

Are exotic natural enemies an effective way of controlling invasive plants?

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Classical biological control (the introduction of exotic natural enemies) is often advocated as a tool for managing invasive species. Here, we review the effectiveness of biocontrol and explore the factors that determine whether it is an appropriate response to the invasive species problem. Although there have been some successes, biocontrol is generally poorly evaluated and, in many cases, its impact is unknown. In particular, there is limited understanding of the nature of the invasive species problem and no clear targets against which 'success' can be gauged. In addition, exotic natural enemies could act as invasive species in their own right. To improve the role of biocontrol in invasive species management, we need a better ecological understanding of the impacts of both the biocontrol agents and the target invasive species.

Introduction

Invasive species (see Glossary) threaten native biodiversity, agricultural productivity and ecosystem functioning, with estimated annual impacts amounting to millions of dollars [1]. Their global significance has prompted a wealth of research aimed at better understanding the processes of invasion and what attributes of either the invasive organism or the environment lead to certain exotic species dominating native communities (see Ref. [2] for a recent overview). Although not without controversy (e.g. Refs [3,4]), one mechanism that appears to be important in determining invasion success is escape from natural enemies [5–9]. If enemy release is important, re-establishing the link between the invader and natural enemies from its native range could provide an effective means of control. This is the aim of classical biological control, which endeavors to introduce host-specific natural enemies from the native range of the invader to reduce populations to levels at which they no longer cause significant agricultural or environmental damage [10–12]. As such, classical biological control represents an interesting situation of using one or more exotic species to control another.

Although biological control can result in sustained control [13], its success is rarely evaluated objectively or quantitatively [13]. Our aim here is to explore this issue to ask whether biocontrol is effective in controlling invasive species. We focus on biocontrol of invasive plants (weeds), although many of the factors that we explore extend to

other taxa such as insects or diseases. We begin with a meta-analysis to evaluate the 'effectiveness' of exotic natural enemies against environmental and agricultural weeds (Box 1), using Australia as a case history (we selected Australia because, along with the USA, it is at the forefront of biological control research and represents current best practice [10,14]). Having defined the state-of-the-art, we examine in more detail what constitutes successful control, to what extent natural enemies alone can meet control objectives, and we highlight some of the unexpected consequences of ineffective control. We conclude with recommendations for better practice to improve the role of biocontrol in invasive species management.

How effective is biocontrol?

Classical biological control has been used for invasive management in Australia for over 80 years. There have been some major successes, with certain weeds all but eliminated (e.g. control of *Opuntia* spp. [15]; *Chondrilla juncea* [16] and *Salvinia molesta* [17]). However, complete control (where the weed is no longer a significant problem) appears to be the exception rather than the rule [14]. Additionally, many estimates of effectiveness are qualitative, providing little detail about the level and extent of control and few insights into the factors that determine its success or failure [18].

Glossary

'Driver' versus 'Passenger' models: contrasting hypothesis for the causes and consequences of plant invasion. The 'driver' model predicts that invaded communities are highly interactive, with native species being limited or excluded by competition from the exotic dominants. The 'passenger' model predicts that invaded communities are primarily structured by non-interactive factors, such as environmental changes, which are less constraining on the exotics and which, therefore, dominate.

Classical biological control (biocontrol): the planned introduction and release of host-specific living natural enemies (such as parasites, pathogens and predators) from the native range of the weed (or pest) to reduce vigor, reproductive capacity, or density in the invaded range.

Ecosystem function: an intrinsic ecosystem characteristic related to the set of conditions and processes whereby an ecosystem maintains its integrity; includes processes such as decomposition, production, nutrient cycling, or fluxes of nutrients and energy.

Enemy release hypothesis: states that the success of an invasive species in the introduced range is due, in part, to their release from the negative effects of coevolved natural enemies left behind in the native range.

Exotic (or introduced) species: is a non-indigenous organism that has been introduced either accidentally or deliberately to a new location.

Invasive species: a species that does not naturally occur in a specific area and whose introduction does or is likely to cause economic or environmental harm.

Weed: a plant growing where it is not wanted and which interferes with the management objectives at a particular location.

