). More recently, the Nagoya Protocol on Access and Benefit Sharing (CBD 2011) also significantly affected the transit of organisms between countries (Cock et al. 2010). The restraints that

surfaced after the signing of the Convention on Biological Diversity (CBD) impacted the exchange of natural enemies all over the world, as national regulations struggle to adopt the international standards for access to genetic resources and for export/import of live organisms (e.g., Coutinot et al. 2013).

As best practices for biodiversity protection, countries have adopted rules and regulations that favor selection of biocontrol agents that do not pose a risk to local biota, usually because they are highly prey/host specific or because they are not able to establish self-perpetuating populations, through implementation of regulatory procedures that include some kind of risk assessment (Barratt et al. 2010). Currently, risk assessments are mandatory in several countries, and should be mandatory in Brazil as well (Shimbori et al. 2022). Adaptation of regulations and legal restrictions for new imports is important to limit the impacts of new invasions. Hajek et al. (2016) commented that the lack of specific regulations has been a problem for microorganism biocontrol agents (viruses, bacteria, fungi, and nematodes), and highlighted the importance of the FAO ISPM3 guidelines (FAO 1996). In Brazil, since publication of the normative instruction IBAMA No. 5 (IBAMA 2016), importing exotic agents without already-established populations in this country requires a risk assessment by the national authority. Since the protocol for risk assessment is not yet established, currently there are no legal means to import a live organism for biological control. The road leading to an effective regulatory process is still long and winding for most nations, especially when harmonization among countries of economic blocs, for example, the Comitê Regional de Sanidad Vegetal del Cono Sur (COSAVE, South America) and the European and Mediterranean Plant Protection Organization (EPPO, Europe), is necessary to achieve this goal (Bale 2011). Geographically isolated countries and blocs made up of fewer countries, such as Australia and New Zealand and the North American Plant Protection Organization (NAPPO, North America), have more advanced regulatory processes (Hunt et al. 2008; Barratt et al. 2018a), in part because of the lower complexity involved.

With the exponential increase in international trade and the intensification of international travel, the resulting high propagule pressure tends to increase the rate of biological invasions (new introductions followed by colonization, expansion of the distribution area, and impacts on native populations) (Simberloff 2009). According to Pimentel et al. (2001), there are at least 120,000 invasive species of plants, animals, and microbes, which constitute one of the main threats to global biodiversity and are causing economic losses of over USD 300 billion annually, for only the six countries evaluated in that study (USA, UK, Australia, South Africa, India, and Brazil). The Invasive Species Specialist Group (ISSG 2018) concluded that the present context may stimulate countries to adapt their rules for importing natural enemies, so that the advantages afforded by classical biological control as a method of combating invasive species, whether by microorganisms or macroorganisms, can be used to the fullest. Lack of taxonomic knowledge of the biological control agents can delay the development of new biological control programs (Maddox et al. 1992; Zucchi 2002), a situation that may be aggravated by inadequate knowledge of the local biota and the low frequency with which pre- and post-introduction monitoring is conducted (Hoddle 2004; Barratt et al. 2006; Hajek et al. 2016).

Therefore, with the intensification of problems associated with biological invasions, an increasingly close collaboration among researchers in different areas of knowledge, i.e., taxonomy, biological control, and ecology, especially conservation ecology (e.g., invasion biology, niche modeling), regulators, and decision-makers will also be necessary. Experiences in earlier classical biological control programs that lacked stronger taxonomic studies, which resulted in failure or non-target impacts, have impacted the perception of these programs so that they are not seen as desirable options and are generally discouraged by regulations and agencies alike. However, international trade continues to intensify, with a consequent rise in introduction rates. As more invasive species are introduced, an increase in demand for classical biological control will follow, as the only viable solution for control in many cases, and this will not be limited to agricultural pests. The role of taxonomy and biological control in this scenario involving the import and release of natural enemies is crucial, due to the increased need for safer and sustainable solutions for the environmental, social, and economic risks imposed by biological invasions, including decreases in food supply, biodiversity, and health security (ISSG 2018).

Applied biological control

Applied biological control, especially inundation biological control, is growing rapidly, which may be associated with the necessity for replacement of the classical model, but also with the possibility of offering both sustainability and profitability at the same time. Even though this method was attempted as early as 1899 in Europe (Decaux 1899), and mass rearing was first used methodically in about the 1930s, in most regions, research on applied biological control as an alternative gained traction around the 1960s (DeBach and Hagen 1964; Ridgway and Vinson 1977; Parra 2014). This growth is often attributed to a greater general awareness of environmental issues following the publication of *Silent Spring* by Rachel Carson (1962) (e.g., Gay 2012).

In Brazil, the biological control market is growing at a fast pace. From 2019 to 2020, the market value of biological control products increased by 42% and from 2020 to 2021

is estimated to rise 33%, for a total net value of BRL 1.8 billion (CropLife Brasil 2022). These numbers are headed by microbial products but arthropods are also following this trend, and with that, the need is also increasing for taxonomic knowledge to identify species and to discover new biological control agents that can be incorporated into production systems. Thus, we have a scientific and technological interaction that proceeds from taxonomy to the market.

