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Classical biological control against insect pests in Europe, North Africa, and the Middle East: What influences its success?

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Abstract

Many factors can affect the success and failure of classical biological control. However, these factors have mainly been studied independently of each other, which leaves their relative importance within the complexity of classical biological control (CBC) programmes unknown. Therefore, we set out to take a more holistic view on the factors that may impact the outcome of CBC of insect pests by insect predators and parasitoids. To this end, we filtered the BIOCAT catalogue to extract entries for the Greater Western Palearctic ecozone and added 15 new explanatory variables. These mainly concerned traits of released biological control agents, target pests, and host plants of the target, but also included the number of introductions for specific agent-target combinations as a management aspect. We then analysed the data regarding three levels of success: agent establishment, impact on the target population, and complete control of the target. Between 1890 and 2010 a total of 780 introductions of insects for biological control were undertaken in the analysed area, constituting 416 agent-target combinations. Overall success of agent establishment was 32%, successful impact of single agents on their target was 18%, and success of complete control was 11%. The number of factors significantly influencing the outcome of CBC decreased with increasing level of success. Remarkably few agent-related factors influenced the success: insect predators as agents decreased the probability of establishment and using oligophagous parasitoids significantly decreased the chances of complete control. Other significant factors were related to traits of target pests or their host plants. For example, sap feeders and target pests attacking reproductive plant parts were more likely to be successfully controlled. The rate of success increased with the number of introductions of CBC agents, in particular against univoltine target pests. These findings suggest that a focus on agent-related traits to increase the chances of successful CBC is not fully justified and should be complemented with the consideration of lower trophic levels and other aspects of CBC, such as abiotic factors and management.

Keywords

BIOCAT, importation biological control, introductions, invasive species

Introduction

Classical biological control (CBC), i.e. the introduction of natural enemies from the region of origin, has proven to be an efficient and cost-effective tool to control invasive insect pests worldwide, including pests of forests and ornamental trees (Van Driesche et al. 2008; Kenis et al. 2017). However, a global analysis of the trends in the CBC of insect pests by insect predators and parasitoids revealed that the success of introduced agents to control a target was only about 10% with only 29% of the target pests being satisfactorily controlled by at least one natural enemy (Cock et al. 2016). This estimation is surely conservative, because it includes many poorly designed CBC programmes and depends on the approach of estimation of the success (Heimpel and Mills 2017). Nevertheless, it raises questions as to why the success is not higher and what can be done to increase the success of CBC.

An impressive amount of theoretical and empirical evidence has been gathered to identify the specific factors that have an impact on the successful outcome of CBC programmes. They can be classified into five categories.

The first three categories are the biotic factors that are inherently bound to the three trophic levels involved in this type of biological control. They correspond to the life-history traits that are involved in the trophic interactions between the pest's host plant, the pest itself, and its introduced natural enemy. When considering which variables within these categories should be addressed to increase the success of CBC, the focus often falls on the highest trophic level, the selection of the biological control agent that is to be introduced. For example, it has been repeatedly suggested that parasitoids are more successful in target control, compared to predators (Hawkins et al. 1999; Kimberling 2004). Similarly, ectoparasitoids have been suggested to be less successful than endoparasitoids, although the reasons for that remain unclear (Stiling 1990), and parasitoids that kill hosts in earlier life stages other than eggs have a higher impact on target populations than those that kill later life stages, such as pupae (Mills 1994). Oligo- or polyphagy has also been suggested as a desirable trait for agents to survive periods when pest densities are low, although, to lower the risk of non-target attacks, the agents should be host-specific (Bale et al. 2008). Traits of lower trophic levels (i.e., target insects and their host plants) that may be related to the success or failure of CBC find, however, very little mention in the scientific literature. Bennett (1974) reviewed some criteria for the determination of suitable targets for biological control, but concluded that almost all pests warrant consideration for biological control. Interestingly, Gross et al. (2005) found that lower trophic level factors such as pest order can successfully predict outcomes in CBC of insect pests. And Kenis et al. (2017) deliver empirical evidence that success rates of agent establishment and target

control were higher in CBC projects targeting pests of woody plants than pests of other types of plants. A reason for this might be that being perennial, trees provide a more stable and predictable environment, when compared to herbaceous plants (e.g., annual plants or crops). Therefore, biological control agents have generally more time to establish and reproduce and might thus be more successful when released against pests of woody plants.

The fourth category of factors that can have an influence on the success of biological control introductions concerns abiotic factors of the environment where introductions are made. An obvious factor may be the existence of physical barriers to dispersal. However, the abiotic factor that is the most considered in relation to the success and failure of biological control is climate. It has been estimated that climate is responsible for about 35% of failures of natural enemy introductions against arthropods (Stiling 1993). Hence, climate-matching models are now widely used to more effectively search for biological control agents that are suited for the climatic conditions of the area of introduction (reviewed by Heimpel and Mills 2017).

The fifth category of factors potentially affecting the success of CBC involves the management of biological control programmes, and in particular release procedures. Some examples for these factors are the timing of release; release location; the quantity, quality, and life-stage of individuals that are released; the number of repeated introductions of an agent species against the same target; or the number of agent species that are released against a specific target (e.g., reviewed by Beirne 1985). However, surprisingly few tools have been developed that may help practitioners to take informed decisions on how to release CBC agents and, all too often, releases become a matter of trial and error.

From the above list of factors that can influence the success of biological control introductions, it becomes sufficiently clear that CBC is very complex and its success depends on proper methods and decisions at different steps of the process. Even if many individual factors have been shown to influence the outcome of introductions, their importance relative to all other factors remains unclear. The main objective of this study is therefore to analyse the relative importance of factors that possibly affect successes and failures of CBC of invasive pest insects using a holistic approach that reflects the complexity of biological control introductions. The analysis is done on the basis of the BIOCAT catalogue of biological introductions (Cock et al. 2016), which we enhanced by adding relatively easily available factors, mainly related to traits of agents, targets, and their host plants, but also one management-related factor. Furthermore, the analysis is restricted to available data from the Greater Western Palearctic ecozone (*sensu* Mitchell 2017; Suppl. material 1: Fig. S1), which includes Europe, North Africa, and the Middle East, on which we had a better knowledge and a better access to information sources, to increase the quality of the data researched rather than the quantity. The study is to be understood as an example of how the relative importance of factors from several aspects of CBC changes, when analysed in a more holistic context. Nevertheless, it may lead to suggested approaches for improving the success of future biological control introductions.

Methods

Data compilation

The basis for all analyses in this report is the BIOCAT catalogue of introductions of insects for the CBC of insect pests (Greathead and Greathead 1992; Cock et al. 2016). The simple spreadsheet database includes information from the published literature up until the year 2010 to provide some details of all biological control agents, target pests, introduction location and date, and the success of the introduction in terms of establishment and various levels of control. Data from 2011 on were not included because they were not yet completely updated at the time of the analysis. A detailed description of the database and an overview of trends in the use of insects for the CBC of insect pests is provided by Cock et al. (2016). For the present analyses, we filtered the database to extract entries for the Greater Western Palearctic ecozone (Suppl. material 1: Fig. S1) and added 15 new variables that were either populated based on existing variables in the database or based on information from published peer-reviewed scientific literature or available grey literature (i.e., reports). The new variables are described below and Table 1 provides an overview of the variables and their categories.

