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Risk Analysis Frameworks Used in Biological Control and Introduction of a Novel Bayesian Network Tool

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Classical biological control, the introduction of natural enemies to new environments to control unwanted pests or weeds, is, despite numerous successful examples, associated with rising concerns about unwanted environmental impacts such as population decline of nontarget species. Recognition of these biosafety risks is globally increasing, and prerelease assessments of biological control agents (BCAs) have become more rigorous in many countries. We review the current approaches to risk assessment for BCAs as used in Australasia, Europe, and North America. Traditionally, these assessments focus on providing assurance about the specificity of a proposed BCA, generally via a list of suitable versus nonsuitable hosts determined through laboratory specificity tests (i.e., by determining the BCA's physiological host range). The outcome of interactions of proposed agents in the natural environment can differ from laboratory-based predictions. Potential nontarget host testing may be incomplete, additional ecological barriers under field conditions may limit encounters between BCA and nontargets or reduce attack levels, and BCAs could disperse to habitats beyond those used by the target species and adversely affect nontarget species. We advocate for the adoption of more comprehensive, ecologically-based, probabilistic risk assessment approaches to BCA introductions. An example is provided using a Bayesian network that can integrate information on probabilities and uncertainties of a BCA to spread and establish in new habitats, interact with nontarget species in these habitats, and eventually negatively impact the populations of these nontarget species. Our new model, Biocontrol Adverse Impact Probability Assessment, aims to be incorporated into a structured decision-making framework to support national regulatory authorities.

KEY WORDS: BAIPA; ecological risk assessment; nontarget impact; probabilistic risk model

1. INTRODUCTION

Considerations of ecological risks have arisen as animportant public concern in response to increasing threats to ecosystems arising from climate change, environmental degradation, and invasive species introductions (Hope, 2006; International Plant Protection Convention, 2014; McDaniels, Axelrod, & Slovic, 1995; McGeoch et al., 2010). Ecological risk assessments seek to provide science-based evidence to inform on the actual risk associated with environmental threats (i.e., the likelihood of an adverse event and the magnitude of the consequences)

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and, hence, support risk managers to mitigate those risks. Threats posed by the introduction, intentionally or unintentionally, of exotic organisms in new environments are particularly concerning. New introductions can affect the functioning of both natural and productive ecosystems, animal and human health, and more generally our environment, economies, and ways of living (Simberloff et al., 2013). For instance, a study of invasive organisms in the United States showed that introduced plants, animals, and microbes are, as a group, potentially causing harm to about 42% of the species listed as threatened or endangered in the United States (; Pimentel, Zuniga, & Morrison, 2005; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). The economic impact associated with these intentional or unintentional introductions amounts to more than US$150 billion annually (Pimentel et al., 2005; inflation corrected for 2020).

Biological control in its classical form refers to the importation of natural enemies, generally insects, from other countries or continents to control unwanted pests or weeds. Such importations are performed with the goal of their permanent establishment, dispersal, and effective control of the target species (TS) in the new range (Eilenberg, Hajek, & Lomer, 2001; Waage & Mills, 1992). Biological control programs present a valuable alternative to the use of synthetic chemical herbicides and pesticides arguably because of their low economic cost/benefit ratio (Heimpel & Cock, 2018; Thomas & Willis, 1998). Nonetheless, concerns about the environmental safety of biocontrol using insects as natural enemies emerged in the 1980s when observations indicated that negative impacts had resulted from some past introductions (Hajek et al. 2016; Heimpel, & Cock, 2018; Howarth, 1983; Simberloff & Stiling, 1996). Historical examples of negative impacts include the release of the Asian ladybird, *Harmonia axyridis*, in Europe and North America (Roy & Wajnberg, 2008) and of the generalist parasitoid fly, *Compsilura concinnata*, in North America (Boettner, Elkinton, & Boettner, 2000). Both species proved efficient natural enemies in the areas of introduction but also led to damage to nontarget native species' populations. More recently, the braconid parasitoid, *Microctonus aethiopoides*, has been shown to attack nontarget native weevils in New Zealand (including in habitats where the TS, *Sitona discoideus*, was not present; Ferguson, Kean, Barton, & Barratt, 2016). In the context of increasing recognition of biodiversity decline, in part related to new and invasive species introductions, assessments for proposed biological control agents (BCAs) have now become more rigorous and risk-averse, focusing on the assurance that the proposed BCA will not attack any species other than the target (i.e., strict host specificity).