Certain characteristics are more relevant for the agents used in applied biological control than for those in classical biological control. Host specificity and establishment, for instance, are not considered necessary or even desirable. Although a few studies have sought to determine the impacts on non-target species, applied control tends to be considered safer, since it can use native species and establishment of self-perpetuating populations is not necessary, therefore having only transient impacts (Lynch et al. 2001; Kuske et al. 2003; Loomans 2021). However, Lynch et al. (2001) noted, based on a literature review, that effects on populations of non-target species are relatively frequent and that in 8% of cases they can be severe (i.e., reducing non-target populations by 40% or more). Therefore, before implementing this method, it is necessary to ensure that any impacts are in fact transient, by using either a non-establishing exotic agent or native agents.

Between 1980 and 2010, applied control developed into a highly organized industry, with at least 230 species available for commercial use; however, the total area treated is still very small, with enormous potential for growth (Collier and Van Steenwyk 2004; van Lenteren 2012; Parra 2014). Taxonomy is essential in helping to prospect for native biological control agents for mass rearing, avoiding the risks of unsuccessful imports, and feeding a rapidly growing industry. More attention to monitoring possible impacts is still needed and naturally must rely on collaborations between taxonomists and applied entomologists.

Regulating agencies also use taxonomic information for applied control. Licenses and registrations of biological agents for commercial use invariably depend on some confirmation of their taxonomic identity, and in many countries, applications are reviewed by experts, including taxonomists (e.g., Mason et al. 2017). In addition, voucher specimens are required to be deposited in permanent entomological collections to ensure that the identity of the registered organism can be reviewed in the future, should the need arise. In Brazil, the Joint Normative Instruction No. 1 of 2019 (MAPA/ANVISA/IBAMA 2019) requires specimens identified by taxonomists to be deposited in accredited collections in order to register an agent.

Another regulatory aspect of applied biological control is the need for quality control of products (natural enemies) produced and sold by companies, which must also be guaranteed by taxonomists. Taxonomic identifications are a necessary step in good-practice protocols for laboratories that produce biological control agents. In addition to consultations and reports by experts, rapid identification techniques can be very useful in certifying mass-reared insects, such as Loop-mediated isothermal amplification (LAMP) and Multiplex PCR, among others. These techniques have been used to identify agricultural pests, particularly groups that are difficult to identify accurately, such as *Helicoverpa* Hardwick (Lepidoptera, Noctuidae) (Amano and Nomura 2020), as well as for mass-reared natural enemies such as *Trichogramma* spp. (Dang et al. 2005; Davies et al. 2006; del Pino et al. 2013; Gonzales-Cabrera et al. 2014; Ivezić et al. 2018, 2021), and will be discussed in more detail in the section "Molecular tools for rapid identification."

The relationship between applied biological control and taxonomy is as important as in classical control. This relationship provides an opportunity for collaboration between the two fields of research and a growing industry providing sustainable solutions for pest control. Two cases involving Trichogramma parasitic wasps illustrate the importance of this closer collaboration. First, Trichogramma galloi Zucchi has become one of the most common commercially produced species in Brazil, thanks to an exemplary model of close collaboration between taxonomy and biological control, as documented by Zucchi (2002). Second, in contrast, identification problems led to the unintended mass rearing and release of 300,000,000 individuals of Trichogramma fasciatum (Perkins) annually for 20 years to control Diatraea saccharalis (Fabricius) (sugarcane borer) in Barbados, because the populations had been mistakenly identified as Trichogramma minutum Riley (Gordh 1977).

Conservation biological control

The central priority of conservation biological control is to create a more complex and diversified agroecosystem conducive to beneficial interactions (Gliessman 2005). The ecological role of biodiversity in agroecosystems is the primary focus of research in this area (Altieri and Letourneau 1982; Andow 1991; Altieri 1999). Methods for conservation biological control are based mainly on culture techniques of habitat manipulation to improve control by the local fauna of natural enemies or by inducing different responses of herbivores to plant diversity (Gurr et al. 2004; Fontes et al. 2020). Conservation biological control is considered an excellent alternative to foster more sustainable agroecosystems, as it requires lower levels of input and promotes higher diversity. However, as this is a complex strategy operating on multiple scales, many issues affecting suppression by natural enemies must be considered and possible limiting factors identified for effective application (Gillespie et al. 2016; Begg et al. 2017). The higher diversity in these agroecosystems requires greater taxonomic knowledge, which may be a limiting factor per se.

As social demands on sustainable production increase (Tracy 2014; Altieri and Nicholls 2020) and options for classical biological control have become restricted, conservation biological control tends to play a larger role in agroecosystems, relying on collaborative research in ecology (including natural enemy dispersal, habitat connectivity and other landscape effects, and trophic interactions), chemical ecology, genetics, insect behavior, and socioeconomic aspects, among others. This multidisciplinary area, encompassing such a vast array of disciplines, is necessarily based on taxonomy, which is essential for recognition of the species of natural enemies and insect pests present in the systems. A vast literature has addressed this ecological service through conservation biological control (for example, Gliessman 2005; Venzon et al. 2021), which has taxonomy as a basic foundation for increasing functional biodiversity.

