



Phylogenetic systematics and integrative taxonomy contribute to weed biological control

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HIGHLIGHTS

- Systematics plays major roles in the efficacy and biosafety of BCW.
- Integrative Taxonomy is fundamental for a correct match of the control agent with the target weed.
- Phylogenetic systematics allows accurate predictions of possible non-target hosts.

ABSTRACT

Taxonomy and systematics are at the base of any biological research, providing the scientific names and evolutionary context to access the biological information needed. The biological control of weeds (BCW), like many other fields, often suffers from the “taxonomic impediment” generated by incomplete taxonomic knowledge or lack of available taxonomic experts on the particular taxa involved (i.e., weed plants and their potential biocontrol agents). Further, most groups with described species require revision by specialists using modern taxonomic methods. Systematists in the different taxonomic groups have the knowledge and experience to perform the accurate identification of the species involved in the study, to recognize if they are non-native species, or if they are new to science. Their expertise is crucial for identifying the organisms involved in BCW, including hybrids or cryptic species. The practice of phylogenetic systematics allows the discovery of evolutionary relationships and natural taxa that are valuable in making host range predictions. This contribution emphasizes the crucial role played by phylogenetic systematics and integrative taxonomy in weed biological control.

1. Introduction

Biological control of weeds (BCW), like many other areas of study in ecology, often suffers from the “taxonomic impediment” generated by incomplete taxonomic knowledge or lack of available taxonomic experts on the particular taxa involved (i.e., weed plants and their potential biocontrol agents). Taxonomic and phylogenetic information is required during the main pre-release and post-release steps of any biological control project (Briese, 2005), their contribution being essential to elucidate the identity and origins of target weed and control agents, to detect issues like hybrids and cryptic species, and to develop host test lists. The identification of target pests and their natural enemies is at the base of any biological control program (Rosen, 1986; Sands, 1997). Accurate identification is associated with efficiency, safety and final success of the biocontrol program, whereas mistakes in the identification of the target weed, the candidate biocontrol agent or both lead to negative consequences, like delays until finding the appropriate biocontrol agent, or they can result in the introduction of the wrong

biocontrol agents (Clewley et al., 2012; Andersen & Wagner, 2016). Moreover, phylogenetic systematics provides natural classifications that, because of their predictive power, are particularly valuable for host-specificity testing (Briese, 2005).

The main goal of this paper was to gain an understanding of the crucial role played by taxonomy and phylogenetic systematics in BCW. With that purpose, it provides a synthetic overview with the objectives: to recognize the contribution of taxonomy (including modern approaches) to accurately identify the target weeds and candidate control agents; to highlight the contribution of phylogenetics to predict the native ranges and possible non-target hosts; and to give examples from real cases illustrative of the topics discussed.

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2. Pre-release studies

2.1. Importance of the taxonomic identification in BCW

2.1.1. Plant identification

The identification of the target weed is paramount in BCW, so that the correct bioecological information (e.g., ecology of the weed, natural enemies) can be searched for the species intended to be controlled. An example that illustrates the fundamental value of the accurate taxonomic identification in BCW, is the case of the floating fern *Salvinia molesta* D.S. Mitchell (Salviniales, Salviniaceae) by weevils of genus *Cyrtobagous* Hustache (Zimmerman, 1993 and references therein). This aquatic plant is native to Brazil, and has become invasive in more than 30 countries, being detrimental to water quality and aquatic habitats. When this invasive plant was first found outside its native range, it was thought to be *Salvinia auriculata* Aubl. *Cyrtobagous singularis* was collected, from the *S. auriculata* native range in Brazil, as a candidate control agent. However, when this species (as well as two other agents, a moth and a grasshopper) were released in the adventive range, they caused very little damage and failed to control the weed. Later examination of the plant and comparison with material held in herbaria in Brazil, demonstrated that the original identification was incorrect, and that the invasive *Salvinia* was a new species, subsequently described as *Salvinia molesta*, and this species also had its own set of specialized herbivores. Among these, was the new species *Cyrtobagous salviniae* described by Calder & Sands (1985). When this species of weevil was released to control the invasive fern, it resulted in an overwhelmingly effective biological control program, not only in Australia but in many other countries (Room 1990). The two weevil species show minor morphological differences, but differ in feeding habits, the larvae of *C. salviniae* burrow into the rhizomes and buds, while those of the other species feed more externally and do not attack the vital parts of the fern (Sands and Schotz, 1985).