The process of species selection for host range testing is always a critical component in risk assessment. It has progressively evolved from the traditional "phylogenetic, centrifugal" approach originally developed for weeds (Wapshere, 1974), where nontarget species (NTS) more closely related to the TS are tested in priority, to a more holistic approach considering both taxonomic and ecological similarities between species (Barratt et al., 1997; Hajek et al. 2016; van Lenteren et al. 2003). Nevertheless, assurance about the specificity of a proposed BCA is typically inferred from the examination of its physiological host range which, of necessity, is undertaken in the laboratory with little evaluation generally possible to determine its ecological host range prior to its release (Barratt et al., 1997; Hajek et al., 2016; van Lenteren, Bale, Bigler, Hokkanen, & Loomans, 2006; Withers & Browne, 2004). Many generalist herbivores or predators are governed less by taxonomic affinities than by ecological or habitat factors (Sheehan, 1986). This is also true for some parasitoids, such as those that specialize in leafminers but that can attack a range of leafminer hosts in different taxonomic orders (Askew, 1994). In this article, we review the main approaches that are currently used for the risk assessment of BCAs. While most proposed BCAs are selected for detailed research on the basis of a narrow host specificity, there are times when the selection of generalist BCAs able to exploit various host or prey species, which thrive in a wide variety of environmental conditions, may be appropriate. Therefore, we do not limit our discussion to specialists alone. We advocate for the adoption of more comprehensive, ecologically-based, probabilistic risk assessment methods, and provide a new tool based on a Bayesian network (BN) model. A retrospective case study demonstrates the use of the model for predictions of the behavior of a BCA in an actual ecological setting and to predict its potential impact on an NTS. The tool enables identification of the key driving influences on the overall impact of the BCA on the NTS, and in this case, shows how the outcome of interactions predicted for the natural environment can differ from laboratory-based predictions.

2. REVIEW OF CURRENT ASSESSMENT FRAMEWORKS

2.1. General Assessment Procedures

The purpose of a risk assessment is to inform on the potential hazards and their probabilities and severities associated with decisions not to make the decision per se. In general, biocontrol risk assessments focus on postrelease impacts on NTS and have the following components (Barratt & Ehlers, 2017; Barratt, Howarth, Withers, Kean, & Ridley, 2010): prediction of release outcomes based on available information; clear depiction of the types, sources, and implications of strengths of evidence and uncertainties on predicted outcomes; use of all available information including research data, technical expert knowledge, and input from stakeholders, including the public; transparent and reproducible assessment procedures; and evaluation of all possible outcomes including those with a low chance of occurrence.

Thomas and Willis (1998) noted that current tests of the degree to which BCAs are specific to their intended TS tend to be highly conservative and are based mostly, or solely, on a physiological match of the agent to the target and some NTS of economic and agricultural importance as determined from laboratory experiments. They recommended increasing the consideration of ecological constraints on the host range of a BCA and the use of empirical data coupled to a risk assessment framework to better estimate potential *in situ* ecological impacts of the agent on NTS. Babendreier, Bigler, and Kuhlmann (2005) suggested using a suite of ecological factors beyond just host specificity for considering potential BCA impacts. These include factors contributing to the temporal and spatial matching of hosts and BCAs, notably dispersal, successful overwintering and establishment, and an evaluation of indirect interactions such as competition. Some of this information can be obtained from previous postrelease studies of the considered BCA conducted elsewhere or from observations on related species. Hopper (2001), De Clercq, Mason, and Babendreier (2011), Barratt, Howarth, Withers, Kean, and Ridley (2010), Barratt and Ehlers (2017), Hajek et al. (2016), and Heimpel and Cock (2018) noted the value of risk assessments, particularly postrelease monitoring and validation of predicted impacts, to reduce uncertainty in subsequent assessments and use of risk-benefit assessments to help guide BCA release decisions. To our knowledge, only New Zealand and Australia incorporate a formal comparison between these risks and benefits into their decision-making process (Barratt & Ehlers, 2017; Heimpel & Cock, 2018; Hinz, Schwarzländer, Gassmann, & Bourchier, 2014; Hunt et al., 2008).

For decisionmakers, all decisions in the real world involve a degree of uncertainty because natural systems are inherently complex. Uncertainty may be part of the environment in which the decision is made and may relate to the analysis of outcomes resulting from the actions or decisions themselves. Uncertainty is a key element of both risk analysis and risk management, and weighing the costs and benefits of potential outcomes with their probabilities is essential to inform and advise decisionmakers. In the Australian and New Zealand Risk Management Guidelines, the definition of risk at a high level has changed from "the chance of something happening that will have an impact on objectives" to "the effect of uncertainty on objectives" (Office of the Prime Minister's Chief Science Advisor, 2016). The European Food Safety Authority (EFSA) defines risk more tangibly as "the inability to determine the true state of affairs of a system" (EFSA Scientific Committee et al., 2018). The latter is appropriate to biological systems where information is usually incomplete and difficult to obtain for resource management decisions (Marcot, 2021).