Current status of the biological control-taxonomy relationship

In general, laws regulating the import and release of biological control agents were tightened from 1980 to 1990. With the possible exception of New Zealand and developing countries where the use of biological control is more recent and the adoption of FAO's ISPM 3 has facilitated regulation (Kairo et al. 2003), it has become much more difficult to introduce exotic species worldwide, including for biological control purposes. Even countries with advanced legislation require lengthy import control processes. Although the number of new introductions has decreased drastically since the 1990s, an increase may become possible after scientific advances in the area, in response to current demand. For example, considering applied biological control in this situation, a company could be discouraged from importing a species with a ready (foreign) technological package, due to the many regulatory requirements. An illustrative example, in this case with a pollinator, is the import and release of the bumblebee Bombus terrestris (L.) (Hymenoptera, Apidae), native to Eurasia and Northern Africa, into South America (Smith-Ramírez et al. 2018; Fontúrbel et al. 2021). After being repeatedly introduced in Chile, it has invaded Argentina and may reach Brazil and Uruguay (Acosta et al. 2016), even though its import was rejected in these countries (Velthuis & van Doorn 2006). This demonstrates the importance of laws that regulate the entry of exotic species (Aizen et al. 2019) and the consequent incentive to prospect for native species, as exemplified by a research grant for bioprospecting Brazilian species of Bombus Latreille for pollination in agriculture, awarded in 2018 by the State of São Paulo Research Foundation (FAPESP) (FAPESP no. 16/21555–9; available at https://bv.fapesp.br/pt/auxilios/ 100336/abelhas-bombus-para-programas-de-agricultural-pollination-bioprospection-of-native-species-of-Brazil/).

Importations of non-native Trichogramma species furnish other examples, because studies on the local fauna of many regions are still incipient, even though this knowledge would be important for furthering the use of Trichogramma in biological control programs (Querino et al. 2010). In almost all habitats, native species adapted to local conditions are already present, an indication that natural parasitism by Trichogramma could be high (Pinto 1999). Cock et al. (2010) confirmed a trend toward an increase in the use of native species. Based on the European market, the authors found that the proportion of native species used for augmentative control grew from 42% in 1960-1989 to 76% in 2000-2009. These trends in the European market may be followed in other parts of the world as regulations became increasingly restrictive, encouraging improvement of taxonomic knowledge and adaptations from the applied biological control industry.

An excellent recent example involving invasive pests, exotic biological control agents, and regulations illustrates how the current situation increases the importance of closer collaboration between applied entomologists and taxonomists. The Asian brown marmorated stink bug, Halyomorpha halys (Stål) (Hemiptera, Pentatomidae), became a serious pest after it became established in Europe and the USA. A classical biological program was initiated in 2005 in the USA by Kim Hoelmer and collaborators, who found an excellent candidate biocontrol agent in Asia, the samurai wasp, Trissolcus japonicus (Ashmead) (Hymenoptera, Scelionidae) (Conti et al. 2021). Years of research in a quarantined facility apparently did not generate data indicating that the samurai wasp could be released in the USA without risks to the environment, which is estimated in terms of non-target effects (Louda et al. 2003). However, in 2014, T. japonicus was found in Maryland (Talamas et al. 2015), as a result of Hoelmer's collaboration with a team searching for native parasitoids on stinkbug eggs (Buffington et al. 2018). This serves as a warning that natural enemies might be inadvertently introduced along with their hosts and of the need for regulations that allow timely screening and assessment of safe and efficient agents, especially considering the increasing flow of international trade. This also shows that close collaboration between a taxonomist and applied entomologists was essential while searching for native agents for biological control. Moreover, this illustrates the role of government agencies and national authorities in plant protection, providing the structure and organization necessary for this relationship to flourish.

The above examples demonstrate the incentive for taxonomy related to native natural enemies. We believe this is a transforming force to strengthen this research field and its relationship with biological control. However, considering the "unnaturally" wide distribution range of many pests and other anthropophilic species, more attention is needed in situations where exotic species are already adapted to a new environment. As border control and quarantine lists are prepared to detect invasive species, natural enemies may also become invasive and identification of species originating from another part of the world may be difficult for many reasons, mostly related to the lack of taxonomic studies. Molecular markers may be the best tools for aiding taxonomy and biological control in such cases.

In conclusion, the legal restrictions intended to protect biodiversity that hinder or prevent importation of species obviously affect efforts for classical biological control, but also impact applied biological control, since the search for solutions would be more and more pushed toward native (or exotic established) species, as the risk assessment and monitoring procedures for introduced species, when they exist, are lengthy and costly. However, for taxonomy, this seems to be a very favorable scenario for further prospecting work that will necessarily involve greater knowledge of the local fauna, and therefore a greater demand for taxonomists. Similarly, regarding the examples of *Bombus terrestris* and Trissolcus japonicus, when prospecting for native agents was encouraged, further incentives in this direction should be expected. This is a very positive situation for conservation biological control, as it does not use exotic species and depends on knowledge of native species, which will be encouraged.

Molecular taxonomy and databases

Molecular markers and their public databases are currently considered highly useful tools in several areas of knowledge. Much of this usefulness relies upon correct association between names and genetic sequences (Schoch et al. 2020). As Strasser (2008) commented, public databases and the use of molecular markers in taxonomy have led to a convergence of natural history practices and the experimental sciences. DNA barcoding, the most prominent of molecular markers used in studies of insects, was proposed originally with the aim of becoming a universal tool for identifying eukaryotic organisms, at the species level, from a DNA sequence (Hebert et al. 2003a). For identification, barcoding would depend on the construction of a database to store sequences of all described species, as well as species not yet described, called the Barcode of Life Database Systems (BOLD Systems) (Ratnasingham and Hebert 2007). This and other molecular markers, and more recently genome-scale studies based on Next Generation Sequencing (NGS), have revolutionized taxonomy, in particular allowing highly refined species delimitation and reconstruction of phylogenies with maximum support, based on a previously unimaginable amount of information. This revolution obviously has profound consequences for collaborations among taxonomists, molecular biologists, and applied entomologists.