Besides traditional morphological identification methods, the use of molecular techniques is increasingly important to identify (and/or delimit) species or genotypes of the weed in order to facilitate surveys of natural enemies (Gaskin et al., 2011). A study by Paterson & Zachariades (2013) on the control of the invasive shrub *Chromolaena odorata* (L.) R. M. King & Rob. is illustrative of the use of molecular evidence to recognize different genotypes of the target weed and their source of origin in the introduced range. The weed *C. odorata* is native to the Americas and the Caribbean and has become invasive in many tropical and subtropical areas of the world. In its introduced range, two “biotypes” of *C. odorata* are recognized based on morphological and ecological attributes, called the Asian/West African (A/WA) and southern African (SA) biotypes, respectively. The insects used as control agents were significantly less effective (most likely because of host-plant incompatibility) in controlling the SA biotype than the A/WA one. Paterson & Zachariades (2013) showed that the biotypes were genetically distinct and that the *C. odorata* invading South Africa (the SA biotype) had its origin in Jamaica and Cuba and was the result of a separate introduction to Africa. These findings indicated those Caribbean islands as the most appropriate region to search for new candidates for the biocontrol of the invasive *C. odorata* in southern Africa.

Identification of different subspecies, hybrids, or haplotypes by means of genetic methods can be very important in BCW, particularly when there is co-occurrence of native and invasive lineages and instances of hybridization. For example, the biological control of the common reed, *Phragmites australis* (Cav.) Trin. ex Steud., in North America is particularly challenging because it is a species that has multiple lineages (subspecies and haplotypes) with different significance for control management and conservation, depending on them being introduced or native (Martin & Blossey, 2013; Lindsay et al., 2023). The geographic co-occurrence of introduced and native lineages (e.g., subspecies), as well as their hybridization, highlights the need to obtain the correct identification of *Phragmites* lineages to ensure the

efficacy and biosafety of the BCW. Although the subspecies may be identified using morphology, a variety of genetic tools are currently available to accurately identify the hybrids and differentiate the invasive and non-invasive haplotypes, as needed to properly design control strategies towards the invaders while preserving the native subspecies (Lindsay et al., 2023).

Another interesting example that highlights the value of combining molecular evidence and morphology to recognize hybrids is provided by Reid et al. (2023b). Based on previous knowledge on the systematics of the native (South African) and invasive species of waterlilies in genus *Nymphaea* L., Reid et al. (2023b) suggested the existence of hybridization between the target weed *N. mexicana* Zucc. and other species in the subgenus. The classification of native and exotic *Nymphaea* spp. in separate subgenera indicated that hybridization between them would be unlikely. This facilitated the design of a control program focused on the search for biocontrol agents with a level of host specificity broad enough to include the plants classified in the target subgenus (the one including the target species *N. mexicana* and its congeners which may share some chemical defenses), but specific enough not to represent a threat to the native waterlilies (classified in another subgenus). Using molecular markers and morphological evidence Reid et al. (2023b) were able to identify hybrids of the invasive weed in South Africa and to detect the putative parents. This was useful to concentrate the surveys of potential compatible biocontrol agents (searched in both the native and invaded ranges) in order to maximize the chances of success of the biological control program (Reid et al., 2023a).

2.1.2. Agent identification

Once the target weed is identified, the surveys searching for biocontrol candidates often result in inventories of natural enemies from which potentially suitable biocontrol agents are chosen (Briese, 2000). At this step, the correct identification of the candidate biocontrol agent/s is of major importance (Andersen & Wagner, 2016).