In the context of risk assessment for BCA applications under the New Zealand Hazardous Substances and New Organisms Act 1996, a preliminary analysis of areas of uncertainty, as expressed by applicants, regulators, and members of the public during the application and consultation process, was carried out to inform future research priorities. Over 250 expressions of uncertainty were grouped into about 30 categories. Among the most frequently mentioned areas of uncertainty were risk of adverse effects on NTS and interpretation of host-range testing data, followed by uncertainty about cultural risks (to values of indigenous peoples), and questions about the existence of natural enemies already present in the new geographical range of the target pest and hence less risky alternatives (Barbara Barratt & Toni Withers, unpublished data).

To help address uncertainty, both semi-quantitative and quantitative (probabilistic) tools have been used in BCA risk assessment processes. They can provide rapid reviews or calculated probabilities of BCA and NTS interactions for either classical biological control (i.e., the introduction of an exotic natural enemy in a new area) or augmentative biological control (i.e., the release of additional numbers of a natural enemy that is already present).

2.2. Semi-quantitative Methods

2.2.1. Description

Semi-quantitative risk assessment methods generally use a system to rate, rank, and combine factors into an overall outcome score denoting the potential efficacy or harm of a BCA. These methods are widely used for the evaluation of risk associated with invasive species and can be instructive in the context of deliberate introductions used in biocontrol programs (Abram & Moffat, 2018). For example, as used with invasive species assessment, Davidson, Fusaro, Sturtevant, Rutherford, and Kashian (2017) applied a risk rating to evaluate the potential of various anthropogenic vectors for introducing aquatic nonindigenous species in Laurentian Great Lakes. Holt et al. (2012) used graphical visualizations of risk and uncertainty scores to evaluate the potential entry, establishment, spread, and impact of pest species.

Semi-quantitative risk scoring has been used to evaluate the potential impacts of BCAs on NTS (van Lenteren & Loomans, 2006). For instance, based on results from laboratory host range testing and literature review, Paynter et al. (2015) obtained risk scores for 22 herbivore control agents established in New Zealand as ratios of their relative performance for target weeds to nontarget plants. They found a clear threshold above which the risk score strongly indicated that nontarget hosts would be used in the natural environment. Similarly, Paynter and Teulon (2019) applied a similar scoring approach for four *Aphidius* BCA species introduced in New Zealand, based on ratios of percent parasitism for nontarget aphid species to target aphid species. High levels of parasitism of NTS in the field were correlated with high risk scores above a certain threshold.

Another semi-quantitative scoring approach is the priority ranking of nontarget invertebrates (PRONTI) tool that is used to rank potential NTS for further risk analysis with a proposed BCA (Todd, Barratt, Tooman, Beggs, & Malone, 2015). PRONTI ranks NTS using scores obtained for five criteria: hazards posed by the BCA (direct and indirect), the likelihood of hazard exposure, ecological impacts of the exposure, species' anthropocentric value, and the degree to which the NTS is testable (Todd et al., 2015).

2.2.2. Advantages and Drawbacks

The primary advantage of semi-quantitative methods is their ability to combine a wide range of qualitative indices into one or several summary scores that can be used for risk ranking. The process is straightforward and repeatable; hence it can be used to support transparent decision making. The possibility to trace back the output to intermediate or initial underlying risk estimates provides end-users with the ability to explain unexpected values in the rankings. An example is the pest risk assessment risk score and uncertainty visualizer developed by the European and Mediterranean Plant Protection Organization (EPPO) (Holt et al., 2012) that provides a one-page graphical summary of about 50 risk scores associated with the entry, establishment, spread, and impact of invasive species. All scores are displayed with a measure of associated uncertainty as estimated by assessors during the risk assessment process. In PRONTI, uncertainty associated with the ranking of each NTS for testing is expressed as the percentage of data that were unknown for each of the five risk criteria and for the calculation of the overall risk score (Todd et al., 2015).

Semi-quantitative models can be quickly adapted to specific needs, provided that the reasons for such updates are objective and well-documented. For instance, additional risk components can be considered or intermediate risk score weightings adapted. The model can be constructed in a stepwise procedure, allowing an initial ranking and shortlisting based on criteria and indices that are considered the most important (hence not all indices necessarily need to be estimated for all tested species). van Lenteren and Loomans (2006), described such a stepwise risk assessment procedure for BCAs, where the decision to advise a release is taken at relevant steps in the process for both augmentative and classical biological control.

The principal drawback of semi-quantitative methods relates to the use of single-point numerical estimates to quantify individual risk components. Point estimates do not provide a means of denoting uncertainty around expected values, and when the amount of uncertainty in each estimate is not communicated with the results, this gives rise to a false sense of precision throughout the entire process. Other simplifying factors that may overstate precision and accuracy include the use of individual component scores established on predetermined semi-quantitative scales, their combinations into overall risk indices using formulae or matrices, and the incorporation of average score values when information is not available. In addition to uncertainty, all numerical estimates can be subject to misunderstandings or errors from the assessors (Marcot, 2021).