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Box 1. Meta-analysis of biological control impact on invasive weeds in Australia

We used meta-analyses to assess quantitatively the effect of biocontrol on weeds in Australia (full details of the methodologies are given in the [Online Supplementary Information](#)). Quantitative data (appropriate for meta-analysis) were available for 130 biocontrol agents established against 39 weed species (representing 65% of weeds and 30% of established agents). Separate meta-analyses were used to assess the impact of biocontrol on a range of life-history and community measurements ([Figure 1](#)). Meta-analyses were also used to investigate how weed type influenced the effectiveness of biocontrol (see [Online Supplementary Information](#)). The results from each study were converted to a common effect size measure, in this case a correlation co-efficient (r). All meta-analyses were conducted using MetaWin software random-effect models (MetaWin 2.1, [81]). The risk of biased results owing to the ‘file-draw problem’ was assessed by calculating fail-safe numbers (N_R), which indicate the number of non-significant, unpublished observations that would need to be added to the meta-analysis to reject a statistically significant result [81,82].

The analyses revealed biocontrol to have a significant impact on six out of the seven selected measurements ([Figure 1](#)). The number, size or biomass of aboveground vegetative components declined in response to attack by biological control agents, although these impacts did not always lead to reductions in reproductive output at the individual plant level ([Figure 1](#)). The effect of biological control agents on belowground parts was less than for aboveground components, although fewer studies included these measurements ([Figure 1](#)). Biocontrol generally reduced target seedling and weed densities; however, these population-scale measurements were only covered by six and 19 (of 290) observations, respectively (seedling $N_R = 2.5$, weed density $N_R = 147$). Only two studies included plant community measurements ($N_R = 0.3$) and both found an increase in the abundance of other plant species with biocontrol, although it is not clear if these were exotics or natives. Both seedling density and plant community effect sizes are not reliable owing to low fail-safe numbers.

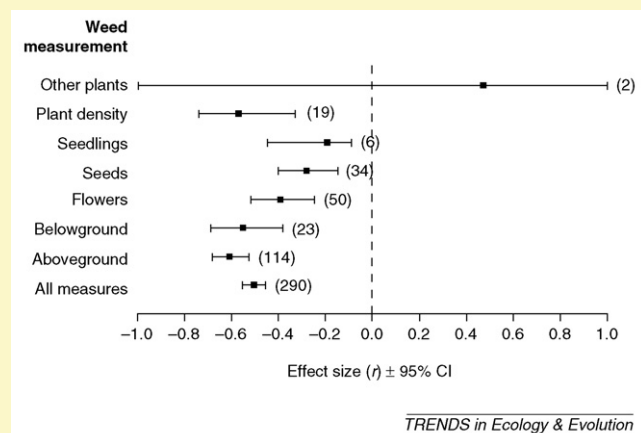


Figure 1. Effect of biocontrol on selected weed measurements. Data presented are mean effect sizes (r) \pm 95% CI, where r represents a correlation co-efficient and effects are considered significant if the 95% CIs do not overlap zero. Numbers in parentheses indicate the number of comparisons for each effect size. Biocontrol had a significant negative effect on most weed parameters, although low fail-safe numbers for seedling density and other plants indicate that these results are not reliable.

To evaluate effectiveness further, we present in [Box 1](#) a meta-analysis in which we determine the effect of exotic natural enemies (including insects, pathogens and mites) on a range of life-history parameters of 39 invasive weeds in Australia. The analysis revealed that appropriate quantitative data evaluating the effectiveness of biological

control exist for 30% of biocontrol agents that have become established and 65% of weed control programmes overall (but see caveats in [Box 1](#)). Where data exist, 75% of observations concentrate on evaluating the effect of a biocontrol agent on individual plant growth and reproductive parameters, rather than on key population-level measures, such as weed density. Given that reductions in plant performance can have little effect on weed abundance [19], such evaluations provide negligible information about actual agent impact.

The impact of biological control on plant community structure or function was also rarely evaluated, with only two studies investigating vegetation changes in response to biological control [20,21]. We also found no empirical studies that linked biological control impacts with increasing agricultural yields or replacement of the target weed by desired native species. These last two results are particularly striking and, although they could reflect a particular lack of data for Australia, other analyses of biocontrol elsewhere [19,22,23] suggest not; it appears we have little quantitative information to assess realistically the overall effectiveness of biological control. This is further confounded by a lack of appropriate benchmarks against which success can be evaluated [18]. Given this, how effective does an agent need to be to be successful? We explore this question by considering some of the different issues that apply to invasive species in agricultural environments (where the drivers are often economic) compared with natural environments (where the focus tends to be on ecological metrics).