- Biological control agent feeding strategy: Either insect predator or parasitoid, based on the taxonomy and description of the species' life-history.
- Biological control agent host range: This variable was divided into four categories: monophagous (feeding on species within the same genus), oligophagous (feeding on species within the same family), polyphagous (feeding on species of several families or orders) or unknown (when no conclusive information about the host range was found). Information was retrieved from the scientific and grey literature. A valuable source for this variable and others related to the agent was Gerber and Schaffner (2016).
- Life-stage killed by the biological control agent: This variable was divided into five categories and populated from the scientific and grey literature. The categories were: eggs, larvae, larvae and adults, all stages, and other. The latter includes rare cases (<20) of more than one killed life-stages, such as eggs and adults, larvae and pupae, pupae, adults, and other combinations.
- Parasitoid feeding behaviour: This variable was created for parasitoids as agents only, which were categorised into endoparasitoids (feeding and developing within the body of their host) and ectoparasitoids (feeding and developing externally on the body of the host).
- Parasitoid brood size: This variable was created for parasitoids as agents only, which were categorised into solitary (only one offspring is ever produced per host) or gregarious (several offspring may be produced from a single host). As the brood size of a parasitoid species can vary depending on the host species or even host size, a parasitoid that has variable brood sizes was considered to be gregarious. The information was retrieved from the literature. In cases for which no information was found, the brood size was categorised as unknown.

- **Parasitoid attack strategy:** This variable was created for parasitoids as agents only, which were categorised into koinobionts (allow hosts to continue to grow in size after parasitism) and idiobionts (the host does not grow in size after parasitism and is often paralysed by the parasitoid). The information was retrieved from the literature. In cases for which no information was found, the attack strategy was categorised as unknown.
- **Target pest feeding guild:** Based on their relative abundance within different feeding guilds, targets were divided into three categories: borers (includes borers, gall inducers, miners, and tubers), defoliators, and sap feeders (mostly Hemiptera). The information was retrieved from the literature.
- **Target pest host range:** The classification was the same as for agent host range, but because of the relatively low frequency of mono- and oligophagous target species, only two categories were created: (1) mono- and oligophagous, and (2) polyphagous. The Crop Protection Compendium (2019) and the Invasive Species Compendium (2019) were the main sources to populate this variable.
- **Target pest voltinism:** Targets that only undergo one generation per year were categorised as being univoltine and those that undergo more than one generation per year as multivoltine. Targets that take more than one year to complete one generation were categorised as being univoltine, and those that may undergo one or several generations per year (e.g. based on climatic conditions) were categorised as being multi-voltine. The information was retrieved from the literature.
- **Host plant attacked by the target pest:** The main host plants of the target insect were categorised as woody, herbaceous, or mixed (woody and herbaceous hosts). The information was mainly obtained from the Crop Protection Compendium (2019) and the Invasive Species Compendium (2019).
- **Plant parts attacked by target pest:** Based on the frequency of occurrence, targets were divided into four categories: shoot (stem and leaves), reproductive (flowers, fruits, seeds), both shoot and reproductive, and other (root, and other combinations).
- **Number of introductions:** For this variable, the database was collapsed to agent species-target species combinations and the number of introductions of one agent species against the same target species into the analysed area was counted.
- **Successful establishment:** This binomial variable was created based on BIOCAT's "Impact code". A "0" was assigned to introductions that led to no, temporary, or not known establishment (impact code <1) and a "1" was assigned to introductions that led to permanent establishment (impact code ≥1).
- **Successful impact:** Also this binomial variable was created based on BIOCAT's "Impact code". A "0" was assigned to introductions that led to no impact on the pest population (impact code <1.5) and a "1" was assigned to introductions that led to either partial control (reduced pest status but other control methods or agents are needed), substantial control (other control methods or agents are needed occasionally or in small areas only), or complete control (no other control required) (impact code ≥1.5).
- **Complete control:** As for successful establishment and impact, this binomial variable was created based on BIOCAT's "Impact code", with the difference that a "1"

was only assigned to introductions that led to complete control of the target (no other control required; impact code =2). All other cases (impact code <2) were assigned a “0”.

Agent voltinism was not considered, because too few agents that were introduced into the analysed area were exclusively univoltine (n = 18).

Statistical analyses

Summary statistics were calculated with various Microsoft Excel functions using two modes: (1) Considering all introductions included in the database regardless if the same species was introduced once or several times against the same target; and (2) collapsing the database to unique combinations of an agent species introduced against a target species (henceforth called agent-target combinations) and keeping track of the number of introductions per unique species combination as a variable (see above), as well as calculating the sums of successful establishment, impact, and control for each combination separately. For the description of the trends over time, a decade is defined as a ten-year period and named based on their shared tens digit, from a year ending in a 0 to a year ending in a 9. For example, the period from 1960 to 1969 is the 1960s.

To assess the effect of the above described factors on (1) agent establishment, (2) impact of the agent on the target, and (3) complete control of the target, three separate Generalised Linear Mixed-Effects Models (GLMMs) with a binomial frequency distribution (logistic regressions) were conducted using the *glmmTMB* function of the package with the same name (Brooks et al. 2017) in R (R Core Team 2019). Success was used as dependent binomial variable and each full model included nine single factors and four interactions (see Table 1) as fixed effects, as well as random effects

Table 1. Independent variables used in the full models for CBC agent establishment, target impact (partial to complete control), and target control (no other control is needed).

| Independent variable | Levels | Description |
|---|------------|--|
| Agent feeding strategy | 2 | predator, parasitoid |
| Agent host range | 4 | mono-, oligo-, polyphagous, unknown |
| Life-stage killed by the agent | 5 | eggs, larvae, larvae & adults, all stages, other |
| Parasitoid feeding behaviour ¹ | 2 | endoparasitoid, ectoparasitoid |
| Parasitoid brood size ¹ | 3 | solitary, gregarious, unknown |
| Parasitoid attack strategy ¹ | 3 | koinobiont, idiobiont, unknown |
| Target feeding guild | 3 | borers, defoliators, sap feeders |
| Target host range | 2 | (1) mono- and oligophagous, (2) polyphagous |
| Target voltinism | 2 | univoltine, multivoltine |
| Plant attacked by target | 3 | herbaceous, woody, both |
| Plant parts attacked by target | 4 | shoot (stem and leaves), reproductive (flowers, fruits, seeds), shoot & reproductive, other (root, and other combinations) |
| Number of (Nº) introductions | Continuous | Number of introductions within agent-target combinations (1–34) |
| Nº Introductions × Agent feeding strategy | NA | Interaction |
| Nº Introductions × Target feeding guild | NA | Interaction |
| Nº Introductions × Target voltinism | NA | Interaction |
| Nº Introductions × Plant attacked by target | NA | Interaction |

¹ Only included as independent variable in models for parasitoids as biological control agents.

on agent and target species to account for correlations within agent-target combinations. The addition of more interaction terms as fixed effects led to problems with model convergence. A separate set of three logistic regressions was conducted for only parasitoids as agents, for which three additional factors were considered (Table 1). All models were tested for collinearity of fixed effects using the *check_collinearity* function of the PERFORMANCE package (Lüdtke et al. 2020). Fixed effects that led to high correlation (variance inflation factor (VIF) >10) or moderate correlation (VIF >5<10) were removed sequentially, starting with the fixed effects displaying the highest VIF, until only low correlations (VIF<5) were present. All models with the remaining fixed effects were then tested for overdispersion of residuals using a Pearson chi-square test.

Results

Spatio-temporal trends of CBC

In Europe, North Africa, and the Middle East, the first recorded introduction of an insect as a biological control agent against another insect was done by Egypt in 1890 with the introduction of the coccinellid *Rodolia cardinalis* from Australia against the cottony cushion scale *Icerya purchasi* (Hemiptera: Margarodidae), an invasive species from Australasia damaging citrus. The introduction was successful in that the agent became established and led to a complete control of the target. From this first case until the year 2010, a total of 780 introductions of insects for biological control of insect pests were undertaken in the analysed area.