S.E. Miller (2007) called the advent of the DNA barcode a taxonomy renaissance. In the area of applied entomology, barcoding could make identification faster and more accessible to anyone, even in the field. To make available such a free tool, for example, via an internet-content search engine such as Google, would require a large investment in developers and means of generating profits that would be reinvested in further development. The main "developers" of these databases are taxonomists who curate information by associating names with DNA sequences based on examination of voucher specimens, and then generating reference sequences that are the basis of DNA barcoding. However, and as is recognized as a bottleneck in barcoding logistics (Borisenko et al. 2009), taxonomists do not receive due recognition for their work or, usually, any kind of compensation. It would be useful for the investment strategies in what S.E. Miller (2007) called the "Taxonomic Enterprise" to be restructured, in order to value and promote taxonomic curation so that all the benefits of public databases could be fully achieved.

Despite the herculean, and essentially impossible, task of sequencing all living species, scientists are increasingly using and expanding the data available for these markers, and the main databases are growing exponentially. DNA barcoding alone (COI) reached 2.5 million sequences in 2018 in the GenBank database (Porter and Hajibabaei 2018), while BOLD reached 11 million COI sequences in 2022, representing approximately 385,000 described species (BOLD 2022) and constituting an invaluable information resource for science. These numbers, although impressive, show that most species are still not represented. The lack of reference sequences is a major problem that is even worse for many poorly known taxa, even at high taxonomic levels. Initiatives to mitigate this problem have emerged, with the potential to use museum specimens (Santos et al. 2022).

An important difference between the BOLD and Gen-Bank databases, which are the two main public databases for DNA barcoding, is that BOLD can be considered a sequence curation tool while GenBank is a repository (Meiklejohn et al. 2019). The issue is recognized by the community, and efforts to improve annotation errors have been proposed for GenBank, but the quality still depends on accuracy and updates from submitters (Bidartondo et al. 2008; Schoch et al. 2020). The few studies reviewing the reliability of the databases regarding taxonomic identification have described some worrying trends. For example, studies on fungi found that 80% of the sequences lack reference vouchers (Bridge et al. 2003; Nilsson et al. 2006). Even with the stricter requirements of BOLD, Meiklejohn et al. (2019) calculated a relatively low accuracy for insect identification ($\sim 35\%$), lower than the GenBank BLAST tool (53%). Thus, although there is a premise that the deposited sequences should be obtained from voucher specimens identified by an expert, the chance of error when using these databases cannot be ignored, as they are public databases. The lack of association between sequences and taxonomic names, whether due to misidentification, lack of comparison with morphologically described species, or simply not assigning a name, is a problem that needs to be addressed and systematized in order to achieve reliability in the use of databases. The debate on this and other points relative to the use of molecular markers in taxonomy is quite intense and extensive (e.g., Meyer and Paulay 2005; Cameron et al. 2006; Begerow et al. 2010; Zhang et al. 2012). The present discussion serves merely to note that end users, applied entomologists especially, should remain aware of these faults, without discouraging the use of markers, as the advantages of this genetic information within the scope of biological control outweigh any of the shortcomings and may not be directly affected by them if the data are treated with due care.

Examples of identification problems in databases are very common-what Collins and Cruickshank (2013) call the "second sin" of DNA barcoding-and can slow the progress of biological control research in very harmful ways. In a recent survey, we found that the name Trichogramma pretiosum Riley, which corresponds to a well-studied species for applied biological control of several of lepidopteran pests, is attributed to 6 distinct molecular taxonomic units (MOTUs) according to the Barcode Index Number (BIN), which could be equivalent to species, for only 75 deposited barcodes. For Telenomus podisi Ashmead (Hymenoptera, Scelionidae), a parasitoid that has been intensively studied for the control of pentatomids, the number of BINs reaches 13 for the~3600 barcodes deposited. Therefore, an unambiguous identification based on DNA barcoding is currently impossible, as is determining which of these MOTUs corresponds to the original names Tr. pretiosum and Te. podisi. It is likely that control programs are being conducted with incorrectly identified wasps, or even that other species are being identified under the names Tr. pretiosum and Te. podisi. Again, the question "What difference does it make, if control is reached?" is pertinent. Among the numerous problems, we can mention the erroneous accumulation of information about biology, ecology, and distribution linked to a species, when this information actually refers to other species. This can lead to a false impression of polyphagy and consequent interruption of classical biological control programs, or even to the attempt to use an agent in applied control of a pest outside the host range of the agent. To put it into perspective, this is exactly the type of problem described by researchers in the past (e.g., Clarke 1993). Howarth (2000) cited the example of sciomyzid flies introduced into Hawai'i for snail control. The program, aiming to introduce the marsh fly Sepedon sauteri Hendel (Diptera, Sciomyzidae), ended up introducing 11 species of flies, and reexamination of the vouchers showed that none of them seemed to be *S. sauteri* (Hardy and Delfinado 1980). Because a permit was issued for that species, there would be no problem with future introductions of *S. sauteri*, even if the actual species has not established. Well-curated reference sequences would prevent these problems.