Control of invasives in agriculture

An effective biocontrol agent should suppress the target to a level at which it no longer poses a significant problem. But what constitutes an acceptably low level and what impact does an agent need to have on the target population to achieve this? Several population modelling studies have explored these questions for particular invasive weed problems (e.g. Refs [24–28]). Here, we adopt a more conceptual approach, taking into consideration some economic perspectives that are relevant to invasive species that impact on agricultural productivity.

In an agricultural context, an invasive plant (or weed) is a problem when its density exceeds a certain threshold at which control is economically justified. [Figure 1a](#) shows illustrative impact-density functions representing two classes of weed with contrasting economic thresholds. A high economic threshold weed would include a weed such as Paterson’s curse *Echium plantagineum*, which is a problem in pastures because it is toxic to livestock. At low densities, livestock can avoid it, so its impact is minimal; however, at high densities, it is eaten, causing weight loss and even death [29]. A low threshold weed would apply to something such as a seed contaminant of grain, such as wild radish *Raphanus raphanistrum* [30]. Even a low level of contamination could have a large impact on the value of the commodity and ability to trade or export ([Figure 1a](#)). A range of other relationships (such as a simple straight line, where impact is proportional to density) can occur, but for brevity we restrict ourselves to these two extremes. Equally, although our focus is on weeds, equivalent linear

and non-linear high and low threshold density–damage relationships exist for pests and diseases [31–36].

These contrasting functions set different backgrounds for measuring the ‘success’ of a biocontrol programme (Figure 1b). That is, for a high threshold weed, there is a large initial benefit in reducing its abundance, whereas, for a low threshold weed, there is little benefit until abundance is reduced substantially. If we now superimpose the costs of biocontrol (Figure 1b), we can identify the point at which there is a net benefit. For the high threshold weed, net benefit accrues early and then gradually reduces to a point where biocontrol is no longer cost effective. The upshot of this is that even small reductions in weed abundance of just 5%, for example, can yield a net benefit (Figure 1b), yet with abundant weed populations remaining, few biocontrol programmes would classify this as a success. By contrast, given the initial insensitivity to change with the low threshold weed, net benefit accrues only after substantial reductions in weed abundance (Figure 1b). As such, it is possible that reductions of even 80–90% could still be considered failures. This has two important consequences. First, it identifies that invasive species (whether plant, pest or pathogen) with low economic or damage thresholds are likely to make difficult targets for biocontrol. Second, although introduction of an individual biocontrol species might be perceived as a failure, the action of several species together could enable the net benefit threshold to be exceeded (Figure 1b) (although this depends on whether successive agents act additively or synergistically, rather than in a substitutive or antagonistic manner).

There have been several cost–benefit studies of biocontrol (e.g. Refs [37–39]) and our current conceptual analysis is not meant to provide an in-depth economic framework. Rather our aim is to demonstrate how the nature of the impact–weed-density function sets the context for defining biocontrol success. Although this might seem obvious, it is striking how few quantitative data are available on the economic impact of weeds (an analysis of weeds in

Australia in 1998 revealed that, for 98% of cases, no information was readily available for the cost of individual weeds [40]; see also Box 1) and how rarely these are used for prospective evaluations [39] to define a ‘bench mark’ for gauging success of control. Such ‘bench marks’ will not only vary between weed species, but also between systems for particular species. A recent study of velvetleaf *Abutilon theophrasti* in soy beans, for example, identified that the level of control necessary to prevent this weed increasing in density was lower in a four-year crop rotation compared with a two-year rotation system, owing, in part, to the increased effectiveness of seed predators in the more diverse rotation system [41].

Control of invasives in the natural environment

For species that invade natural environments, the concerns tend to relate to impacts on biodiversity and associated ecosystem functioning. However, although the threat of invasive species to natural biodiversity is considered high, again there are few data available on the relationship between weed abundance and impact [11,40,42]. Where studies have been done, they tend to explore correlative relationships rather than determine causality [42]. This issue, at least in part, has led some to question the extent to which invasive species are a direct cause of biodiversity decline (e.g. ‘drivers’) or whether they are themselves simply responding to other forms of ecosystem change (e.g. ‘passengers’) [43].