From the 1890s to the 1960s the number of introductions per decade steadily increased up to a maximum of 120 attempts (Fig. 1A). Only in the 1940s the number briefly recessed, coinciding with World War II. After a maximum of CBC attempts in the 1960s, the increasing use of widely available chemical insecticides can be linked to the lower number of CBC agent introductions in the following three decades. However, in the 2000s a steep decline followed, which brought the number of introductions down to only 20. This low number of introductions can be attributed to emerging concerns towards the use of CBC, especially regarding adverse nontarget effects on native biodiversity (Howarth 1983, 1991). Over the whole period, the majority of the introductions (83%; Fig. 1B) were done against pests of woody plants, and thus, the above-described trends are dominated by those introductions.

The success of the introductions varied over time, but in contrast to the number of introductions, it does not exhibit an equally clear trend (Fig. 1C). While establishment and impact remained relatively high until the 1940s, successful control steadily declined until the 1950s. The reasons for this remain unclear, but may be due to the fact that, at first, CBC was used against the most obvious targets, while it became more experimental after that. From the 1940s to the 1990s, successful establishment increased, while control and impact increased as well, but at a lower rate, starting in the 1950s and 1960s, respectively. From the 1980s and 1990s to the 2000s, a decline at all levels of success is

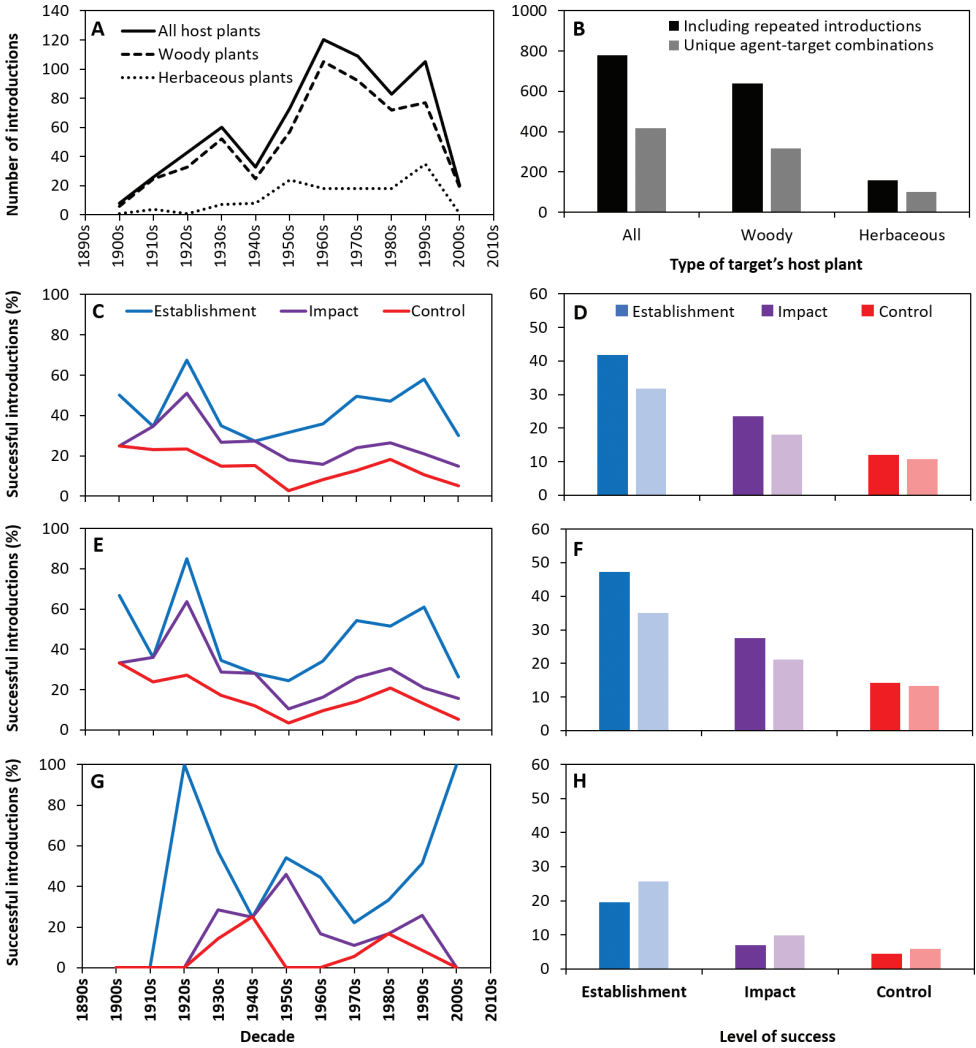


Figure 1. Number and success of classical biological control (CBC) introductions. Upper two panels **A** number of introductions of CBC agents per decade introduced in Europe, North Africa, and the Middle East against pests on (full line) all plants, (dashed line) woody plants, and (dotted line) herbaceous plants **B** total number of introductions for all target host plants, woody plants, and herbaceous plants (black bars) including repeated introductions of agents against the same target and (grey bars) for unique agent-target combinations. Note that some targets feed on both woody and herbaceous plants. Lower six panels: Percentage of successful biological control introductions (left side) per decade and (right side) overall, against pests on **C, D** all plants **E, F** woody plants, and **G, H** herbaceous plants. Success was measured in terms of (blue line) agent establishment, (purple line) partial to complete control of the target (i.e., impact), and (red line) substantial to complete control (i.e., control). Repeated introductions within specific agent-target combinations are included in the calculation of the percentages per decade and in full-coloured bars. Light-coloured bars indicate percentages based on unique agent-target combinations.

visible, which could possibly be attributed to the fact that in this period, the selection of a CBC agent became increasingly based on its specificity and less on its efficacy. The overall success of agent establishment was 41.8% (and 31.7% when excluding repeated introductions of same agent-target combinations and analysing the best possible outcome), 23.6% for impact on the target (18.0% without repeated introductions), and the overall success of complete target control was 12.1% (10.8% without repeated introductions) (Fig. 1D). When analysing the temporal trends of successful CBC against pests of woody and herbaceous plants separately, it becomes evident that also here the patterns of success for woody plants (Fig. 2E) followed closely the pattern of all introductions combined, while the ones for herbaceous plants were more erratic (Fig. 2G), due to the low number of introductions in some decades (Fig. 1A). The overall success of CBC was considerably higher when targeting pests of woody plants, compared to those of herbaceous plants (Fig. 1E–H): The success of establishment was more than twice as high for woody plants (47.2 vs. 19.5%), the impact on target pests was almost four times as high (27.5 vs. 6.9%), and the control of pests more than three times as high (14.2 vs. 4.4%). When including repeated introductions, the overall success of CBC of all pests together (Fig. 1D) and pests of woody plants (Fig. 1F) was always higher than for unique agent-target combinations. However, for pests of herbaceous plants (Fig. 1H), it was the opposite because of several unsuccessful repeated introductions, such as the two-spotted stink bug *Perillus bioculatus* (Hemiptera: Pentatomidae) that was introduced to Europe 19 times against the Colorado potato beetle *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) without any successful establishment, impact, or control.

Eight countries were responsible for more than two thirds (70.5%) of all introductions: Israel (16.3%), Italy (14.0%), Former USSR (10.1%), France (7.3%), Greece (7.1%), Spain (6.0%), Egypt (5.3%), and Cyprus (4.4%). Within these countries, the percentage of complete target control was very variable, ranging from 19.1 in Spain to 5.5 in Israel (Table 2).