2.3. Quantitative (Probabilistic) Methods

2.3.1. Description

Quantitative risk assessment methods generally use a probabilistic approach based on key input variables such as ecological traits of the species of interest and their environmental associations. Wright, Hoffmann, Kuhar, Gardner, and Pitcher (2005) demonstrated the use of precision (decision) trees with an analysis of the impact of the egg parasitoid, *Trichogramma ostriniae*, on the European corn borer, *Ostrina nubilalis*, in the United States. Decision trees are a type of probabilistic decision model that incorporates parameter variability as a measure of uncertainty, and where the system is described based on the relationships between key parameters, decision points, and potential outcomes (Varis 1997). The "tree" allows an easy visualization of the joint probabilities that each of a number of contingencies will occur, and the "branches" in the tree allow the paths to these outcomes to be identified.

The EPPO Standard PM6/4 "Decision-support scheme for import and release of biological control agents of plant pests" provides a decision-support procedure for evaluating BCAs of plant pests based on the probability of BCA establishment and spread and assessment of potential environmental consequences (EPPO, 2018). The results are similarly expressed as probabilities of outcomes, although the input variables used in the assessment may derive in part from expert knowledge elicitation and might be qualitative or quantitative.

Besides probabilistic decision models, quantitative simulations and analytic models also have been developed to inform biocontrol decisions. For example, Grevstad (1999) developed a stochastic simulation model of BCA establishment that provides quantitative results to help inform decisions on BCA introduction. Rees and Hill (2001) used analytic and simulation models to assess the viability in New Zealand of European gorse, *Ulex europaeus*, under varying levels of seed survival-related factors as well as other site disturbances.

Another approach gaining favor in evaluating risk and management solutions for invasive species, and introduction of BCAs, is the use of BN models (Holt et al., 2018; Jamieson et al., 2013, 2016; Mengersen et al., 2012; Wright et al., 2005). BNs can link physiological and ecological input variables using conditional probabilities to calculate posterior probabilities of specified outcome states, such as degree of potential spread of and injury by invasive species (Marcot, Hoff, Martin, Jewell, & Givens, 2019; Wyman-Grothem, Popoff, Hoff, & Herbst, 2018).

2.3.2. Advantages and Drawbacks

The main advantage of probabilistic risk assessment methods is their capacity to quantify the sources and implications of uncertainty. For ecological systems, this is more meaningful than procedures that rely on single-point estimates, which do not represent variability, including seasonal, habitat or genetic variability, or assessment uncertainty, such as occurs when experts are unsure or diverge in their opinions. Kenis et al. (2012) presented a hierarchical scoring system to improve consistency among experts' opinions while performing assessments of environmental impacts of alien plants, invertebrate plant pests, and pathogens. The experts/assessors select their modal score for risk factors (low, medium, or high, for most variables) but also assign them a level of uncertainty (high, medium, or low, which automatically assigns the chosen modal score a probability of 60%, 74%, or 94%, respectively). The probability distribution of other scores is then determined by a matrix system based on the probability distribution of the input scores. Probabilistic methods can be used to investigate the worst case (high probability of impact) and best case (low probability of impact) scenarios and to identify the effectiveness of risk factors by use of sensitivity and influence analyses. Such analyses can be used to justify a degree of precaution in the interpretation of predictions and provide justification for further data collection to reduce major uncertainties.

Probabilistic models such as this can be readily tested, updated, and improved with new information for any of the input variables. Kaufman and Wright (2017) used decision trees to estimate overall probability distributions of parasitism for three introduced parasitoids that attack an endemic Lepidoptera species in Hawaii, based on habitat overlap, seasonality, and observed direct impacts in other countries. These models could be adapted quickly should new data become available, for instance, to test new parasitoids (self-introduced or envisaged for release), or to consider another nontarget host.

Probabilistic risk assessment methods will often require more data than other approaches, and not all of them can handle large or complex species networks. If they do, there is likely to be a large amount of information required to untangle the main ecological interactions. In cases where accurate estimates of probability distributions cannot be obtained for input variables, the precision of the projected outcome(s) might be limited (especially if these are the most effective risk factors, although the system's sensitivity to that uncertainty can be documented). Complex models may be associated with difficulties to correctly display the ecological causal links leading to the projected outcome(s) or to explicitly denote all the sources and the propagation of uncertainties. The BN-based assessment approach presented below addresses the advantages and some of these drawbacks.