Numerous case studies are already known about systematic research generated in response to requests related to the development of a biological control program. Particularly in the New World tropics, it is not unusual that when potential control agents are found, they belong to groups that are little or scarcely studied and often represent species new to science. For example, Bickel and Hernandez (2004) searched for potential control agents, from the native Neotropical range, of the water hyacinth *Pontederia crassipes* Mart., a harmful invasive weed in the Old World tropics, where it had no natural enemies. They discovered and described nine species of phytophagous diptera of genus *Thrypticus* Gerstäcker, which develop in *P. crassipes* and some other Pontederiaceae. Interestingly, the *Thrypticus* species differed in important biological features and the comparative study led to discover a clade of species having particular oviposition characters associated with bio-ecological features that make them more likely to be effective biocontrol agents (Bickel and Hernandez, 2004; Hernández et al., 2004).

Another example also illustrates the importance of taxonomic expertise in BCW. Alonso-Zarazaga & Sánchez-Ruiz (2002) performed a study to solve taxonomic problems that emerged in the context of biocontrol programs for thistles (*Carduus* spp. and *Onopordum* spp.) using weevils as control agents. They revised the *Trichosirocalus horridus* (Panzer) species complex (Coleoptera: Curculionidae) and described two new cryptic species, one from Spain and the other from Australia (introduced). The discovery of these two species helped to explain the different food preferences observed between populations or strains of the control agent that was previously thought to be a single species. The systematic revision by Alonso-Zarazaga & Sánchez-Ruiz (2002) provides fundamental information to re-examine voucher material and data from those biological control programs that have released weevils of this complex, in several countries, under the name *T. horridus*.

Historically, biological control programs as well as taxonomy have relied mostly on morphological characters to identify organisms, sometimes with the addition of biological data like host-plants and life

history information. However, during the last decades there was a revolution, based on the increasing possibility of using molecular evidence. Molecular evidence is now used together with morphological, ecological and other sources of data to discover and describe species, and this is known as “integrative taxonomy” (e.g., Toševski et al., 2013). The use of molecular tools to identify specimens is becoming a common practice. These methods compare diagnostic sequence data (for instance, the COI 5P fragment of insects) to sequences in a reference data base. However, molecular diagnoses and identifications are usually not that simple and require research by experts in the particular taxa. Of course, the genetic databases (e.g., GenBank, BOLD) are more useful or reliable for deeply studied taxa, but less so for insufficiently known groups, and there are some problems arising from misidentified species in the genomic databases. The use of molecular tools to identify species has limitations, and particularly in animal taxonomy, the use of COI for delimiting species should be integrated with other data, including morphology (Ahrens, 2024). Despite the limitations they may have, molecular sequence data have important applications in BCW (Goolsby et al., 2006b; Gaskin et al., 2011). Nuclear and mitochondrial DNA sequences can be useful to: make or confirm identifications; to discover or distinguish cryptic species; to recognize sub-specific lineages and hybrids; to associate life stages (e.g., larval and adult); and to associate sexually dimorphic specimens.

The usefulness of molecular tools to distinguish cryptic species is critical in BCW. Particularly among phytophagous insects, cryptic species or morphologically very similar species are common and they may differ in host-range and/or efficacy as biocontrol agents. An illustrative example is the case by Paterson et al. (2019) involving the control of the invasive water hyacinth *P. crassipes* in South Africa, by two cryptic species of plant bugs (Hemiptera: Miridae) *Eccritotarsus catarinensis* (Carvalho) and *E. eichhorniae* Henry. These mirids were originally considered as a single species but with two lines, one from Brazil and other from Peru. However, further studies suggested they were cryptic species, as evidenced by their genetic differences (Taylor et al., 2011) and reproductive isolation (Paterson et al., 2016). Moreover, detailed taxonomical study led to the finding of morphological differences and the description of a new species (Henry, 2017). Paterson et al. (2019) performed a study of both species to evaluate them as biocontrol agents. They compared host-specificity and efficacy of the two cryptic species and found significant differences in performance between them, depending on temperature.