CBC attempts were conducted for a total of 416 agent-target combinations. From these combinations, 78% of the agents were parasitoids (Fig. 2A), within which endophagous, solitary, and koinobiont parasitoids dominated (Fig. 2D–F). The majority of agents were known to be either oligophagous (39%) or polyphagous (35%) and fewer are described as monophagous (13%). For 13% of the analysed targets, no information was found about their specificity (Fig. 2B). Biological control agents attacking larvae (36%) or larvae and adults (30%) were clearly predominant (Fig. 2C). Considering the targets, sap feeders, polyphagous, and multivoltine species dominated (Fig. 2G–I). Furthermore, 70% of the targets were pests of woody plants and the majority fed on shoots, or shoots and reproductive plant parts (Fig. 2J, K). In most cases (74%), only one introduction per agent-target combination was done, and in only 11 cases, the number of introductions was above eight (mean = 1.9; Fig. 2L).

CBC agents released in the Greater Western Palearctic ecozone for the described time period belonged to 33 insect families. Within the agent-target combinations, four

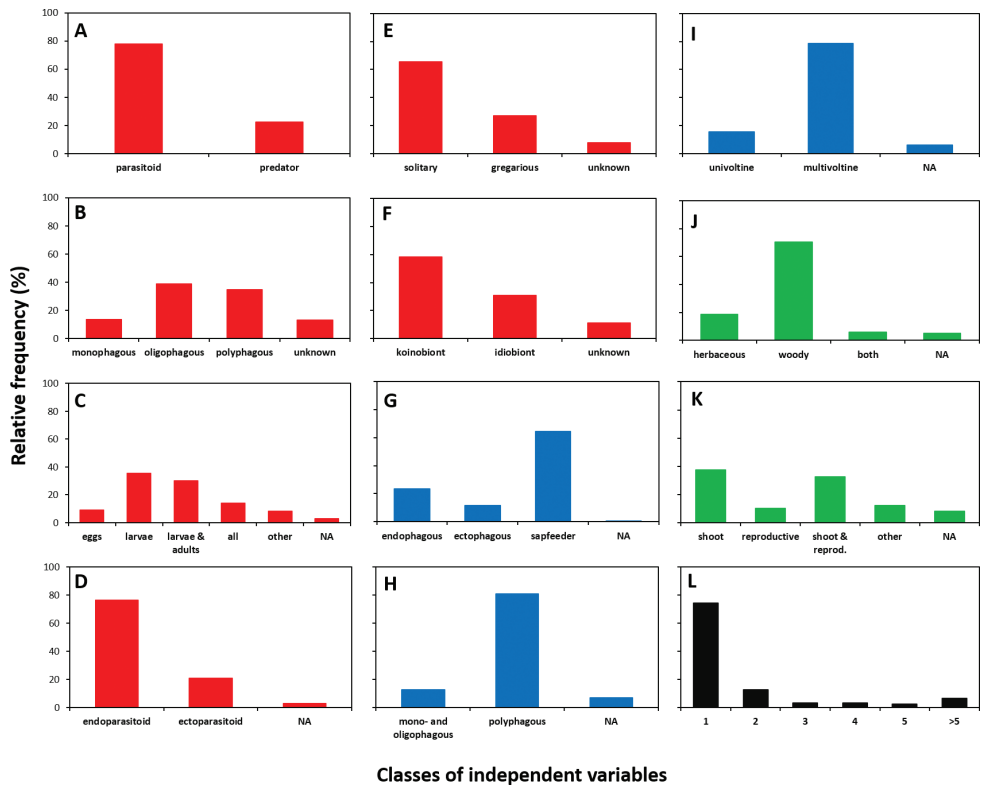


Figure 2. Relative frequency of independent variable classes related to (red bars) biological control agents, (blue bars) biological control targets, (green bars) host plants of targets, and (black bars) management **A** agent feeding strategy **B** agent host range **C** life-stage killed by the agent **D** parasitoid feeding behaviour **E** parasitoid brood size **F** parasitoid attack strategy **G** target feeding guild **H** target host range **I** target voltinism **J** plant attacked by target **K** plant parts attacked by target, and **L** number of introductions within agent-target combinations.

insect families made up 72% of all agents, with the three most abundant ones (Aphelinidae, Encyrtidae, and Coccinellidae) being agents attacking targets belonging to the insect order Hemiptera (Fig. 3A). When plotting the successful complete control against the relative abundance of agent families, the overall trend is positive, showing that the most often used agent families (especially Aphelinidae, Encyrtidae, and Coccinellidae) are also most successful. Only Braconidae stand out to contribute below average to target control (Fig. 3B). When considering the relationship between establishment and impact on target species, most agent families are very close to the positive regression line ($R^2=.61$) and only Ichneumonidae stand out, as none of the established agents of this family had a considerable impact on target populations (Fig. 3C).

With 36 insect families, the biological control targets were similarly diverse as the agents. However, the top 72% of targets comprised eight families, which is twice the amount of the top agent families. Not surprisingly, the six most abundant target fami-

Table 2. Countries in Europe, North Africa, and the Middle East and their respective number of introductions of biological control agents, agents established, targets impacted, and targets controlled. Target impact is defined as partial (reduced pest status) to complete (no other control needed) control and target control is defined as substantial (other control needed occasionally) to complete control. Percentages (numbers in parentheses) are calculated for all countries for which at least 10 introductions are recorded in the BIOCAT database.

| Country | Number of introductions | Agents established Number (%) | Targets impacted Number (%) | Targets controlled Number (%) |
|-----------------------|-------------------------|----------------------------------|--------------------------------|----------------------------------|
| Israel | 127 | 43 (33.9) | 15 (11.8) | 7 (5.5) |
| Italy | 109 | 48 (44.0) | 30 (27.5) | 20 (18.3) |
| Former USSR | 79 | 20 (25.3) | 12 (15.2) | 6 (7.6) |
| France | 57 | 24 (42.1) | 16 (28.1) | 4 (7.0) |
| Greece | 55 | 20 (36.4) | 12 (21.8) | 8 (14.5) |
| Spain | 47 | 30 (63.8) | 25 (53.2) | 9 (19.1) |
| Egypt | 41 | 14 (34.1) | 7 (17.1) | 6 (14.6) |
| Cyprus | 34 | 22 (64.7) | 5 (14.7) | 3 (8.8) |
| Former SFR Yugoslavia | 21 | 0 (0.0) | 0 (0.0) | 0 (0.0) |
| Former Czechoslovakia | 19 | 3 (15.8) | 0 (0.0) | 0 (0.0) |
| Turkey | 17 | 10 (58.8) | 7 (41.2) | 2 (11.8) |
| United Kingdom | 15 | 4 (26.7) | 3 (20.0) | 2 (13.3) |
| Germany | 14 | 5 (35.7) | 5 (35.7) | 0 (0.0) |
| Morocco | 13 | 8 (61.5) | 3 (23.1) | 2 (15.4) |
| Poland | 13 | 1 (7.7) | 1 (7.7) | 0 (0.0) |
| France (Corsica) | 11 | 10 (90.9) | 8 (72.7) | 3 (27.3) |
| Oman | 11 | 8 (72.7) | 2 (18.2) | 2 (18.2) |
| Portugal | 8 | 6 | 3 | 3 |
| Switzerland | 8 | 6 | 6 | 2 |
| Georgia | 8 | 4 | 4 | 2 |
| Malta | 6 | 4 | 4 | 3 |
| Tunisia | 6 | 5 | 3 | 2 |
| Ukraine | 6 | 2 | 0 | 0 |
| Iran | 5 | 1 | 0 | 0 |
| Russia | 5 | 1 | 1 | 0 |
| Syria | 5 | 5 | 0 | 0 |
| Austria | 4 | 3 | 1 | 1 |
| Algeria | 3 | 2 | 0 | 0 |
| Belgium | 3 | 1 | 1 | 1 |
| Spain (Canary) | 3 | 2 | 1 | 0 |
| Czech Republic | 2 | 2 | 0 | 0 |
| Hungary | 2 | 0 | 0 | 0 |
| Ireland | 2 | 2 | 2 | 2 |
| Portugal (Azores) | 2 | 0 | 0 | 0 |
| Spain (Balearic) | 2 | 2 | 1 | 0 |
| Sweden | 2 | 2 | 2 | 1 |
| Yemen | 2 | 1 | 0 | 0 |
| Afghanistan | 1 | 1 | 0 | 0 |
| Azerbaijan | 1 | 0 | 0 | 0 |
| Croatia | 1 | 0 | 0 | 0 |
| Denmark | 1 | 1 | 1 | 0 |
| Greece (Crete) | 1 | 1 | 1 | 1 |
| Greece (Rhodes) | 1 | 0 | 0 | 0 |
| Italy (Cuneo) | 1 | 0 | 0 | 0 |
| Jordan | 1 | 1 | 1 | 1 |
| Lebanon | 1 | 0 | 0 | 0 |
| Portugal (Madeira) | 1 | 0 | 0 | 0 |
| Saudi Arabia | 1 | 1 | 1 | 1 |
| Slovenia | 1 | 0 | 0 | 0 |
| Uzbekistan | 1 | 0 | 0 | 0 |
| Grand Total | 780 | 326 (41.8) | 184 (23.6) | 94 (12.1) |