Besides identification, DNA barcoding has also been used in taxonomy as a tool for species delimitation and is regarded as a fundamental link between traditional taxonomy and the "DNA world" (Hubert and Hanner 2015). However, contrariwise, there is a lack of connection between the "traditional" taxonomy and the "molecular" taxonomy along the lines proposed by Sharkey et al. (2021), that is, replacing the entire description with only a genetic sequence, a couple of photographs and a list of material examined, which seems worrying to us. Generating and analyzing sequences that are considered unique and assigning names to these sequences could drastically accelerate knowledge of biodiversity (Godfray 2002; Hebert et al. 2003b). However, applying the methods used by Sharkey et al. (2021) would generate this knowledge at the expense of loss of centuries of scientific history, as the names and all scientific research linked to these names cannot be accessed for species without available molecular markers. Unfortunately, this is still the case for the vast majority of species already described (see, however, Santos et al. 2022). Meier et al. (2022) discussed the issues of the approach taken by Sharkey et al. (2021), pointing to the increasing availability of large throughput imaging and sequencing, and the advances in algorithms that can integrate multiple sources of data, as sound solutions for the taxonomic impediment, by providing taxonomists with a solid foundation for species descriptions.

There are serious criticisms of the way that taxonomic units are delimited based on molecular markers, and whether there is coherence between these methods and species concepts, so that species can be explicitly delimited by comparison of their genetic sequences (e.g., DeSalle et al. 2005; Meier et al. 2006; Rubinoff et al. 2006; Lowenstein et al. 2009; Zamani et al. 2021). Therefore, combination of different models with transparency and reproducibility of the methods is strongly recommended (Meier et al. 2022). Additionally, a combination of multiple loci may be necessary for delimitation (Heraty 2004, 2009). Some examples from parasitoids, such as the Peristenus pallipes complex (Zhang et al. 2012), the Aphelinus varipes complex (Heraty et al. 2007), and certain species of Trichogramma (Stouthamer et al. 1999; Pinto et al. 2002, 2003; Cruaud et al. 2018, 2019), demonstrate that divergence in a single gene region may not correspond to reproductive isolation, and even the use of more than one region may not be sufficient (e.g., Zhang et al. 2017), requiring further mating-compatibility studies in different populations (e.g., Vickerman et al. 2004).

These problems are inherent to the field of taxonomy, in regard to the evolutionary process and its multiple levels, and demonstrate that in many cases there is no simple solution other than a closer collaboration among scientists in several fields, including taxonomy, ecology, evolutionary biology, applied entomology, and even behavioral ecology.

Criticisms aside, it would be extremely advantageous, not only from the point of view of biological control, if the taxonomic challenges posed by all pests and biological control agents could be solved by obtaining a DNA sequence. The entire movement around the development of these markers, such as DNA barcoding, revolves around this possibility. The identity of an organism, however, depends on the taxonomic work involved in attaching the name to the marker. Without this work, the only possible statement is that the sequence obtained is equal to some, or different from all, of the sequences deposited in the databases. Therefore, it makes no sense to name sequences, and so taxonomic work remains relevant in all its complexity. This is a long-standing discussion (e.g., Tautz et al. 2003; Lipscomb et al. 2003; Wheeler and Valdecasas 2005; Hickerson et al. 2006; Carvalho et al. 2007; Packer et al. 2009; Zamani et al. 2021) that is beyond the scope of the present article, although some points are still controversial. However, it is necessary to point out that solutions such as DNA taxonomy or cybertaxonomy are proposed to accelerate taxonomy but depend on the growth of taxonomic foundation. Therefore, we agree with Carvalho et al. (2005) and Engel et al. (2021), in that fighting taxonomic impediment instead of creating shortcuts for the lack of taxonomists is the only way to achieve meaningful goals for any science based on biodiversity.

In the context of biological control, we can imagine a scenario that illustrates the possibilities and limitations of using molecular markers and databases, as follows:

Imagine a Brazilian research group that finds a natural enemy with high potential for use in biological control. The species cannot be identified immediately, so the first step is to obtain sequences from a molecular marker, and here the DNA barcode is chosen. The sequence is compared to the sequences in BOLD and GenBank and an identical sequence is found. The researchers, here in Brazil, discover that the other sequence was deposited by researchers in South Africa. Both groups are studying the same pest, which has a worldwide distribution, and the parasitoid apparently dispersed along with the pest. The two groups begin to exchange information and develop an international research program for mass rearing and release of this natural enemy. Groups in Europe and Australia are are evaluating the possibility of importing specimens for introduction. Finally, the only active taxonomist specializing in the taxon responds to the

request to identify the parasitoid. While in the process of retiring, he receives the material and responds with a name and a publication attached: "This species, Aa aa, described by me 40 years ago, is present in all biogeographic regions (except Antarctica) and was introduced from Europe to the Americas, Africa, and Australia. It was studied for decades without success for the control of the target pest. In the 1990s the studies were abandoned because its release did not result in a significant reduction of the pest populations." Most programs did not keep specimens and the only voucher specimens from these research programs are in very poor condition and scattered in collections around the world, except for material studied by the taxonomist. In conclusion, applied entomologists should use protocols similar to those followed by insect collectors, that is, collecting, assembling, tagging, and preserving specimens, which will be of great value in any biological control programs that may be implemented at any time.

An inherent advantage in comparing molecular markers is their universality and accessibility. The process of detecting that the same entity occurs at isolated points on the planet is fast and reliable. In the above hypothetical example, this could immediately draw researchers' attention to the disjunct distribution, possibly reflecting human action. This feature is very useful, especially for species that live in proximity to or associated with anthropic environments, such as pests and their natural enemies (Andersen et al. 2019).

