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Opinion

Trait-based approaches to predicting biological control success: challenges and prospects

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Identifying traits that are associated with success of introduced natural enemies in establishing and controlling pest insects has occupied researchers and biological control practitioners for decades. Unfortunately, consistent general relationships have been difficult to detect, preventing *a priori* ranking of candidate biological control agents based on their traits. We summarise previous efforts and propose a series of potential explanations for the lack of clear patterns. We argue that the quality of current datasets is insufficient to detect complex trait–efficacy relationships and suggest several measures by which current limitations may be overcome. We conclude that efforts to address this elusive issue have not yet been exhausted and that further explorations are likely to be worthwhile.

Highlights

Across many organisms, there is clear evidence that there are traits associated with successful establishment after being moved to new regions by human activities.

Among predatory and parasitoid insects that have been, for decades, intentionally imported to combat insect pests, there is little clear evidence that any particular traits influence their success as biological control agents.

We argue this is not due to traits having no influence on success but more likely to the insufficiency of existing data and consequent constraints on analyses used.

We provide a roadmap towards improved predictions of how traits, and combinations of traits, affect natural enemy suitability as biological control agents.

More accurate forecasting of outcomes of biological control introductions would aid importation decisions based on potential risks and benefits of such interventions.

The quest for traits associated with success in biological control

Biological pest control has been practiced for over three millennia [1], but the deliberate introduction of natural enemies to control invasive pests (**importation** or **classical biological control**, see Glossary) emerged as a discipline following the highly successful suppression of the cottony cushion scale *Icerya purchasi* in California by an introduced predatory beetle and a **parasitoid** fly from Australia in 1888 [2]. Since that time, over 250 species of invasive insects and weeds have been controlled using biological control introductions [3]. In addition to important benefits to agriculture, these cases of invasive species control have produced immense benefits in terms of environmental and human health, including reducing reliance on chemical pesticides [4], protection of native biodiversity [5], and the alleviation of poverty in low-income countries [6]. However, not all biological control introductions have resulted in pest suppression [7], begging the question of which ecological conditions and traits of agents contributed to successful outcomes [8]. Efforts to answer this question generated the hypotheses that successful agents should be specialised on the target pest, and that they should exhibit high **attack rates** through short **handling times** and/or high fecundity [9,10]. Additional traits identified as promising included rapid and **gregarious** development (for parasitoids) [11,12].

As the number of biological control importations increased, it became possible to create databases on the performance of agents. For example, the BIOCAT database [7,13] includes records of 6158 introductions, in which 2384 potentially beneficial arthropod species were released against 588 invasive arthropod pest species in 148 countries. Such databases can be augmented with trait information on agents and pests, providing opportunities to address hypotheses about success using a comparative approach. Nevertheless, identifying influence of an agent's traits on the likelihood of success has been frustratingly difficult. Past analyses have, in general, failed to detect clear patterns associating agent traits with biological control success, other than some inconsistent signals of agent type (predator vs

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parasitoid) and specificity (summarised in Table 1). For example, Seehausen *et al*. [14] concluded that 'remarkably few agent-related factors influenced success' and Jarrett and Szűcs [15] stated that 'no overwhelming evidence was found that any one of the five parasitoid traits analysed on their own would predict variation in establishment success'. Here, we propose a series of explanations and suggest how to improve pattern detection. We focus on the importation of biological control agents (mainly insect predators and parasitoids) against insect pests, but insights may be relevant for **augmentation** or **conservation biological control**, and additional pest taxa.

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Potential explanations

The failure to detect consistent patterns that link natural enemy traits to biological control success may simply indicate that such patterns do not exist. We find this unlikely because patterns of success are found in relation to agent taxonomy, suggesting that related species share at least some traits that correlate with success. Instead, we propose that patterns of success related to traits do

Table 1. Summary of studies (ordered chronologically) aiming to detect correlations between natural enemies' traits and their success in biological control programmes