3. INFORMING DECISIONS BASED ON ASSESSMENT PREDICTIONS

3.1. Problem Summary

In evaluating outcome probabilities to advise on the risk of a proposed BCA introduction, the problem is to make predictions for a system that does not yet exist. The accuracy of the assessment depends on the veracity of assumptions of how BCAs respond to their new environments. Besides lack of accuracy is the uncertainty arising from partial information and incomplete knowledge, lack of field monitoring, environmental variability, and untested species interactions. To account for uncertainty, ideally, a quantitative BCA risk analysis framework would account for the phenology, dispersal ecology, reproductive biology, physiological tolerance ranges, habitat selection, and host species selection of the BCA, as well as similar attributes of target and potential NTS, and the spatial distribution of environmental conditions at introduction sites and adjacent locations within the BCA's potential dispersal range. It is likely many such attributes will not have been empirically studied and assessments will rely on expert judgment using rigorous methods for expert knowledge elicitation to make this robust.

A probabilistic framework can be useful to depict knowledge levels and propagation and implications of uncertainty on predicted outcomes. Probabilistic frameworks useful for describing causal dynamics in complex systems include structural equation models (Dawid, 2015) and directed acyclic graphs (Pearl, 2000), the latter of which can be most usefully represented with conditional probabilities in the form of BNs.

3.2. BNs

BNs (Korb & Nicholson, 2011; Pearl, 1988) are an increasingly popular paradigm for reasoning under uncertainty. BNs are directed acyclic graphs, in which nodes represent variables and arcs represent direct probabilistic relations. For a BN that has discrete or discretized variables, the relationship between variables is quantified by conditional probability tables (CPTs) associated with each node (an example is provided in Supplemental Note S1). BNs allow for a wide range of inferences about the modeled system to be made in an efficient way. Users can set the values of any combination of nodes in the network that they have observed, relegating unobserved variables to their prior probability distributions, and all evidence propagates through the network, producing a new posterior probability distribution for each variable in the network. In this context, the reasoning required is a predictive one; given a scenario of a proposed BCA and NTS, a BN model can be used to incorporate evidence about the species, their biological features, and environments, to compute the quantitative likelihood of impact. Sensitivity analysis in the form of influence runs (Marcot, 2012) is used to explore the influence of the input variables on the output posterior probability distribution. This is done by sequentially selecting each state of the input variable, updating the BN, and recording the range of the output variable's posterior probabilities in a tornado plot.

Over the past 20 years, BNs have been widely used in ecological modeling (see section 5.2.3 in Korb & Nicholson, 2011). In biosecurity modeling, BNs have been developed for pest detection and eradication (Burgman et al., 2010; Dambacher, Shenton, Hayes, Hart, & Barry, 2008; Horton, Evans, James, & Campbell, 2009; Murphy, Jansen, Murray, & De Barro, 2010; Peterson, Rieman, Dunham, Fausch, & Young, 2008) and for import risk assessment (Hood, Barry, & Martin, 2009; Jamieson, Woodberry, McDonald, & Ormsby, 2016; Mengersen et al., 2012). There have been several assessments of BNs as biosecurity tools (e.g., Baker & Stuckey, 2009; Hood et al., 2009; Hosack, Hayes, & Dambacher, 2008; Walshe & Burgman, 2010; Wintle & Nicholson, 2014). To our knowledge, BNs have never been used for biological control risk assessments.

4. BN MODEL FOR BCA RISK ASSESSMENT

4.1. Evaluation Components in a Classical Biological Control Program

A classical biological control program can be viewed as the deliberate introduction of an invasive organism (the BCA), where one aims to maximize the invader's ability to suppress a target organism (usually a pest or a weed) while typically ensuring safety to otherwise valued NTS (native or beneficial introduced species). The target organism is often an invasive species itself; hence, potential BCAs are commonly searched for in the area of origin of the target (Fig. 1—selection of BCA). The list of BCA candidates is then refined based on a preliminary evaluation of each candidate's ability to control the TS, balanced with a consideration of the negative effects it could cause in the introduction area. Impacts on NTS are primarily considered, which can be initially drawn from observations of current interactions between the BCA and related or valued species in its area of origin. At this stage, the estimated outcomes of the BCA introduced in a new environment rely principally on assumptions.

An assessment of the physiological host range of a candidate BCA is the typical first step in addressing its potential impact on species in the proposed area of introduction. It is usually determined prerelease, based on choice and other response tests evaluating the attacking behavior and reproductive success of a BCA with selected NTS (Fig. 1—assessment of BCA in quarantine). Physiological host range testing is often used to discard BCA candidates with a host range wider than just the target. Properly testing all species that could be threatened by the introduction of the BCA is difficult in practice due to frequent issues sourcing, rearing, or synchronizing both the NTS and the BCA (or their appropriate life stages). The physiological host range of a BCA, as evaluated in the laboratory, may significantly differ from its ecological host range, which requires the consideration of other field constraints, such as habitat or seasonal matching.