If, in this hypothetical example, the natural enemy species had been given a second name, Aa bb, in a taxonomic study based exclusively on molecular markers, the problem would not have been noticed. The species would be identified as Aa bb by the association between the marker and the name; however, all previous knowledge of the species Aa aa would be ignored and there would even be a risk of attributing the origin of the species to a place where it was introduced. Even if it were technically possible to mass-rear and release such a species with modern techniques, the valuable knowledge already generated would have been wasted. Likewise, if the sequences in databases had been incorrectly assigned to a different species, all sorts of problems related to misidentification could follow. As DeBach (1960) commented, "a natural enemy species, perhaps undescribed and new to science, but wrongly given the name of a described species, may be as effectively hidden as if it was never collected."

NGS and museomics

The increasing ease of obtaining genome-scale data following rapid advances in High Throughput Sequencing technology is generating new and exciting possibilities (e.g., Wen et al. 2017). Some have claimed that this new genomic era could mean the end of DNA barcoding (Taylor and Harris 2012; Joly et al. 2014), while others have highlighted the complementarity of genomics and DNA barcoding (Grant et al. 2021). In fact, most of the applications of genomics in taxonomy are related to the reconstruction of phylogenies, improving our understanding of the evolution of life and consequently our classifications. This knowledge can be particularly important in risk assessments, as discussed by Barratt et al. (2018b). It is possible, however, for an extended concept of DNA barcoding to integrate genomic data (Coissac et al. 2016). For example, Allio et al. (2020) developed a pipeline for mitogenomic data extraction from UCE (Ultra Conserved Elements) libraries, retrieving COI barcoding and confirming identifications with 100% success. As demonstrated by Cruaud et al. (2019), it is now possible to generate genomic data from minute parasitoids, which can be important for molecular taxonomy in support of biological control.

The emerging field of historical DNA or museomics is being supported by NGS techniques (Raxworthy and Smith 2021), for example, Target Enrichment using UCE, because of the high rates of success for degraded samples (Blaimer et al. 2016; Zhang et al. 2019). Mini-barcodes have also proved useful for museum specimens (Van Houdt et al. 2010). Research in this area will be essential to fill the gaps in reference sequences in DNA databases for described species, improving both species identification and discovery.

Molecular tools for rapid identification

Numerous diagnostic methods based on molecular-biology techniques have been developed in the last two decades. Some have recently become popular because of their usefulness in diagnosing COVID-19 (Amaral et al. 2021), such as LAMP (Loop-mediated isothermal amplification), developed for rapid amplification of DNA with high specificity using six different primers (Notomi et al. 2000). LAMP is currently considered one of the most versatile methods for identifying organisms, as it does not require equipment for electrophoresis or real-time monitoring. This method is accurate, inexpensive, and can be used for on-site identification, such as during monitoring surveys (Notomi et al. 2015). Other examples are PCR-RFLP and multiplex PCR, which can distinguish among numerous target species with conventional PCR equipment but are not adapted for large samples. On the other hand, real-time PCR and ddPCR are excellent alternatives for rapid analysis of multiple samples but require expensive equipment (Amano and Nomura 2020).

These methods are increasingly used to identify pests and invasive species. LAMP, for example, is being used to identify quarantined species on-site (von Felten 2017, in Switzerland), especially fruit flies (Blaser et al. 2018; Sabahi et al. 2018; Blacket et al. 2020; Kitano and Takakura 2020; Dermauw et al. 2022), using a portable device. LAMP is also helpful for field identification, especially when specimens cannot be reliably identified using traditional methods (e.g., a stage or sex is not morphologically useful for accurate identification): Agarwal et al. (2020; 2022) for the fall armyworm, Spodoptera frugiperda (J.E. Smith), and the grape phylloxera, Daktulosphaira vitifoliae (Fitch); Rako et al. (2021) for the Khapra beetle, Trogoderma granarium Everts. All these methods only detect predefined targets for which the primers need to be designed, and may not be sensitive for some lineages such as biotypes (e.g., Hsieh et al. 2012). Therefore, development of tools for biological control, and more broadly for integrated pest management (IPM), requires close collaboration between taxonomists and molecular biologists.

The same technology can be used to detect infections by Wolbachia (Gonçalves et al. 2014) and other symbiont bacteria that might reduce the ability for establishment and biological control due to cytoplasmic incompatibility (Sinkins et al. 1995). The ability to detect infections is guite useful, considering new introductions and the effect of bacterial symbionts on the life history of their hosts, as exemplified by the introduction of *Encarsia* spp. into the USA (Gebiola et al. 2016b). This example involves a complex taxonomic history of two cryptic species, Encarsia inaron (Walker) and E. partenopea Masi, both introduced into the USA as populations from two different localities, but under the same name. Gebiola et al. (2016b) demonstrated not only that these are two species, but also that they are infected by different bacteria, causing cytoplasmic incompatibility, one by Wolbachia and the other by Cardinium. This case draws attention to the risks of mixing populations with different bacteria that may cause reproductive failure, or any important change in fitness, in imported biological control agents. Luckily, the populations imported into the USA were from two different, reproductively isolated species, and that particular biological control program is considered a textbook example of success.