Study	Agents' traits considered	Statistical approach	Success measures	Main conclusions
Kimberling [21]**:** Compiled a database from current and historical literature for 87 non-native insect biological control species in the continental USA	Thirteen **life history traits**, all considered as categorical: predator/parasitoid, host specificity, sex ratio, **voltinism**, oviposition site, host stage attacked, developmental time, feeding life stage, **endo-/ecto-parasitism**, host mortality per agent, searching efficiency, dispersal ability	Stepwise logistic regressions	Reduced population levels of a target host/prey below the economic injury level, or a significant decrease in pesticide applications in at least one region	Released parasitoids are more likely to control a pest than predators. High host specificity and multi-voltinism significantly contribute to the likelihood of success.
Stiling and Cornelissen [58]**:** Compiled a dataset based on 145 studies describing cases of biological control attempts worldwide	Agent guild (predator, parasitoid), pest guild (parasite/pathogen/herbivore), host specificity (generalist/specialist)	Analysis of within- and between-guild heterogeneity in effect sizes; comparison with χ^2 distributions	Establishment, target fecundity, developmental time, mortality, parasitism, predation, and/or abundance before and after agent releases	Biological control efficacy is higher for predators compared to parasitoids, and tends to be higher when agents are generalists than when they are specialists.
Rossinelli and Bacher [59]**:** Compiled a dataset of 254 imported and released parasitoid species	Specificity (number of documented hosts), endo-/ecto-parasitism, body size	GLMM including agent taxonomy and biogeographic origin as random factors	Establishment	Establishment success increases with host specificity.
Seehausen *et al.* [14]**:** Used a subset of the BIOCAT database considering 780 introductions of 416 target-agent combinations	Six traits of the agent: guild (predator/parasitoid, specificity (**monophagous**, **oligophagous**, **polyphagous**), feeding behaviour (endo-/ecto-parasitism), life stage attacked, brood size (solitary/gregarious), attack strategy (**idio-/koinobiont**)	GLMM	Establishment, impact on the target population, and complete control of the target	Insect predators are less successful in establishing post-release than insect parasitoids. Oligophagous agents are less likely to completely control the pest.
Jarrett and Szucs [15]**:** Used a catalogue of introductions in North America [17], augmented by data on life-history traits of 132 parasitoid species and their herbivorous hosts	Five parasitoid traits: specificity (phylogenetic host range), developmental stage attacked, idio-/koinobiont, endo-/ecto-parasitism, solitary/gregarious	Bayesian models accounting for host and parasitoid phylogenies	Establishment	Parasitoids with a wide host range are more likely to establish when the target is also a generalist.
Wyckhuys et al. [60]**:** Considered 108 separate biological control introductions in the Mariana Islands (USA) and Easter Island (Chile)	Specificity (parasitoids with fewer than 10 known hosts considered specialists)	χ^2 tests	Establishment and partial-to-good control of target insect pests	Specialist species have slightly higher establishment rates than generalist species.

exist but that current databases – as extensive as they may seem – lack sufficient information either on success measures or on the relevant traits to allow adequate statistical power. We further consider the possibility that such patterns are too complex or confounded by environmental contexts to be detected by standard analyses. We summarize these limitations and potential solutions in Figure 1 and discuss them in detail in the next sections.

Limited and biased datasets

Regulations related to biological control are likely to limit the accumulation of data and to introduce biases in the available databases. In particular, a more risk-averse approach to releases began in the 1990s following the recognition of **nontarget effects** attributable to previous releases of generalist agents [3]. This resulted in declining rates of new introductions worldwide [7,16] and to preferences for introducing agents that had already successfully controlled target pests elsewhere [17]. To reduce occurrence of nontarget effects, the current importation of

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Figure 1. The problem (blue box), possible explanations (grey boxes), details (green boxes), and possible solutions (yellow boxes) for the lack of consistent patterns regarding the influence of natural enemy traits on the likelihood of biological control success. (Illustration by Daniella Möller)

Glossary

Attack rate: number of prey/hosts attacked by a predator/parasitoid per time unit.
Augmentation biological control: release of mass-reared natural enemies to control pests.
Conservation biological control: environmental protection and promotion of naturally occurring natural enemies, by preserving them, and providing them with, resources.
Endo-/ecto-parasitism: parasitoid development while feeding from the host internally/externally.
Gregarious: parasitoid in which multiple offspring develop from an individual host.
Handling time: time taken for a predator/parasitoid to handle each prey/host.
Hyperparasitoid: parasitoid which parasitises another parasitoid species.
Idio-/koinobiont: parasitoid of hosts that cease/continue development upon parasitism.
Importation (classical) biological control: intentional introduction of a natural enemy (biological control agent) from the native geographic range of an exotic pest, aiming for long-term control.
International Organization for Biological Control (https://www.iobc-global.org/): nonprofit international organisation promoting biological control worldwide.
Life history traits: characteristics related to the timing and magnitude of major events in the life of an organism, e.g., developmental time, age at maturation, fecundity, clutch size, egg size, and lifespan.
Mono-/oligo-/polyphagous: feeding on one/few/multiple types of food: an indication of dietary specialization level.
Nontarget effect: adverse effect imposed by a biological control agent on organisms that are not the intended target pest.
Parasitoid: insect that completes its development feeding from the body of another (individual) arthropod, eventually killing it, and is free-living as an adult.
Plant secondary defences: plant metabolites that act as anti-herbivory compounds.
Principal component analysis (PCA): dimension reduction technique for analysing large datasets containing many quantitative dimensions/features per