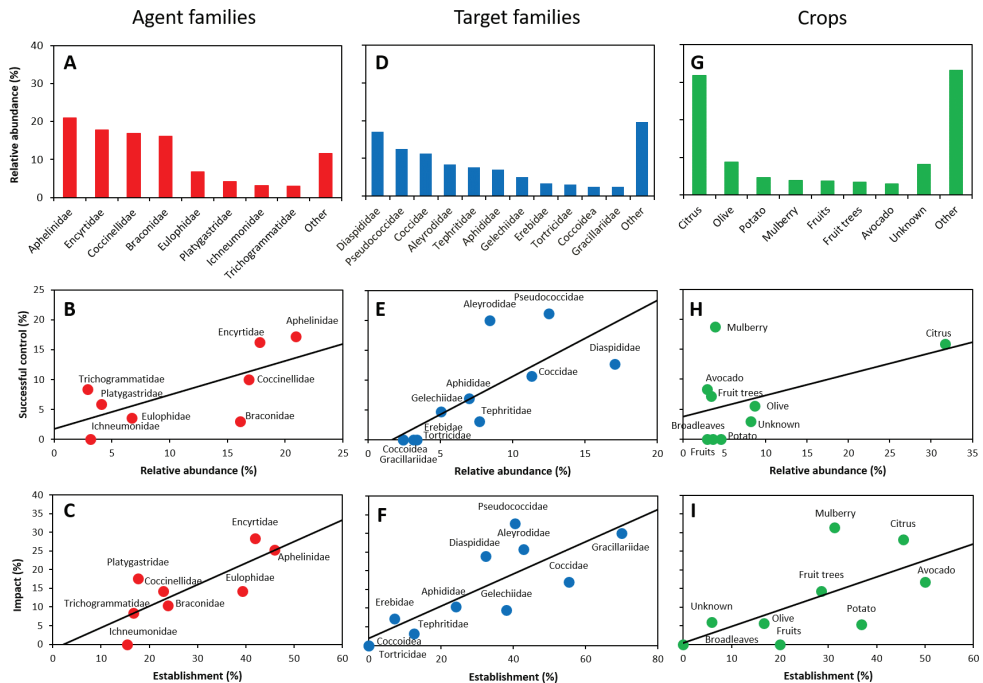


Figure 3. Descriptive statistics of (red) biological control agent families, (blue) biological control target families, and (green) plant groups. Upper row: Relative abundance of **A** agent and **D** target families, and **G** crops represented in introductions for biological control against insects in the analysed area (Europe, North Africa, and the Middle East). Middle row: Relationship between the relative abundance of **B** agents **E** targets, and **H** crops in all introductions and successful complete control of the target. Lower row: Relationship between the percentage of agent establishment and the percentage of partial to complete control (impact) of the target for the most abundant **C** agent and **F** target families, and **I** crops. Repeated introductions of agent-target combinations are not considered.

lies (Diaspididae, Pseudococcidae, Coccidae, Aleyrodidae, Tephritidae, and Aphididae) belong to the order Hemiptera, the insect order in which the above described majority of agent families are specialised (Fig. 3D). Given their relative abundance, the successful control of pests belonging to the families Aleyrodidae and Pseudococcidae is above average (Fig. 3E) and agents also have an above average impact on Pseudococcidae when considering their percentage of successful establishment (Fig. 3F).

Almost one third (31.7%) of crops attacked by the target pests were citrus, followed by olive (8.7%), potato (4.6%), mulberry (3.9%), various fruits (3.6%), various fruit trees (3.4%), and avocado (2.9%; Fig. 3G). A wide variety of other crops including woody and herbaceous plants were included into the category “other”, which made up 33.2% of all crops attacked. In 8% of all cases no information about the attacked crop was found. Considering these relative abundances, the success of controlling mulberry pests was clearly above average, while none of the pests of other fruits and potato were completely controlled (Fig. 3H). Also, when considering the relationship between suc-

Table 3. Analysis of Deviance Tables (Type II Wald chi-square tests) for fixed effects of the logistic regressions testing the factors influencing biological control agent establishment, impact of the agent on the target species, and complete control of the target species, considering **A** all biological control agents (predators and parasitoids) and **B** parasitoids as biological control agents only.