Rapid molecular diagnostics is useful for quality control in biofactories. For parasitoids, most published studies have used Multiplex PCR for rapid identification of *Trichogramma* species (Dang et al. 2005; Davies et al. 2006; del Pino et al. 2013; Gonzales-Cabrera et al. 2014; Ivezić et al. 2018, 2021), with some exceptions in Braconidae (Gariepy et al. 2005) and Encyrtidae (Rugman-Jones et al. 2011). Studies with LAMP are more recent, and this technique is more widely used in pest detection (e.g., Jenkins et al. 2012), with some examples for parasitoids such as the study by Nam et al. (2022) to identify two species of *Diadegma* Foerster (Ichneumonidae) that parasitize the diamondback moth, *Plutella xylostella*.

Recent examples

Numerous control programs have demonstrated the importance of population-level studies in the evaluation of agents. This has been discussed since the first papers on the relationship between taxonomy and biological control (e.g., Sabrosky 1955). A classic example of the importance of considering strains and populations in biological control occurred in New Zealand, when the beetle parasitoid Microctonus aethiopoides Loan (Hymenoptera, Braconidae) was imported and released at two different times, to control two different pests, and achieved different outcomes, demonstrating the importance of taxonomy in risk assessment for biological control. The first strain has a broader host range and had success in controlling the lucerne weevil, Sitona discoideus Gyllenhal (Coleoptera, Curculionidae) (Goldson et al. 1990; Ferguson et al. 1994; Barratt et al. 2018b), but commonly attacks native species (Aeschlimann 1995; Barratt et al. 1997). The second strain was imported after careful risk assessment, has a narrow host range, and achieved relative success in controlling the clover root weevil, Sitona obsoletus (Gmelin), with no significant non-target effects (Goldson et al. 2005; Gerard et al. 2011; Basse et al. 2015). Since the early studies, infraspecific variation within M. aethiopoides has received some attention (e.g., Aeschlimann 1983a, 1983b; Adler and Kim 1985), although not primarily concerned with host range and non-target effects (Aeschlimann 1980). The difference in outcome related to non-target effects can be attributed to considerably better knowledge of the parasitoids' infraspecific taxonomy, the phylogeny of its weevil hosts, the host preferences of each parasitoid strain (Phillips et al. 2008; Barratt et al. 2018b), and better regulation processes.

However, in taxonomic practice, the importance of the species as a fundamental unit predominates. Even if the species concept is well established, it may be insufficient to identify populations with desirable characteristics for biological control. A more in-depth study may be needed to reveal cryptic species, biotypes, or populations with relevant adaptations. Therefore, integrative taxonomy that addresses intraspecific variation, using phylogeographic analyses, for example, can be decisive to achieve satisfactory results in a close collaboration between taxonomy and biological control (Huang 2020). A series of studies on Trichogramma has demonstrated the importance of data integration, not only for species delimitation and reproductive isolation within a species complex (e.g., Pinto et al. 2003), but also for demonstrating intraspecific variability in certain parasitoids, such as Trichogramma marandobai Brun, Moraes and Soares (Vieira et al. 2015) and Tr. pretiosum (Querino et al. 2002; Viana et al. 2021).

A study on euphorines (Hymenoptera, Braconidae) exemplified this situation using integrative taxonomy, where molecular data predominated in species delimitation (Zhang et al. 2017). The authors concluded that a complex of nine nominal species of the Peristenus pallipes group, previously delimited essentially based on ecology and morphology (Goulet and Mason 2006), was in fact composed of only three species. This conclusion has important consequences for biological control, as well as for the definition of conservation priorities, since the species as previously understood would have more-restricted distributions and host ranges. Zhang Y.M. et al. (2017) recognized the importance of studying the group at a population level, investigating microevolution within the complex. However, with current knowledge, it is impossible to determine whether at least some of the previously recognized species actually correspond to distinct populations or lineages. Likewise, although a complex of cryptic species that are notoriously difficult to distinguish were more clearly delimited, an even greater level of detail would be necessary to select biological control agents. We agree with Huber et al. (2021) that the classification proposed by Goulet and Mason (2006) may be more useful to select strains for biological control.

The taxonomic revision of Trichopoda Berthold (Diptera, Tachinidae) by Dios and Nihei (2020) reveals the complexity of this topic, as they showed that a group of species widely studied in biological control is a polymorphic species (quite the opposite of a group of cryptic species), while differentiating other species of this group, previously considered cryptic, based on morphology. The genus Trichopoda has a native distribution in the Nearctic and Neotropical regions. This recent revision demonstrated the extremely complex taxonomic history of the group, with 16 synonyms for Trichopoda pennipes (Fabricius), including names also used in biological control, such as T. giacomellii (Blanchard) (Dios and Nihei 2020). Trichopoda pennipes was supposedly introduced into several countries to control Nezara viridula (L.) (Hemiptera, Pentatomidae), a pest with worldwide distribution and important in numerous crops, especially soybean. Instead of the widely distributed and well-studied T. pennipes, the species that actually established populations in Europe was Trichopoda pictipennis Bigot (Dios et al. 2021). The entire history involving these species began a century ago, due to the interest in controlling a serious agricultural pest, and at that time the identity of accidentally introduced organisms had not been established. Notwithstanding, modern taxonomic studies have not been able to elucidate the nature of the populations and possible subspecies that compose T. pennipes, so that the differences among these lineages, which may be important for biological control, are still obscure. This example demonstrates the lack of studies on important and taxonomically challenging groups, as well as the limitation of taxonomic studies based only on morphology, without molecular and ecological data (Packer et al. 2009). Complex groups with cryptic and polymorphic species, and important differences at the infraspecific level, as in *Trichopoda*, should be studied using a combination of methods to clarify the extent of population and species diversity.