The fundamental role of expert taxonomists for solving complex systematic issues of potential control agents toward implementing a biological control program, is illustrated by several case studies. For example, Toševski et al. (2013) applied an integrative taxonomic approach, using different sources of evidence, to study weevils of genus *Mecinus* Germar (Coleoptera: Curculionidae), postulated as good candidates for the biological control of two *Linaria* spp. (Plantaginaceae), invasive toadflaxes of European origin in North America. Results from the comparative and phylogenetic analyses, based on morphological characters, nuclear and mitochondrial molecular markers, and bioecological data, suggested the weevils were in fact not one but a complex of several cryptic species, which differ in host-plant choices.

2.2. The predictive power of natural classifications in BCW

There are currently no doubts about the advantages of having classifications that are consistent with phylogeny (Wiley & Lieberman, 2011). One of the most valuable properties of natural classifications is their predictive power (Farris, 1979). In BCW the classification (=phylogeny) can be used to determine or predict: the native range or region of origin of pests and biocontrol agents; host-plant associations or host ranges (real and potential) of biocontrol agents; and establishment success of biocontrol agents (Andersen & Wagner, 2016; Hinz et al., 2019).

2.2.1. The role of phylogenetic analyses to predict the native range

The use of phylogenies to predict region of origin can be of interest in BCW to match the target pests with potential biocontrol agents (Goolsby et al., 2006b). An illustrative case study is Goolsby et al. (2006a). They used phylogenies to evaluate genetic diversity and region of origin of the climbing fern, *Lygopodium microphyllum* (Cav.) R. Br., an invasive plant in Florida Everglades (USA), and of its potential control agent, the mite *Floracarus perrepa* Knihinicki & Boczek. Phylogenetic knowledge of the weed and control agent allowed for the determination of the most closely matched indigenous population of the plant to invasive populations, and the populations of the mite collected from that same region were the most harmful to the plant, and hence the most effective biocontrol agents.

Another case study, on the biocontrol program of the weed saltcedar *Tamarix* spp. in USA (Williams et al., 2014), exemplifies how phylogenetic studies at the population level can be used to find out whether the species is native or exotic and to determine the possible source/s of origin of the exotic lineage/s. The research by Williams et al. (2014) found that the invasive weeds were two species of Asian origin. Then, some species of leaf beetles in the genus *Diorhabda* Weise (Coleoptera: Chrysomelidae) were introduced from Asia as effective biocontrol agents (DeLoach et al., 2014; Mc Kay et al., 2018).

2.2.2. The role of phylogenetic analyses to prepare a test list for host specificity testing

The phylogeny of the plants and of the candidate biocontrol agents can be useful to predict host associations. Accurate predictions of non-target hosts are fundamental for risk assessment in any BCW program. The basic assumption is that closely related herbivores (i.e., control agents) often have closely related host-plants (Winkler & Mitter, 2008; Futuyma & Agrawal, 2009). This “phylogenetic conservatism” can be valid in many cases because the biocontrol agents of interest in BCW are specialist herbivores that feed and oviposit on only one or few host plants, which are often closely related; i.e., related herbivores often share similar host preferences (Futuyma & Agrawal, 2009). Such phylogenetic conservatism is also expected in other intimate biotic interactions involved in biocontrol programs (e.g., parasites/pathogens and their hosts). However, caution must be taken because phylogenetic tracking is not the only possible co-evolutionary pattern of herbivore and hostplant associations, since other factors (e.g. ecological, behavioral) can also determine the evolution of host-choice (e.g., Jousset & Elias, 2019).

In BCW, the predictive power of (natural) classifications is useful to prepare plant lists for tests of susceptibility of non-target plants. The “centrifugal phylogenetic approach” (Wapshere, 1974; Briese, 2005; Hinz et al., 2019) consists of designing the list of test plant species by selecting a larger number of plant taxa that are more closely related to the target weed and progressively decreasing it towards taxa that are less closely related. This is because it is expected that plants more closely related to the target weed share (by common descent) traits important for host selection by the specialist phytophages, i.e., they have higher chances to be selected/attacked by the biocontrol candidate than more distantly related species that may not have such traits. The use of the centrifugal phylogenetic method for selecting test plant lists has improved considerably since the earlier implementations, particularly thanks to the availability of more accurate plant phylogenies to guide selection of plants to be tested, and because knowledge on evolution of host-choice and behavior of the insects is also taken into account (Briese, 2005).