| Variable | Establishment | | | Impact | | | Control | | |
|---|-----------------|----|-------------------|-----------------|----|---------------|-----------------|----|---------------|
| | χ^2 -value | df | P | χ^2 -value | df | P | χ^2 -value | df | P |
| (A) All agents (Predators and parasitoids) | | | | | | | | | |
| Number of (№) introductions | 17.9290 | 1 | <0.0001 | 12.5121 | 1 | 0.0004 | 0.7041 | 1 | 0.4014 |
| Agent feeding strategy | 6.3983 | 1 | 0.0114 | 1.6525 | 1 | 0.1986 | 0.1924 | 1 | 0.6609 |
| Agent host range | 2.8100 | 3 | 0.4219 | 4.0226 | 3 | 0.2590 | 5.3605 | 3 | 0.1472 |
| Target feeding guild | 17.3652 | 2 | 0.0002 | 8.9079 | 2 | 0.0116 | 7.6286 | 2 | 0.0221 |
| Target host range | 0.2938 | 1 | 0.5878 | 0.6057 | 1 | 0.4364 | 1.0514 | 1 | 0.3052 |
| Target voltinism | 0.4109 | 1 | 0.5215 | 0.1767 | 1 | 0.6743 | 0.0001 | 1 | 0.9915 |
| Plant attacked by target | 1.5464 | 2 | 0.4615 | 2.4780 | 2 | 0.2900 | 1.7736 | 2 | 0.4120 |
| Plant parts attacked by target | 12.5481 | 3 | 0.0057 | 0.5769 | 3 | 0.9017 | 0.6256 | 3 | 0.8906 |
| № Introductions × Agent feeding strategy | 0.0556 | 1 | 0.9491 | 0.0556 | 1 | 0.8136 | 1.0702 | 1 | 0.3009 |
| № Introductions × Target voltinism | 5.2701 | 1 | 0.0217 | 4.5016 | 1 | 0.0339 | 3.2968 | 1 | 0.0694 |
| (B) Parasitoids only | | | | | | | | | |
| Number of introductions | 11.9774 | 1 | 0.0005 | 9.0146 | 1 | 0.0027 | 0.0037 | 1 | 0.9518 |
| Agent host range | 2.1136 | 3 | 0.5492 | 5.6368 | 3 | 0.1307 | 8.9607 | 3 | 0.0298 |
| Agent feeding behavior | 0.0299 | 1 | 0.8627 | 0.0153 | 1 | 0.9017 | 0.1627 | 1 | 0.6867 |
| Agent brood size | 1.3036 | 2 | 0.5211 | 0.4971 | 2 | 0.7799 | 0.0119 | 2 | 0.9941 |
| Agent's attack strategy | 1.3689 | 2 | 0.5044 | 2.0629 | 2 | 0.3565 | 1.1576 | 2 | 0.5606 |
| Target's life-stage killed by agent | 1.7470 | 3 | 0.6265 | NA | NA | NA | NA | NA | NA |
| Target feeding guild | 6.4020 | 2 | 0.0407 | 12.7859 | 2 | 0.0017 | 11.6543 | 2 | 0.0029 |
| Target host range | 0.0110 | 1 | 0.9164 | 1.3492 | 1 | 0.2454 | 1.0008 | 1 | 0.3171 |
| Target voltinism | 0.7702 | 1 | 0.3802 | 1.9263 | 1 | 0.1652 | 1.3506 | 1 | 0.2452 |
| Plant attacked by target | 1.5567 | 2 | 0.4592 | 3.4705 | 2 | 0.1764 | 3.3887 | 2 | 0.1837 |
| Plant parts attacked by target | 5.9048 | 3 | 0.1163 | 0.6848 | 3 | 0.8768 | 0.3072 | 3 | 0.9587 |
| № Introductions × Target voltinism | 4.8460 | 1 | 0.0277 | 4.9852 | 1 | 0.0256 | 4.4323 | 1 | 0.0353 |

successful establishment of agents and their impact on targets, mulberry pests were clearly impacted above average (Fig. 3I). Introductions of CBC agents against pests of all forest trees together (e.g. eucalyptus, pine, fir, which are among others within the category “other”) represented 11.5% of all introductions. From these, 14.6% led to agent establishment, 10.4% to impact on the agent, and 10.4% to complete agent control.

Main drivers of CBC success

The explanatory variables ‘number of introductions × plant attacked’, ‘number of introductions × target feeding guild’ and ‘life-stage killed by the agent’ were removed from all but one of the regressions due to high collinearity. The variable ‘life-stage killed by the agent’ remained in the regression analysing the success of establishment of parasitoids as CBC agents.

For all CBC agents together, the number of explanatory variables significantly influencing the outcome of CBC decreased with an increasing level of success, i.e. from establishment to impact to control (Table 3A). While for target control only the target's feeding guild was a significant variable, the impact of the agent was also significantly influenced by the number of introductions and the interaction of ‘number of

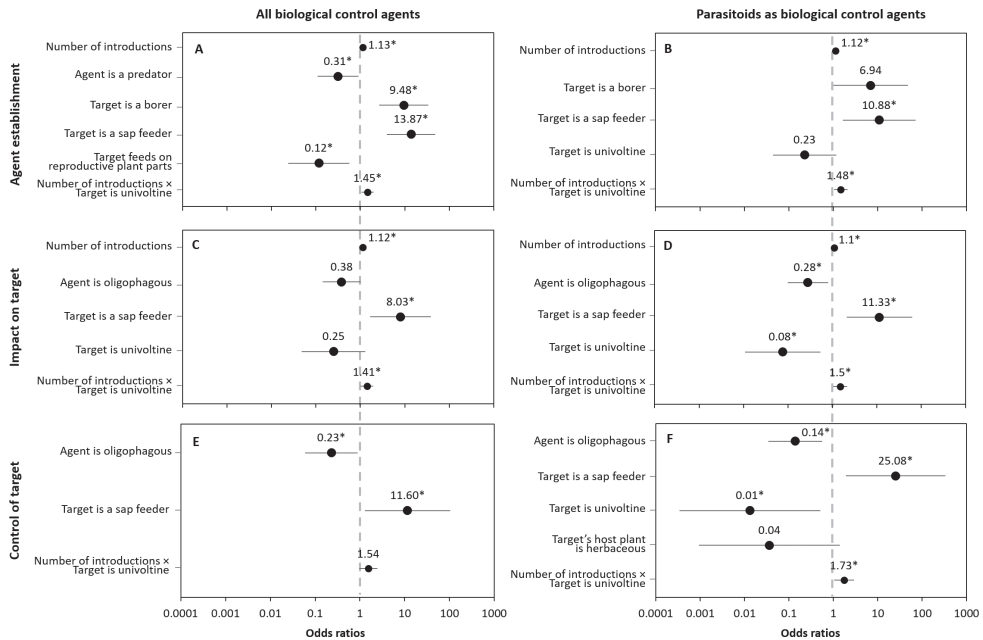


Figure 4. Back-transformed (odds ratios) significant estimates and 95% confidence intervals from the logistic regression determining the factors negatively (<1 , on the left of the dotted line) or positively (>1 , on the right of the dotted line) influencing the success of biological control introductions, for (left panels) all biological control agents and (right panels) parasitoids as biological control agents. Success was measured as (upper panels (A, B)) establishment of the agent, (middle panels (C, D)) impact on the target (partial to complete control), or (lower panels (E, F)) substantial to complete control of the target. Estimates with numbers followed by an asterisk (*) are statistically significant at $\alpha=.05$, those without an asterisk at $\alpha=.1$.

introductions × target voltinism', and agent establishment additionally by the agent's feeding strategy and the plant parts attacked by the target.

In contrast to models for all CBC agents together, for parasitoids the number of significant explanatory variables remained the same at all three levels of success (Table 3B). For all three models, the explanatory variables feeding guild and the interaction 'number of introductions × target voltinism' were significant. For agent establishment and impact on the target, the single variable of the number of introductions was also significant, but for target control the third significant variable was the agent's feeding behaviour.

The models' estimates for predators and parasitoids together revealed that keeping all other variables constant, the odds for agent establishment significantly increased with the number of introductions against specific agent-target combinations, when the target was a borer (endophagous) and when it was a sap feeder, as well as by an interaction of the number of introductions and the target being univoltine. But agent establishment significantly decreased when the agent was a predator, and when the target fed on reproductive plant parts (Fig. 4A; Suppl. material 1: Table S1). The only difference when analysing parasitoids as CBC agents alone was that borer as targets only had the tendency ($.05 > \alpha < .10$) to increase the success of establishment (Fig. 4B; Suppl. material 1: Table S2).