natural enemies in many countries is essentially limited to species with specialized diets [18], confounding *post hoc* attempts to test whether specialisation affects pest control efficacy. While regulatory agencies evaluate ecological information about prospective agents before they are imported and released, funding for biological control programs is rarely extended beyond the release of natural enemies. This regretfully limits follow-up studies on the consequences of the releases [19], reducing information on success. Finally, failed projects are perhaps less likely to be reported than successful ones, potentially biasing the databases further [7].

observation, increasing the interpretability of data.

Solitary: parasitoid in which single offspring develop from an individual host.

Uniform manifold approximation and projection: novel machine learning technique for nonlinear dimensionality reduction.

Voltinism: the number of broods or generations of an organism per year.

Inconsistent measures of success

The different ways of measuring the success of biological control agents can further complicate attempts to identify general patterns. A common measure of success is whether populations of introduced agents establish after release [20]. However, life-history traits that facilitate establishment might trade off with those contributing to pest control (see 'Trade-offs between traits' below). Another measure of success is the impact of the agent on pest populations. Impact has been evaluated in various ways, with some studies considering any reduction in the pest population, others considering only reduction below a certain threshold, and yet others only complete eradication (Table 1). Perhaps most relevant to agricultural crop protection is whether an agent reduces the need for insecticide use against its target [14,21]. However, decisions on whether to apply chemical control are not only based on pest population densities. Socioeconomic factors, such as farmers' beliefs and risk-sensitivity, peer advice, cost of pesticide treatment, type of damage caused by the pest, and cash value of the crop, are also considered [22], potentially obscuring the importance of biological traits.

Limited information on traits

The low number of traits considered in analyses of biological control databases (typically <10; Table 1) may further limit the ability to explain biological control outcomes. Most traits considered in past analyses of success are coded as qualitative traits, such as specificity (monophagous vs polyphagous), oviposition strategy (**solitary** vs gregarious), and reproductive mode (sexual vs asexual). The limited availability of quantitative data on traits may reduce the explanatory power of statistical analyses and misrepresent the ecology of the agents [23]. Most analyses focus on traits that are related to direct interactions between pests and control agents, whereas the persistence and efficacy of agents also depend on traits that determine their sensitivity to local environmental conditions (see also 'Variable environmental contexts' below). Environmental tolerance traits such as desiccation resistance, heat tolerance, and inundation resistance may be particularly important since they determine how organisms cope with extreme weather conditions [24,25].

Trade-offs between traits

Ecological and life-history trade-offs may further obscure the contribution to success of any single independent trait. For example, high fecundity is often considered desirable as it may allow agents to attack many pest individuals and to experience rapid population growth. However, investment in fecundity can come at the expense of other traits such as longevity, egg size and dispersal ability [26–28] all of which may influence success. Moreover, the allocation of resources between fecundity and other traits may be highly dependent on environmental conditions (see also 'Variable environmental contexts' below). For example, in a simulation model of parasitoid life history evolution [28], the optimal allocation between egg load, egg size, and adult longevity, depended on host and food availability in the environment, in agreement with empirical data comparing parasitoid traits in natural versus agricultural environments [29,30]. Thus, traits that promote success under certain environmental conditions may not guarantee high performance in others.

Gregariousness in parasitoids, particularly species with large clutch sizes, has also been suggested to benefit biological control, as this increases the number of offspring produced per host and therefore the reproductive rate of the agent [20]. However, under conditions of egg limitation, a larger clutch size would necessarily lower the number of hosts attacked and hence reduce immediate pest suppression [11]. Similarly, short developmental time is considered preferable in biological control agents [12] but is likely to trade off with other fitness-related traits, such as adult lifespan [31].

As a final example, high specificity is often assumed to correlate with high efficiency in locating, attacking, and overcoming host or prey defences, as well as with lower risks of nontarget effects [32]. However, it may trade off with the ability of an agent to exploit alternative resources, and hence to overcome environmental fluctuations and periods of low pest density [20,33,34].