In the last two examples, the lack of close collaboration with applied entomologists may have rendered taxonomists less sensitive to the level of refinement required in biological control, which is often on the threshold between cryptic species and populations (subspecies) or geographic forms within a species with distinct biological characteristics such as preferences in oviposition and host range (e.g., Pinto et al. 2003; Goldson et al. 2005; Huang 2020; Seehausen et al. 2020). In view of the enormous gap in knowledge of species, which is considerably larger for parasitoids and microorganisms, and the taxonomic impediment, particularly the lack of professionals with training in taxonomy, taxonomists may find themselves faced with the need to decide between dedicating their time to detailing nuances of a species' microevolution or to revising a larger group such as a genus or tribe. Choosing the second option seems naturally more acceptable at this juncture. However, in some cases, taxonomists have been able to solve questions at the three taxonomic levels (alpha, beta, and gamma), largely using molecular data, but also based on morphological knowledge and other sources. The Euphorinae (Braconidae) provide some good examples, where the identities of species of Peristenus Foerster (Zhang et al. 2017) and Eadya Huddleston and Short (Peixoto et al. 2018; Ridenbaugh et al. 2018), two important genera in biological control, were clarified concurrently with the phylogeny of the subfamily (Stigenberg et al. 2015; Zhang et al. 2018).

An essential practice: taxonomic validation

Taxonomic validation, as defined by Packer et al. (2018), is a three-step process during the identification of an organism in any study using scientific names, in order to confer falsifiability on identifications presented in publications. In general terms, taxonomic validation consists of (i) a description of the identification procedure, (ii) an explanation of the concept used for a given taxon, and (iii) a designation of a collection for deposit of voucher material. As most studies based on biodiversity, including applied studies, have species as their fundamental unit, the possibility of replicating and falsifying identification results through correct and explicit methods must be an integral part of sound scientific activity. However, only 1.8% of studies in entomological journals evaluated by Packer et al. (2018), on various subjects, reported conducting these three steps that allow replicability of the taxonomic information. This is alarming, since the possibility of changes in taxonomic concepts, together with potential identification errors, can make a significant part of published information completely unverifiable and thus unusable. With taxonomic validation, it is possible to trace back and correct errors without losing information, either by simply verifying that the concept used is outdated or by checking voucher specimens.

Deposit of molecular marker sequences in public databases is another very useful practice in the taxonomic validation process, and should be followed whenever possible, along with citation of accession numbers in publications. Importantly, even in cases where the identification has been carried out by means of comparison with molecular markers, it is essential that all three steps be taken. In this case, the species concept must be explained upon citation of taxonomic works that associate the sequences of markers with the names, given the lack of reliability of public databases.

In order to clarify the species concept used, and in some cases as part of the description of the identification procedure, it is necessary to cite taxonomic works that enable identification of taxa whose names are mentioned in the publication. The suggestion by Packer et al. (2018) is quite timely, as it allows tracing the taxonomic concept underlying the identification, based on the most relevant bibliography at the time, that is, not necessarily the original description, but the work that contains the most recent concept followed by the authors. This is expected to alleviate one of the primary aspects of the crisis in taxonomy, through the considerable increase in the number of citations.

Numerous articles have discussed the problem of lack of citations of taxonomic articles (e.g., Drew 2011; Meier 2017), despite the undeniable importance of this field (Mayr 1968; Danks 1988). Here, we must emphasize that the common practice of not citing taxonomic articles is not only unjustified but also harmful to taxonomy and to the proper development of biological sciences that have biodiversity as their primary focus of study. The discovery, delimitation, and naming of a species, as well as the creation of tools for its identification, open a multitude of possibilities of use for this name and all the scientific communication surrounding it. Imagine if Trichogramma galloi, currently one of the most commercially important species in Brazil for biological control, had not been studied and described in such a way as to make its identity clear, what would have become of the over two thousand scientific articles on this species? Adding the original description (Zucchi 1988) and the main published identification keys (Querino and Zucchi 2005, 2011, 2019), these taxonomic works have been cited 93 times,² which means that less than 5% of the publications using the name

Tr. galloi cited references that could help to ensure the correct use of the name as part of their results.

We understand taxonomic validation to be essential for both taxonomy and biological control, and more broadly for the biological sciences. All aspects of this process are customary practices in taxonomy, which denotes the advantage of close collaboration between applied entomologists and taxonomists and tends to improve the taxonomic validation process in publications in applied entomology, which is often overlooked. Much has been said in recent years about a taxonomic renaissance (e.g., S.E. Miller 2007), or even a new era of cybertaxonomy (e.g., Wheeler 2007; Hita-Garcia et al. 2019). However, the problems related to the "taxonomic impediment" remain serious and the crisis in taxonomy is still worrying. Fortunately, many journals have begun to require one or more steps of taxonomic validation in their publications, which we regard as one of the main actions toward valuing taxonomy by peers. These steps should increase the number of citations and show the true importance of taxonomic research as an enabler of rather than an impediment to work focused on biological diversity.

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Data Availability All data generated or analysed during this study are included in this published article.

Declarations

Conflict of interest The authors declare no competing interests.

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² Based on a search in Google Scholar, accessed on June 13, 2022.

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