The phylogeny of the target plant is fundamental to the design of host-range testing. The application of the phylogenetic approach clearly had a positive effect in minimizing risks of damage to non-target organisms (Hinz et al., 2019). It is also important to consider the phylogeny of the biocontrol agent as well as its close relatives. Several studies on phylogenetic patterns of phytophagous insects and their host plants suggest that host-choice by the insects is often based on particular

plant features (e.g. chemical cues) (Jousselin & Elias, 2019). Hence, potential biological control agents and close relatives are likely to feed on plant species with similar features to those of the target weed, which are, therefore, more likely to be at risk of non-target impacts (e.g., Rapo et al. 2019). However, such similarity could be due to common ancestry (phylogenetic relatedness) or because of convergence (independently evolved) (Jermy, 1984; Mitter et al., 1988); i.e., the control agent and relatives may be specialists on plants that have particular features shared by common descent (the plants are closely related) (e.g. Rasmann & Agrawal 2011), but they also could be associated with unrelated plants that are similar in feature/s or resources tracked by the phytophagous agent (e.g., Kergoat et al., 2005; Hinz et al., 2008). As many examples demonstrate, a biocontrol candidate that was originally considered a single species, may contain subspecies or be a complex of cryptic or morphologically very similar species that differ in their host choice. The phylogeny and pattern of host-choice of control agents can provide valuable information to design host range tests. These should include both close relatives of the target weed and other plant species that are fed on by close relatives of candidate agents, as these plants may be more distant relatives with shared features through convergent evolution that make them more likely to be suitable host plants to the candidate agent (Simmons & Blossey, 2023).

Applying the phylogenetic criterion is often difficult or not possible because not all current formal classifications are based on phylogeny, and some may contain artificial, non-monophyletic groups, making the accurate prediction of host range difficult. For example, biological control programs for *Lantana camara* L., a major invasive pantropical weed, have a long history with several instances of non-target attacks (Hinz et al., 2019). A common factor behind these negative outcomes was the lack of proper host-specificity testing based on a phylogenetic hypothesis of *Lantana* L. and allied genera within the Verbenaceae (McFadyen et al., 2003; Briese, 2005). A recent phylogenetic molecular study of *Lantana* and allied genera performed by Lu-Irving et al. (2021) will be valuable to the biocontrol program, considering that besides some invasive weeds, like *L. camara*, the group has many species of ethnobotanical, ornamental and economic significance. Moreover, the resulting phylogeny shows the non-monophyly of the genera *Lantana* and *Lippia* L., and that the small clade containing *L. camara* is more closely related to a group of species currently classified in the genus *Lippia* than to other *Lantana* spp.

Another case study that exemplifies the improvements in the methods to predict host ranges involves research towards the control of the Russian thistle *Salsola tragus* L., invasive in USA, by a potential control agent, the eriophyid mite *Aceria salsolae* de Lillo & Sobhian. Several studies were performed to test host-specificity of this mite in order to evaluate its risk to non-target plants. The first host-specificity tests (Smith et al., 2005) were based on the available taxonomic data of the plant, traditionally classified in Family Chenopodiaceae. Accordingly, the sampling was more intensively done in the tribe Salsoleae (subfamily Salsoloideae). The list did not include species of genera *Bassia* and *Kochia* because they were classified in a different subfamily (Chenopodioideae). However, a molecular phylogenetic study by Berner et al. (2009) found that *Bassia* and *Kochia* were the closest relatives to *Salsola*. Then, Marini et al. (2021) performed new tests in the laboratory and in the field to evaluate the risk, now including these potentially suitable non-target plants. They concluded that, in the field, the mite is not a risk to any of the non-target native or economic plants in the USA.

Phylogenies are still unavailable for many taxa (either the target weed and/or the control agents), particularly when dealing with hyperdiverse taxa, their phylogenies may have not been studied yet or there could be conflicting hypotheses about the relationships. For example, Cabrera Walsh & Maestro (2017) had to consider a larger plant list for testing the host-specificity of the weevil *Listronotus elongatus* (Hustache), candidate agent to control the aquatic weed *Hydrocotyle ranunculoides* L.f., native of the Americas and invasive in Europe. The

difficulty was because the plant has a conflictive phylogenetic placement, either in Araliaceae or in Apiaceae.