Variable environmental contexts

Biological control success, as well as the set of traits associated with it, may strongly depend on the environmental context under which the agent is expected to perform efficiently [35,36]. These may include specific attributes of the target pest and the crop plant, as well as larger-scale environmental factors (Figure 2). Regarding pests, it is well known that some taxonomic groups of herbivores are more likely to be controlled than others [8,37]. For example, target pests feeding on plant sap (mostly in the insect order Hemiptera) are more often successfully controlled than those feeding on other plant parts [14] and have become frequent targets of biological control programmes. In addition, traits of the pest are likely to interact with traits of the agent in determining control success, yet such interactions are only rarely considered [15].

Other factors of importance may be related to the characteristics of the agricultural environment and of the crop plant. Agroecosystems often differ greatly from natural areas in foraging environments and community structure [38–40]. Crop domestication generally selects for increased palatability, which is often coupled with decreased production of **plant secondary defences**. Such changes may affect the performance of agents through multiple direct and indirect mechanisms [41–43]. Abiotic conditions, such as temperature and humidity, are also of high importance, especially in the context of global climate change [44,45]. Finally, biotic interactions, such as the occurrence of competitors and natural enemies of the agent itself (e.g., **hyperparasitoids**), may further affect biological control outcomes [8].

Potential solutions

Based on the above, we propose that patterns linking the traits of introduced agents to their success in controlling invasive insect pests are highly complex, potentially involving interactions and trade-offs among traits; many of which are dependent on the environmental context. We argue that the complexity of the expected patterns in relation to agent traits calls for richer datasets to improve statistical power and allow for more sophisticated analyses. Below, we suggest ways by which this could be achieved.

Improved data

We call for clearly defined guidelines to monitor and evaluate the success of biological control introductions, including guidelines for post-release monitoring [7]. These would ideally be developed at the international level, promoted by bodies such as the **International Organization for Biological Control**. In addition, we suggest adopting a consistent metric to evaluate the pest suppression performance of natural enemies. Quantities such as the *q* value, the ratio of the pest population in the presence and in the absence of a certain agent [9], can provide estimates of the population-level impact of the introduced agent. We propose that *q* values be