Components related to the initial selection of candidate BCAs are shown in the top part of the diagram (green-colored box). This evaluation usually consists of a pre-import analysis of the biology and behavior of the agents in the area of origin of the pest or weed.

4.2. BAIPA

We propose here a new tool to assess the potential negative ecological impacts of candidate BCAs on individual, at-risk NTS. The BAIPA uses a probabilistic BN-based model to combine nine evaluation components to assess the probability that an introduced BCA will reduce the population of a specified NTS in a specified habitat (Fig. 2). The model evaluates key species interactions, such as the frequency of encounters between the BCA and the NTS (based on local species abundances and the possibility of spatial and temporal overlap) and the local frequency of successful attacks (based on likely interactions between the BCA and the NTS) and considers potential indirect effects to estimate the overall probability for population impact (Table I). All evaluations are based on an extrapolation from the situation where the BCA successfully establishes and controls the original TS in all habitats where the target occurs.

BAIPA aims to support management decisions in biological control programs (Fig. 1—assessment for release decision). The outcome from BAIPA (component 9 in Fig. 2) indicates that the probability of a reduction in the population of the selected NTS following release of the BCA is either minimal (supporting a decision to release), too great (supporting a decision not to release), or too uncertain (supporting a requirement for more information on the BCA and/or NTS to enable a technically justified decision to be made). BAIPA is built on a discrete BN comprising the nine evaluation components described in Table I. Throughout the evaluation components, the BN propagates uncertainty by calculating posterior probability distributions among the states of each model variable; a greater spread of probabilities among variable states denotes greater uncertainty. A more detailed description of all model variables and their possible states are provided in Table S1, including the descriptions of the main relationships between variables that have been used to quantify the CPTs. A case study is presented below on assessing the potential negative impact on a native wee-