Recently, a few studies have adopted manipulative approaches, based on invasive species removal, to better quantify impact and causality, and to distinguish between these ‘driver versus passenger’ models [44,45]. These studies demonstrate mixed results. Hulme and Bremner [45] showed an increase in species richness of up to 25% in response to removal of Himalayan balsam *Impatiens glandulifera* from riparian communities in north-east England; a result consistent with the ‘driver’ model. By contrast, MacDougall and Turkington [44] showed that, whereas some native plants responded positively to the removal of

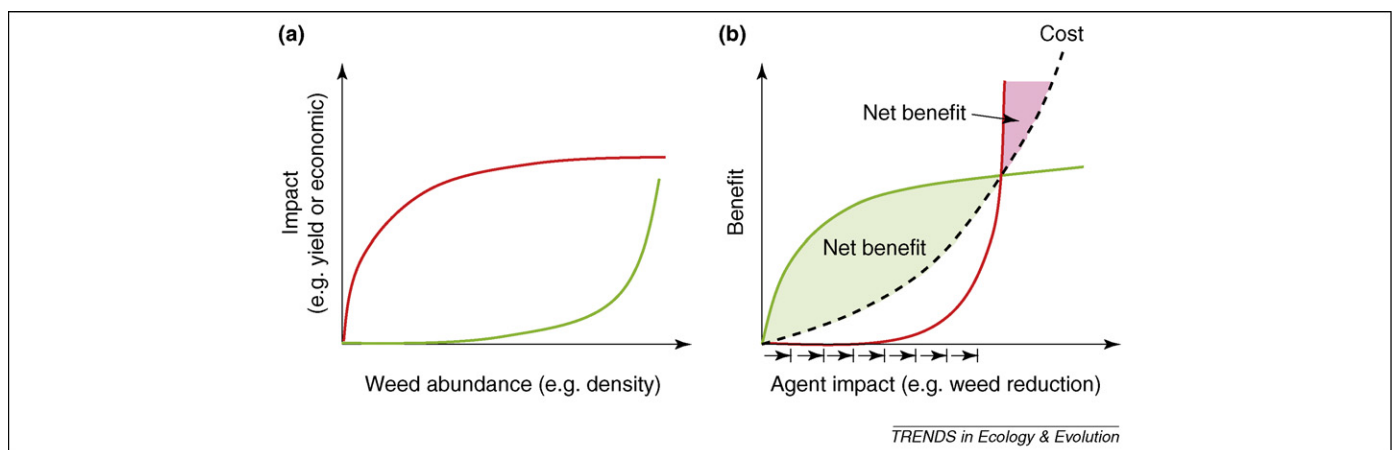


Figure 1. The benefits of biocontrol for an agricultural weed. (a) The economic impact of individual weeds varies from those causing minimal impact until a certain threshold density is exceeded (green line; e.g. Paterson’s curse *Echium plantagineum*), to those with high initial impact even at low densities (red line; e.g. wild radish *Raphanus raphanistrum*). (b) For the high threshold weed (green line), a single biocontrol agent that causes even a relatively small reduction in weed abundance from an initial high level (impact of individual agents indicated by arrows below the x-axis) can deliver a net benefit (green-shaded area). For the low threshold weed (red line), there is only a net benefit (red-shaded area) when weed abundance is reduced below a threshold, even if control is substantial (because weed impact is high, even at low abundance). The costs of biocontrol are represented by an increasing nonlinear function to capture the probable escalating costs of reducing the abundance of a weed to ever-decreasing levels. An ineffective biocontrol agent could still deliver the net benefit, if it acts additively (as indicated by sequential arrows) or synergistically with other agents.