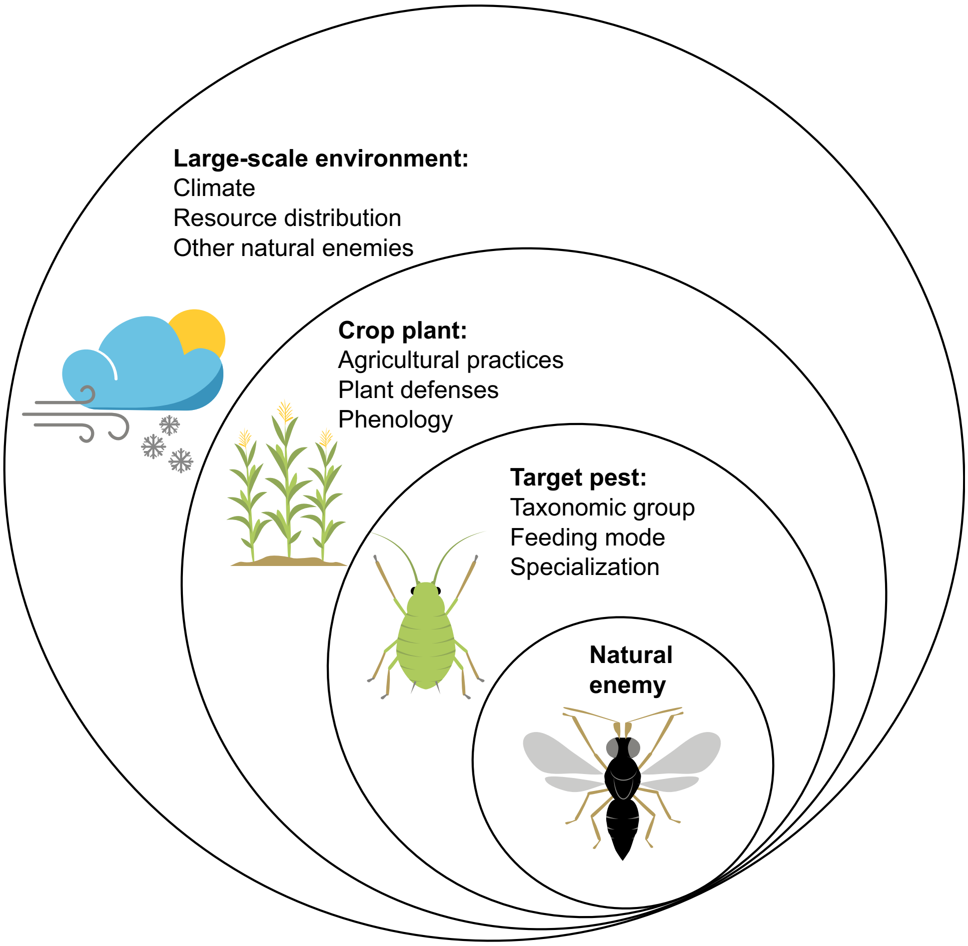

Figure 2. The complexity of the environmental context in which a biological control agent is expected to perform efficiently, including characteristics of the herbivore pest, crop plant, large-scale environmental effects, all of which may obscure patterns related to biological control success in relation to natural enemy traits. (Illustration by Daniella Möller).

retrospectively estimated for past biological control projects where possible, and projected for future projects where appropriate information is available from past releases or system-specific population modelling. When estimating the q value is not feasible, we suggest semiquantitative estimation of the degree of success (e.g., no establishment, establishment with no impact, and establishment with low, intermediate, or high impact on the pest population).

Statistical power to identify genuine effects increases with sample size. For example, traits that correlate with invasion success have been successfully detected for various taxa using large datasets (Table 2). Given the declining rate of new biological control introductions, we suggest combining previous, independently compiled, data sets on biological control outcomes. We also propose enriching the datasets with information on unintentional colonization by natural enemies, which can occur after an exotic pest invades a new region [46]. Leveraging information from both successful and failed accidental biological control interactions could help identify natural enemy traits that promote pest control and reduce some of the biases of current databases. Existing datasets that include some of this information [47,48] could serve as a starting point.

Table 2. Examples of trait-based analyses in invasion biology (ordered chronologically)

Organisms	No. of species in database	No. of traits tested	Statistical approach	Traits associated with invasiveness	Refs
Plants	1218	19	Regression trees	Early flowering, tall stature, generative reproduction, number of ploidy levels, opportunistic dispersal	Pysek *et al.* [61]
Birds	428 (2760 invasion events)	9	GLMM, PGLS	Favouring future over current reproduction	Sol *et al*. [62]
Mammals	518	8	Phylogenetic GLMM in Bayesian framework	High reproductive output, long reproductive lifespans	Capellini *et al*. [63]
Reptiles/ Amphibians	402/147	7/5	Phylogenetic GLMM in Bayesian framework	Large clutches and frequent reproduction	Allen *et al.* [64]
Fish	6293	6	Hedge's *d,* permutational multivariate analysis of variance,	Large body size, high longevity, greater size at maturation, delayed maturation and high fecundity	Liu *et al*. [65]
Woody plants	857	45	boosted regression tree models, principal coordinate analysis	Vegetative reproduction, long-distance seed dispersal	Nunez-Mir *et al*. [66]
Plants	395	7	PCA, GLM, PGLS	Different leaf traits (related to metabolic rates and leaf economics) associated with different measures of invasion success and impact	Liao *et al*. [67]
Marine invertebrates	387	12	Fuzzy correspondence analysis, regularized discriminant analysis	Intermediate body size, high longevity, high fecundity, suspension feeding, other traits related to brooding	Quell *et al.* [68]

Intentional biological control introductions are analogous to biological invasions because they involve the establishment and spread of an exotic species in a new geographic area. The table shows that, in several groups of organisms, traits associated with invasiveness have been identified. With large enough databases and appropriate statistical analyses, it is thus possible to discover how traits influence exotic species' abilities to establish and spread in new environments. Abbreviation; PGLS, phylogenetic generalized least square model.

Finally, we suggest enriching the available biological control datasets with additional traits of natural enemies. This can rely on existing datasets compiled in the context of studying arthropod life history evolution [49,50], as well as on ongoing projects aiming at compiling new trait data [51] (https://github.com/ShareTraitProject/ShareTrait). While physiological traits may be particularly difficult to measure, standardised protocols to facilitate cross-species comparison have recently been developed [25].