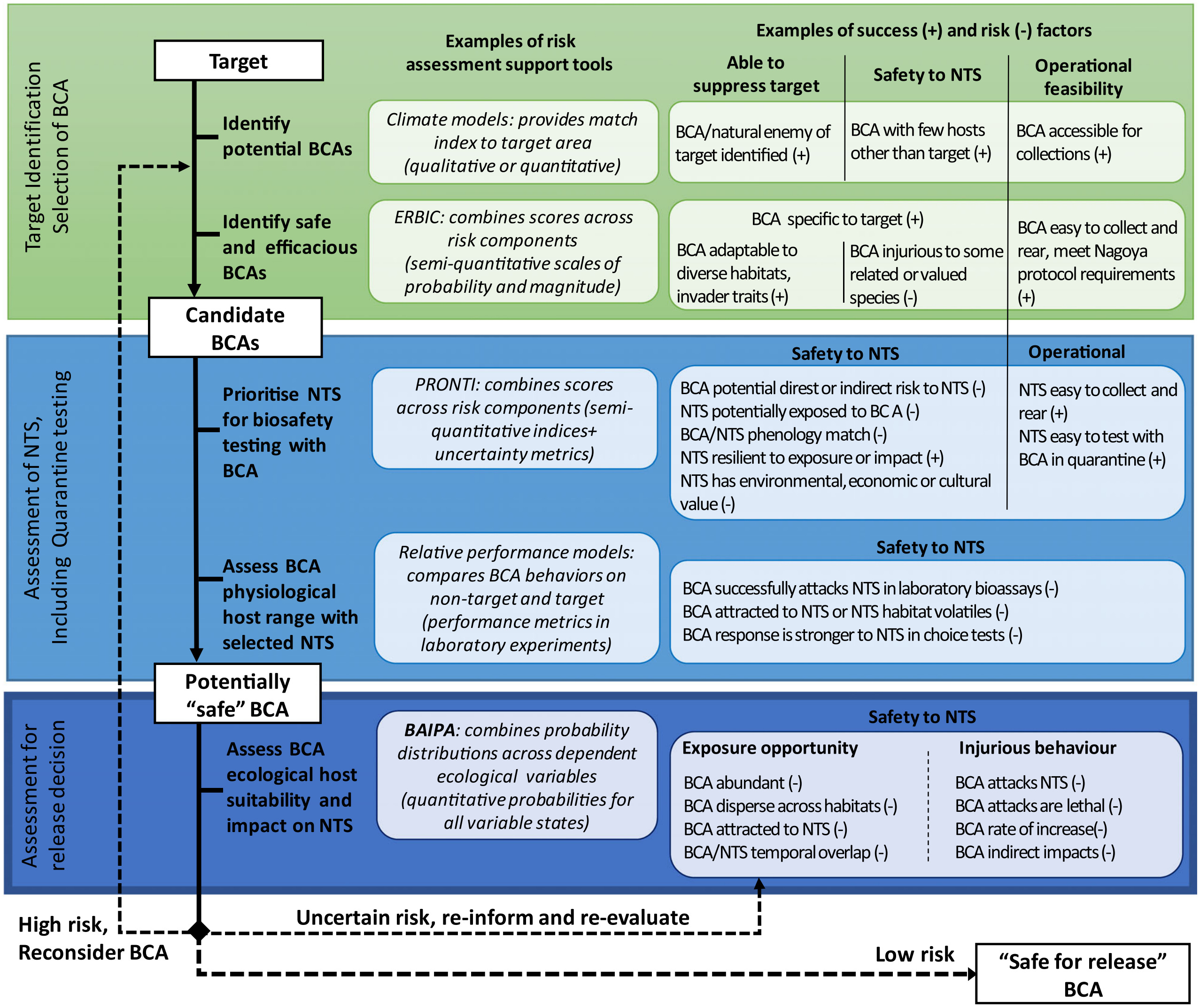

Fig 1. General evaluation components in the risk assessment of a biological control agent (BCA). Components related to the assessment of candidate BCAs for the area of introduction are shown in the bottom part of the diagram (blue-colored boxes). This part of the evaluation usually consists of the selection of non-target species (NTS) and testing in quarantine conditions (assessment of the physiological host range of the candidate BCA) and a general evaluation for release (assessment of the ecological host range and potential impact of the candidate BCA should it be released in the natural environment). The Biocontrol Adverse Impact Probability Assessment (BAIPA) aims to advise whether a BCA is low risk (safe for release), high risk (unsafe for release), or the risk level is too uncertain (more information is required) for each NTS identified to be at risk. ERBIC = Evaluating Environmental Risks of Biological Control Introductions into Europe (Van Lenteren et al., 2003); PRONTI = Priority Ranking of Non-Target Invertebrates (Todd, Ramankutty, Barraclough, & Malone, 2008; Todd et al., 2015).

vil species (NTS) associated with the introduction of a BCA targeting a pest weevil (TS) in New Zealand.

4.3. Case Study and Application

The lucerne pest, *S. discoideus* (Coleoptera: Curculionidae), a weevil first recorded in New Zealand in 1974, rapidly became recognized as a serious pest affecting lucerne (alfalfa, *Medicago sativa*), a perennial legume (Goldson, Frampton, Barratt, & Ferguson, 1984). The introduction in 1982 of a hymenopteran endoparasitoid, *M. aethiopoides* (Braconidae: Euphorinae), successfully reduced *S. discoideus* populations providing benefits to farmers (Goldson et al., 1993). Concerns arose when it was discovered that 19 species of nontarget weevils were attacked in