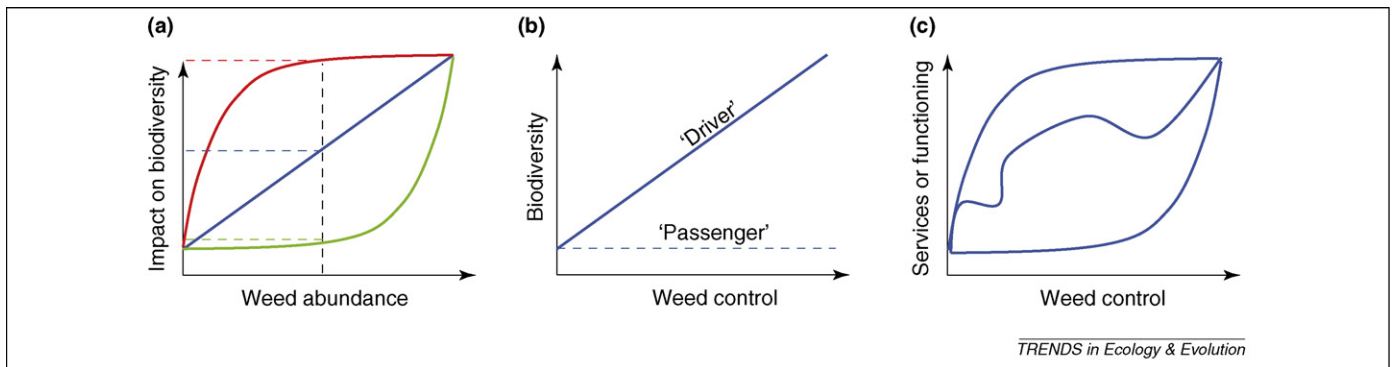


Figure 2. The benefits of biocontrol for an environmental weed. **(a)** Impact of a weed on biodiversity can follow a saturating function (red line), can be more or less proportional to abundance (blue line), or can exhibit a threshold effect with negligible impact until weed abundance is high (green line). These contrasting damage functions can produce quantitatively different benefits for biodiversity for a given level of control (dotted lines). However, these functions assume a causal relationship between weed abundance and biodiversity. If the weed is the ‘driver’ of biodiversity change [(b), solid line], then control will deliver a biodiversity benefit (example given for the linear impact function); Alternatively, if the weed is a ‘passenger’ and biodiversity loss is due to some other environmental factor, even complete control might fail to deliver a biodiversity benefit [(b), dashed line]. Moreover, even if there is a biodiversity benefit, the return of associated ecosystem services and function can be complex (c). Function might return at a higher rate than biodiversity (upper line), at a slower rate (lower line), or can exhibit an idiosyncratic pattern (middle line), depending on the order and rate at which functionally significant elements of biodiversity reassemble.

two dominant exotic grasses (*Poa pratensis* and *Dactylis glomerata*) in north American oak savannah, almost half showed either no response or a decline in cover; a result at least partly consistent with the ‘passenger’ model. Moreover, the study of Hulme and Bremner [45] revealed that non-native species accounted for more than one-third of the additional species found in removal plots. Such compensatory response in the abundance of non-native species has implications for whether conservation or biodiversity goals are met, even where the weed is controlled. Indeed, a common observation in the biocontrol of weeds is that one weed is replaced by another [46], creating, in effect, an ‘invasive species treadmill’.

The information above identifies several issues that underlie the ‘effectiveness’ of biocontrol of environmental weeds. Similar to the agricultural scenarios, we illustrate these with some conceptual models (Figure 2a–c). First, the nature of the weed abundance–impact function sets a proximate target for the level of control required to deliver measurable success. Again, we can expect a range of relationships, including saturating functions with high initial impact at low population levels (e.g. suggested impact of leafy spurge *Euphorbia esula* on rangeland grasses in Canada [47]), impacts that increase linearly with abundance (e.g. suggested impact of broom *Cytisus scoparius* on native species richness in Australia [48]) and non-linear threshold relationships with impact accelerating after abundance exceeds a certain level (e.g. suggested impact of Cape ivy *Delairea odorata* on native plant species richness in California [49]). Given these relationships, a specified reduction in weed abundance would be expected to deliver quantitatively different impacts on biodiversity (Figure 2a). However, if the weed is a ‘passenger’ rather than a ‘driver’ of biodiversity change, its control will not necessarily deliver any biodiversity benefit (Figure 2b). Furthermore, even if the weed is the cause of initial biodiversity loss, it need not follow that its removal will result in communities returning to their initial states.

Regardless of the mechanism of biodiversity loss, if native species are seed or dispersal limited, then their

capacity to recolonize will be constrained [50]. In addition, the presence of invasive species can change aspects of the local and regional abiotic (e.g. nutrient cycling [51], soil sedimentation [52], fire regime [53]) and biotic (e.g. soil microbial community [54,55], trophic structure and food-web interactions [56,57]) environments. Such invasion legacies highlight the importance of not only understanding the long-term effects of species invasions [57], but also the consequences of removal [58] and processes of recovery to ensure the restoration of structurally similar communities [11,45,59–61].