Improved analyses

A major challenge for trait-based analyses of success is the identification of the relevant taxonomic level for consideration. Analyses of biological control datasets are typically conducted on taxonomically broad sets of organisms, such as across insect natural enemies or across all hymenopteran parasitoids. However, as the taxonomic breadth considered increases, the diversity of ecological contexts and interactions being considered also rises, to the point where patterns may become too complex to be detected. As evidence, prior analyses that have detected strong influences of traits on the success of invasive species tended to focus on more specific taxa [52] (Table 2). In the context of biological control, it might also be useful to focus on a certain group of pests or a specific crop. For example, success was found to increase with fecundity among parasitoid species established against lepidopteran pests, but this pattern does not occur consistently across higher level taxa [53]. Reducing the taxonomic breadth of trait-based analyses may thus pay off, despite decreasing the generality of the conclusions.

Generalised linear models (GLM) [54] is an appropriate statistical approach for investigating biological control outcomes, either as binary (success vs failure) or continuous responses such as the q value. In such analyses, multiple candidate explanatory traits can be evaluated together, while controlling for phylogenetic relationships between agents, and between pests [55]. In addition, it would be appropriate to include some information as random effects (generalised linear mixed models; GLMM) [56] to account for multiple cases that represent the same agent species, the same pest, the same cropping system, or the same region. Model specification (i.e., the choice of explanatory variables and interaction terms to be included in initial statistical models) can be guided by theoretical developments in our understanding of eco-evolutionary trade-offs, implying specific interaction terms between agent traits or between traits and environmental variables [27,28]. This would result in more meaningful model fits to data and would also enable evaluation of the models and identification of required improvements.

A more exploratory approach would be to utilise dimensionality-reduction data visualisation techniques that cluster together trait combinations associated with successful pest control. This could be carried out naïvely with standard **principal component analysis (PCA)** or using more sophisticated machine learning approaches, such as **uniform manifold approximation and projection** (UMAP) [57]. Importantly, such data exploration methods should not replace the statistical procedures mentioned already, but rather provide supporting analyses that can guide research in fruitful directions and generate working hypotheses regarding trait combinations that promote biological control success.

Past studies relating the traits of exotic species to invasion success (Table 2) have used a range of statistical techniques that remain underutilised in analyses of biological control datasets (Table 1).

Concluding remarks

After more than 50 years of discussion, there is still no consensus as to which traits of a released arthropod agent can predict success in controlling pest species. The only trait that has been somewhat consistently identified as important, high target specificity, is already being used as a prerequisite for importation as it reduces the risk of non-target effects. One option is to abort the mission and concede that the exploration of life history and other traits of natural enemies is not useful for predicting or understanding biological control success. We suggest, however, that our abilities to address the question have not yet been exhausted. Specifically, we point out that patterns may be too complex to be detected when using current datasets. Better incorporation of mechanistic, theoretical approaches for data generation, accumulation, and analysis may help in disentangling some of these complexities. While enriching the datasets in a meaningful way is likely to be difficult and time consuming, we suggest that this will be an ultimately worthwhile way to overcome constraints on using more powerful and sophisticated statistical analyses. It may allow us to detect not only patterns related to biological control but also to understand related ecological, evolutionary, and environmental processes that occur when organisms are introduced into new environments (see Outstanding questions).

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Declaration of interests

No interests are declared.

Outstanding questions

Which traits of introduced natural enemies (biological control agents) make them more, or less, successful in controlling insect pests? Attempts to address this question have often failed, which we suggest is due to the complexity of ecological mechanisms influencing the strength of top-down population suppression, and the paucity of comprehensive data sets.

How can we use trait-based approaches to improve biological control practice? We suggest promoting the use of consistent measures of success, enriching databases with control attempt outcomes and with more traits of agents, controlling for environmental contexts, and improving the statistical approaches used to analyse datasets.

How does optimal allocation to different traits vary across different environmental contexts? Traits, and their combinations, that contribute to success, may differ according to the environment under which biological control agents are expected to perform efficiently. If we can identify context-specific beneficial traits, we can likely use this information to improve success rates.

What are the size requirements for a trait-based biological control database? To achieve sufficient statistical power to identify traits that predict biological control success, larger and more complete databases are needed, especially to explore potential interactions between multiple traits, and also with environmental effects.

What is the optimal taxonomic level for trait-based biological control predictions? Some taxa (genera/families) of natural enemies provide better biological control than others, and some taxa of target species are better regulated by natural enemies than others. Analysis of new, larger, databases will likely identify taxon-specific traits related to positive biological control outcomes.

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