3. Post-release studies

At the final steps of any biocontrol project, it is expected that the released biocontrol agent successfully establishes at the selected sites followed by its spread through the range of the weed (Briese, 2000). The contribution of taxonomic expertise is also highly valuable during the post-release monitoring phase of biocontrol programs. In some cases, it is necessary to compare agent populations in the indigenous distribution with those in the invaded distribution using genetic techniques.

3.1. Identification of agents after release

Post-release monitoring of control agents in the field to evaluate their effectiveness to control the weed can be challenging, particularly when the released agents were not genetically homogeneous and intra- or interspecific hybridization between them occurs (Szűcs et al., 2018). Hybridization among biocontrol agents produces novel genetic combinations that can affect their fitness and adaptive ability. Hence, hybridization among control agents can have important consequences (either neutral, positive or negative) on the effectiveness of the biocontrol programs (Szűcs et al., 2018). For example, Knutson et al. (2019) found hybridization between three leaf beetle species of *Diorhabda* (Coleoptera: Chrysomelidae), released for the biological control of tamarisk in Texas and New Mexico (USA). Post-release monitoring of the biocontrol agents was important to evaluate the establishment success, dispersal, non-target attack, and long-term impact on the targeted weed. Post-release detection of the hybrids *in situ* was done by detail morphological and genetic studies, made possible thanks to basic knowledge from the taxonomic revision of the species involved (Tracy & Robbins 2009).

Another example is provided by Hopper et al. (2019), who documented the interspecific hybridization among two South American weevil species, *Neochetina bruchi* Hustache and *N. eichorniae* Warner (Coleoptera: Curculionidae), introduced into many countries worldwide for the biocontrol of *P. crassipes*. To evaluate whether co-introduction of *N. bruchi* and *N. eichorniae* resulted in hybridization, they first used diagnostic morphological characters of each species to identify possible hybrids between them (individuals with ambiguous traits). By applying molecular markers to putative hybrids and exemplars with typical features of each species, they corroborated hybridization, but its consequences for the biological control program remain to be evaluated.

4. Conclusion

The focused perspective offered in this review highlights the contribution of modern taxonomy and phylogenetic systematics to the efficacy and biosafety of weed biological control. Their crucial role in correctly matching the control agent with the target weed and accurately predicting possible non-target hosts is demonstrated in numerous case studies, some of them chosen as examples in this overview.

Systematic biologists that are experts in the taxa of interests are the best partners for an effective BCW program. They know the recent advances in the taxonomy and classification of the species, they have updated literature and contacts with other taxonomy experts that may help. They usually know about the most recent phylogenetic hypotheses, and may even have unpublished information on the biology of the organisms of interest. Taxonomists have the knowledge and experience to perform accurate identification of the species involved in the study, or to recognize if they are non-native species, or if they are new to science. Their expertise applied in biocontrol studies can be crucial for identifying the challenging organisms often involved in BCW, like hybrids or cryptic species. Molecular tools for confirming species identification are helpful and becoming common practice, but they can only illuminate,

not replace, the taxonomic expertise required based on morphological evidence. The crucial value of taxonomy and phylogenetic systematics in biological control is clearly recognized and documented in numerous case studies in the present and previous contributions. On the other side, BCW represents a source of opportunities to perform systematic studies on taxa that would otherwise be unlikely to be conducted or at least not performed in detail.

Well beyond just providing an identification service, experts in the different taxonomic groups often contribute with fundamental systematic research required to ensure an effective and successful biological control program. Numerous case studies documented in the literature on BCW worldwide demonstrate that systematists often undertake detailed taxonomic and phylogenetic studies under the motivation of a BCW program. BCW is clearly interdisciplinary, fostering reciprocally illuminating research lines. Collaborative research between biological control scientists and systematic biologists is the key for a successful BCW program and a source of progress in different fields of science.

CRedit authorship contribution statement

Adriana E. Marvaldi: Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The author declares that she has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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