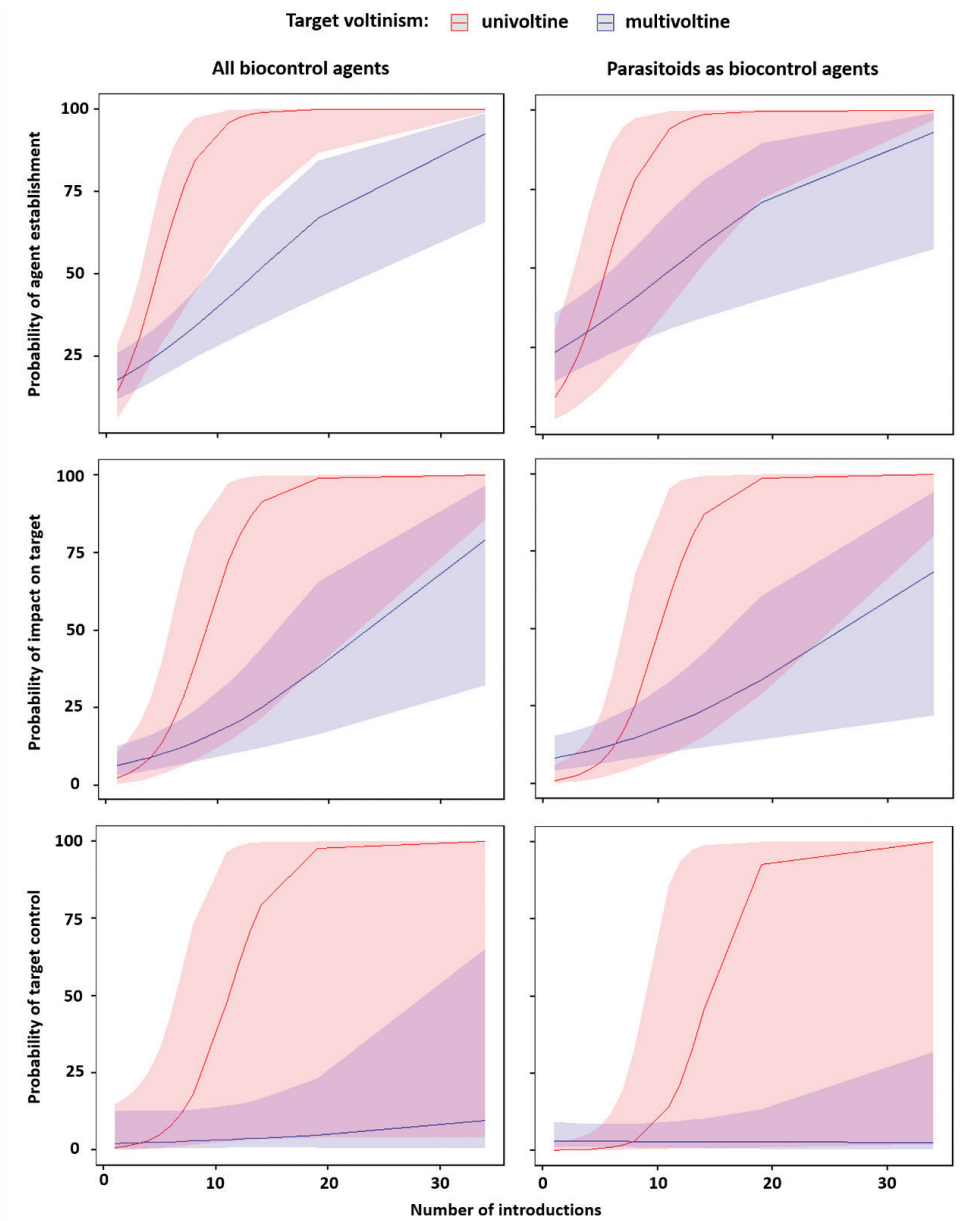


Figure 5. Model predictions for the influence of the interaction between number of introductions within agent-target combinations and target voltinism (red=univoltine, blue=multivoltine) on the probability of (upper panels) agent establishment, (middle panels) impact on target, and (lower panels) target control, by (left panels) all biological control agents and (right panels) only parasitoids as biological control agents.

The impact on targets was also positively influenced by the number of introductions against specific agent-target combinations, by sap feeders as targets, and by the interaction of the number of introductions and univoltine targets, but only had the tendency to be negatively influenced ($.05 > \alpha < .10$) when agents were oligophagous and

targets univoltine (Fig. 4C; Suppl. material 1: Table S1). The latter two estimates significantly negatively influenced the impact of parasitoids on targets (Fig. 4D; Suppl. material 1: Table S2).

The odds to control a target significantly decreased when the agent was oligophagous but significantly increased with sap feeders as targets. It had also the tendency to be positively influenced by the interaction of ‘number of introductions × univoltine targets’ (Fig. 4E; Suppl. material 1: Table S1). However, for control by parasitoids, additionally univoltine targets significantly decreased the odds of target control but the interaction term ‘number of introductions × univoltine targets’ significantly increased it. Furthermore, there was a tendency of herbaceous host plants of target pests to decrease the odds of control (Fig. 4F; Suppl. material 1: Table S2).

A graphical analysis of the interaction between the number of introductions and target voltinism for each level of success separately (establishment, impact, and control) shows that for both univoltine and multivoltine targets the probability of success increased with the number of introductions. However, for univoltine species an asymptote at 100% probability of success was reached at 10–20 introductions, while for multivoltine species the relationship was rather linear, with a decreasingly steep slope at increasing levels of success (establishment > impact > control; Fig. 5). For parasitoids alone, the only difference is that there was more overlap in the confidence intervals at the level of agent establishment and less variability in the probability of agent control for multivoltine species at high numbers of introductions (Fig. 5).

Discussion

The overall success of biological control introductions of insect predators and parasitoids against herbivorous insects in Europe, North Africa, and the Middle East is comparable to the success of CBC worldwide (Cock et al. 2016). The dominance of introductions against pests of woody plants, however, is markedly higher in the area analysed here (70%), when compared to the worldwide percentage (55%; Kenis et al. 2017). This can be attributed to the high number of introductions against pests on citrus, e.g. in Israel, Spain, and Italy.

Until the 1990s, it was common practice to collect several agent species in the area of origin of the target and release them with no or only a minimum of studies in the invasive range of the pest. Our analysis shows that in Europe, North Africa, and the Middle East these rather uninformed and hasty introductions led to a slight increase in agent establishment but less frequently to a sufficient impact on the target. Furthermore, these introductions were often only attempted once for any given agent species, which can explain the high percentage of one-time introductions for agent-target combinations (74%). In fact, as has also been shown in a global analysis of the BIOCAT catalogue (Cock et al. 2016), the percentage of success in terms of establishment, impact on the target or target control, seems to be independent of the number of species introduced for the biological control of a given pest. However, it seems undeniable that

the period of uninformed introductions decreased the overall percentage of success, when compared to the time between the 1900s and 1940s. Concerns of undesirable non-target effects beginning in the 1980s (Howarth 1983, 1991) and the resulting focus on specificity and less on efficacy of CBC agents, led to a further decrease of success until the 2000s. Thus, within one century of CBC in Europe, North Africa, and the Middle East, no overall increase in success was achieved, indicating that new ideas are needed about how to increase the success of CBC against insect pests.

On the other hand, we show here that for the agent-target combinations for which introductions have been repeated several times, a positive correlation between the number of introductions and success was found. There are several possible reasons why repeated introductions of the same agent against one target may lead to a higher probability of success. For example, if several introductions were made from different source locations, the more diverse genetic sources of the agents may lead to a higher possibility that at least one of the strains can well adapt to the new environment in the location of release (Hopper et al. 1993; Hoddle et al. 2015; Leung et al. 2020). On the other hand, a biological control agent might also have been introduced against the same target in different countries within the analysed ecozone, increasing the chance of finding a suitable habitat or climate in at least one of them. While the BIOCAT catalogue offers information on the source and release country for the agents, it is a tedious work to investigate the pathways of agents once they were introduced the first time into an ecozone. It might be possible to do it for some case studies but a detailed analysis of these possible mechanisms is beyond the scope of this study. There might also be a bias towards higher success with increasing numbers of introductions, i.e., when an agent from one source location was introduced into several locations because it already successfully controlled a target somewhere else. An example from our analysis are parasitoids of the family Aphelinidae, which once proven successful in aphid control, have been introduced more often and increased the percentage of successful control. Lastly, it is also possible that there is simply a positive learning curve with the number of introductions, so that success was warranted after a couple of failures from which the biological control practitioners could learn.