Finally, it is likely that, in many cases, the ultimate goal of controlling an invasive species is to restore not only biodiversity, but also the associated ecosystem functions. Understanding the relationship between biodiversity and ecosystem function is a major focus of contemporary ecology (for a recent synthesis, see Ref. [62]). Two insights that are particularly relevant are that re-establishing structurally similar communities does not necessarily ensure effective ecosystem function [60,63], and that the order of species assembly can have a marked impact on the pattern and rate of functional recovery [62–65]. The governing process is the overlap between ‘response’ and ‘effect’ groups [63,64,66]. That is, if functionally significant species respond rapidly to removal of the invader, then ecosystem services can recover in advance of biodiversity, whereas if functional species respond slowly, then even substantial recovery in biodiversity will not necessarily result in restoration of function (Figure 2c).

Ineffective biocontrol and non-target effects

An ongoing debate concerning invasive species and biocontrol relates to the potential for exotic natural enemies to have negative impacts on non-target biodiversity (e.g. Refs [67–70]). A recent contribution to this debate has highlighted a potential link between impact (or lack thereof) on the target, and impact on non-targets [71–73]. The mechanism centers on the potential for even a highly specific weed biocontrol agent to act as resource subsidy, promoting indirect effects on non-target species.

The impact or efficacy of the agent is important because an effective agent will drive down the target population and, if host specific, should track the food source and exhibit a commensurate decrease in numbers. An ineffective agent, however, will not reduce its food source and so could reach and maintain high population densities. These superabundant biocontrol agents can boost populations of predators or parasitoids, leading to indirect effects via apparent competition (as suggested for a tephritid fly released for biocontrol of bitou bush *Chrysanthemoides monilifera* ssp. *rotundata* in Australia [74]) and even cascading effects on reservoirs of vertebrate diseases such as hantavirus (suggested for two gall fly species introduced against spotted knapweed *Centaurea maculosa* in the USA [73]). Host specificity testing (now stringent in most biocontrol programmes) will tend to minimize the direct environmental risk of biocontrol introductions. However, this does not guarantee against indirect impacts via 'resource subsidy' effects. Such mechanisms identify a further need to better understand and predict the efficacy of a biocontrol agent

Conclusion

To some extent, the success of using one invasive to control another depends on the objectives of the programme and how high the 'the bar is set'. The focus of many biocontrol programmes is to identify candidate agents, screen for host range and, if suitable, release the agents into the new environment. If the 'bar is set' at the level of release and establishment, then biocontrol generally attains a high level of proximate success. However, the ultimate measure of success is a significant reduction in weed abundance, with subsequent benefits for productivity or biodiversity and associated services. Although it might seem harsh to 'set the bar' this high, few biocontrol programmes monitor or quantify success at this level.

These assessments challenge us to place biocontrol (and other control practices) in a more holistic framework for invasive species management, which draws on mechanistic ecological insights to understand the cause of the initial problem, quantify its impact and determine the full consequences of control efforts [11]. In practical terms, this means, for example, pre-release manipulative studies such as invasive species removal [44,45]; enemy exclusion and/or enemy addition studies to investigate the role of natural enemies on plant performance and population regulation [5,75]; common garden experiments with variable resources to explore the interaction between resource availability and enemy release [8,9]; re-seeding experiments to examine the effect of recruitment limitation on native species restoration [44,76]; and long-term quantitative post release monitoring of biological control agents [12,77–79].

There is also considerable potential for utilizing population and climate modelling to inform selection of agents and identify the best targets for control (e.g. Refs [24–28,80]). Biocontrol programmes do not routinely include such research and it has been argued that the benefits from successful biocontrol exceed the costs of the failures [70]; however, given the pressing nature of invasive species problems, the unique potential of biocontrol to deliver

sustained control and the already considerable expense and effort of introducing a novel agent (whether good or bad), it would seem in the interests of biocontrol practitioners, the agencies who support their activities and the end beneficiaries, to better quantify the impact of biocontrol to answer our original question and ultimately improve (cost)effectiveness.

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2007.03.003.

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