Regardless of the underlying mechanisms discussed above, we found that as few as 10 introductions increased the mean probability of agent establishment to 75% for univoltine species, and with 20 introductions success of CBC increased on all levels (establishment, impact, and control) to near 100%. However, those results were biased by the facts that in only 2.6% of agent-target combinations more than 10 introductions have actually been done, and that only 15.4% of targets were univoltine species. Nevertheless, it emphasizes the importance of the number of introductions for specific agent-target combinations for the success of CBC.

Interestingly, remarkably few agent-related factors significantly influenced the success of CBC. The odds of establishment decreased when agents were predators, a finding that has been repeatedly confirmed empirically by comparing the success of predators and parasitoids used in CBC programmes (e.g., Hawkins et al. 1999; Kimberling 2004; MacQuarrie et al. 2016; Kenis et al. 2017). The higher success rate of parasitoids

as well as the fact that they are generally more specific to their target than predators have led to them being used more often in CBC (Greathead and Greathead 1992; MacQuarrie et al. 2016; Kenis et al. 2017).

Furthermore, oligophagy of agents was negatively related to the impact and control of targets, which holds true when considering all CBC agents together or only parasitoids. Considering agent host range as a single factor, the overall success of target control was 21%, 8% and 10% (or 28%, 7%, 11% when considering repeated introductions) for mono-, oligo-, and polyphagous agents, respectively, which would suggest that rather monophagy is an advantageous characteristic over oligo- and polyphagy. Given the relatively low number of agents that were considered monophagous in this study (13.5%), the effect of agent host range on the success of CBC should be further assessed in a multiple regression context including data from additional regions of the world. Interestingly, oligo- and polyphagy have been mentioned in the literature as a desirable trait for CBC agents, e.g., to survive periods when target pest densities are low by switching to other prey/hosts (Bale et al. 2008). Nowadays, an insect's high degree of specificity to the target species is often a requirement for the import of a species as a CBC agent to prevent negative impacts on non-target species. However, host specificity can only be determined through extensive laboratory studies or field surveys before and after the introduction of a species. In the past, those studies were rather uncommon. While pre-release host specificity assessments are now routinely done in new CBC programmes, post-release monitoring studies are still not common (Van Driesche et al. 2008; Hajek et al. 2016). Therefore, it can be assumed that we overestimate host specificity in many cases, especially when relying on information from older studies, where no or few investigations of this CBC agent trait were done.

The factor with the strongest influence on the chances of success of CBC was related to the trophic guild of the target insect: sap feeders were the target feeding guild most likely to be successfully controlled. This result is consistent in our analyses through all levels of success and for both parasitoids and all agents combined. It is also consistent with results from previous analyses, where 'Homoptera' were repeatedly found to be the group of insect pests with the highest number of agent releases, establishments, and successful control (Hall and Ehler 1979; Hokkanen and Sailer 1985; Stiling 1990; Greathead and Greathead 1992). Also when considering specifically CBC attempts against insect pests of trees, the current suborder Sternorrhyncha was found to be targeted most often and with the highest percentage of success (Kenis et al. 2017). Examples for this in the region analysed here are (1) the eucalyptus psyllid *Ctenarytaina eucalypti* (Hemiptera: Psyllidae) that was targeted four times in Europe (France, Ireland and the UK) by the Australian parasitoid *Psyllaephagus pilosus* (Hymenoptera: Encyrtidae), each time leading to a complete control of the pest (Hodkinson 1999); and (2) the cottony cushion scale *Icerya purchasi* (Hemiptera: Monophlebidae), which attacks citrus trees and was targeted 13 times (each time in a different country of the Greater Palearctic Ecozone) by the cardinal ladybird *Rodolia cardinalis* (Coleoptera: Coccinellidae), resulting in 9 cases (69%) of the introductions to complete control of the target pest (Greathead 1976). Also in a global analysis of the BIOCAT catalogue,

Heimpel and Mills (2017) found success rates against sap sucking hemipteran insect families (Aleyrodidae and Aphididae) to be the highest. As possible reasons for this higher success, Mills (2006) suggested that compared to parasitoids of lepidopterans, parasitoids of “homopterans” have more frequently multiple generations per host generation and typically a broader range of host stages available for attack. However, one has also to consider a possible sampling bias in our analysis as 6 of the 10 most targeted insect families were sap feeders, the majority of which are pests of citrus.

Our analysis only comprises a limited number of factors from the various aspects of CBC that have been reviewed so far. Many other factors may significantly influence the outcome of biological control introductions. In our opinion, especially climate matching and management factors such as the timing, the quantity, and quality of CBC agents being released deserve more attention to increase the success of CBC programmes. However, for the majority of the introductions that have been done, the principal challenge might be the limited availability of information about many of the potentially important factors explaining their success or failure. To further advance in this direction, more data have to be gathered, for which a more rigorous documentation of CBC programmes and a wider availability of these data to scientists and biological control practitioners are paramount. Additionally, our analysis was restricted to data from Europe, North Africa, and the Middle East. Because results may change among ecozones, BIOCAT data from other ecozones or for the whole world should also be analysed.

Conclusions

The finding that only few CBC agent-related factors significantly influenced the success of CBC suggests that the reoccurring focus on agent-related traits is not justified and should be redirected to include lower trophic levels and other aspects of CBC, such as abiotic factors (i.e., climate) and management (e.g., release procedures). Indeed, Gross et al. (2005) already demonstrated that factors related to biological control targets and their host plants can effectively help to predict the success of introductions. Our study confirms this finding and identified factors of different aspects (agent, target, target host plant, and management) that significantly affect CBC at several levels of success: (1) Predators as CBC agents decreases the chances of establishment and oligophagous agents decrease the chances of impact and control; (2) sap feeders as targets increase the chance of success at all levels, borers as targets increase chances of agent establishment, and univoltine targets decrease the chances of impact and control; (3) when reproductive plant parts are attacked by the target the chances of agent establishment decrease; and (4) increasing numbers of introductions of the same agent against a specific target increases the chances of agent establishment and impact on targets. The latter also extends to target control by parasitoids when targets are univoltine. A summary of the results for woody plants can be found in the supplements (Suppl. material 1: Fig. S2).

The results from this study should be understood as a first step to give the incentive for a holistic, rather than an independent consideration of factors affecting the success of CBC. The analysis of the entire BIOCAT catalogue or an updated version including the more recent introductions should lead to further insights and help to develop decision support tools to increase the success of CBC at all levels.

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Supplementary material I

Supplementary tables and figures

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Data type: Tables and figures

Explanation note: **Table S1.** Model coefficients (estimate \pm standard error) and their level of significance in the logistic regressions for all biological control agents (predators and parasitoids) analysing variables impacting agent establishment, agent's impact on the target, and target control. **Table S2.** Model coefficients (estimate \pm standard error) and their level of significance in the logistic regressions for parasitoids as biological control agents, analysing variables impacting agent establishment, agent's impact on the target, and target control. **Figure S1.** The Greater Western Palearctic ecozone (sensu Mitchell 2017), comprising Europe, Northern Africa, and the Middle East, for which area the BIOCAT data were analysed here. **Figure S2.** Summary of the results for woody plants, depicting the percentages of overall success of biological control (red circles) for pests of woody plants with borers, defoliators, or sap feeders as target pests; predators or parasitoids as classical biological control (CBC) agents; and (black) single or multiple releases of an agent against the same target.

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