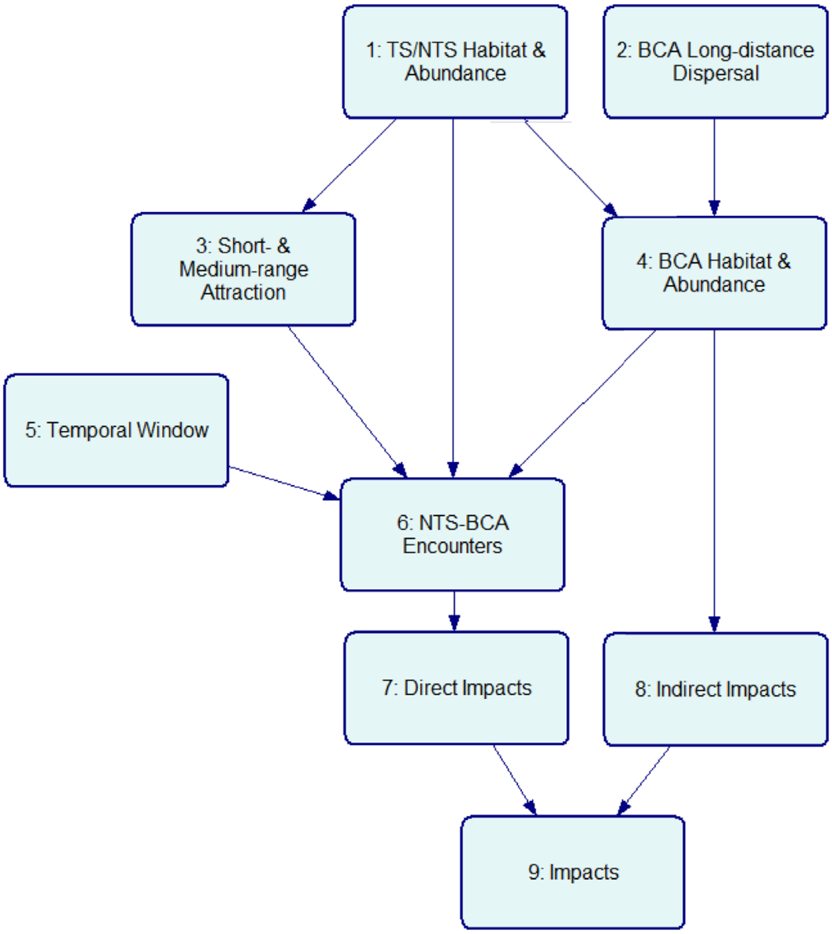

Fig 2. High-level structure of the Bayesian network (BN) model used to assess the nontarget impacts of BCAs. The "Biocontrol Adverse Impact Probability Assessment" (BAIPA) tool comprises nine interconnected BN model components (Table I) to assess the ecological overlap between a BCA and a nontarget species (NTS) (components 1 to 6), and their physiological matching and potential for direct and indirect impacts (components 7 to 9). Data on the target species (TS) is also used.

the field, 14 of which are native species (Barratt & Johnstone, 2001; Barratt et al., 2007, 2010). The nontarget parasitism associated with the introduction of *M. aethiopoides* in New Zealand provides an interesting case of a BCA initially expected to establish only in the receiving environment (lucerne crops and pastures) but which has now established populations in natural ecosystems (mainly mid-altitude native tussock grasslands that are habitats for native weevil species). *Microctonus aethiopoides* has a weak flight capability and the propensity of *M. aethiopoides* to colonize remote habitats may principally occur via the large numbers of parasitized adult weevils dispersing away from lucerne crops to aestivate in distant sites (Barratt et al., 2010; Ferguson, Kean, Barton, & Barratt 2016). Whether the observed nontarget parasitism results principally from summer "spillover" from lucerne crops or from the locally sustained reproduction of *M. aethiopoides* on NTS in these remote habitats or both remains unclear (Ferguson et al. 2016). Here, we use this example to retrospectively test BAIPA for its ability to assess the probability a BCA will have a negative effect on NTS populations. Table S2 provides summaries of existing knowledge and their interpretation as probability distributions used to inform input variable states for this case study.

Before beginning the assessment, the assessor must clearly define the identity of the BCA, TS, NTS, and one or multiple habitats of interest to evaluate. BAIPA is run separately for each habitat to be tested. We suggest that the habitat of BCA introduction should be tested first, then the habitat where the TS and the NTS are the most likely to coexist, then "refuge" habitats for the NTS (e.g., native environments). "Fact sheets" should be provided by the applicant for this purpose, including a collation of available information on the presence and abundance of the different species (see Table S2 for an example). This information will often be incomplete, but the

Table I. Model Components in Biocontrol Adverse Impact Probability Assessment (BAIPA). The High-Level Structure of the Bayesian Network (BN) Model is Shown in Fig. 2. A full Data Dictionary, Including Detailed Nodes and States Definitions, is Provided in Table S1. The Model is Run Separately for each Combination of Biological Control Agent (BCA), Target Species (TS), Nontarget Species (NTS), and Habitat

Model Component	Description	Input Required from Assessor
1. TS/NTS habitat and abundance	States the abundance of the TS and NTS populations within the considered NTS habitat	Size and stability of the TS population in habitat[a] Size and stability of the NTS population in habitat[a] Spatial proximity to nearest TS habitat (if TS absent)[a]
2. BCA long-distance dispersal	Evaluates the frequency at which BCA individuals disperse outside their habitat of introduction	Long-distance passive dispersal ability of the BCA[b] Long-distance active dispersal ability of the BCA[b]
3. Short- and medium-range attraction	Evaluates whether BCA individuals are attracted to the NTS within the considered NTS habitat	Direct attraction of BCA to NTS (medium-distance)[b] Indirect attraction of BCA to NTS (medium-distance)[b] Direct attraction of BCA to NTS (short-distance)[b] Indirect attraction of BCA to NTS (short-range)[b]
4. BCA habitat and abundance	Evaluates the abundance of the BCA population within the considered NTS habitat	No input required, determined by other factors in the model
5. Temporal window	Evaluates the level of activity of the BCA during the period when susceptible life stages of the NTS are present, within the considered NTS habitat	Seasonal match between the NTS and the BCA[b,c] Reproductive phenology of the BCA[b]
6. NTS-BCA encounters	Evaluates the frequency of encounters between the BCA and the NTS within the considered NTS habitat	No input required, determined by other factors in the model
7. Direct impacts	Evaluates whether the introduction of the BCA has a direct negative impact on the NTS population within the considered habitat	Frequency of attacks when BCA encounters NTS[b] Mortality frequency of NTS after attack[b] Frequency of non-lethal attacks that affect the fitness of NTS[b]
8. Indirect impacts	Evaluates whether the introduction of the BCA has an indirect negative impact on the NTS population within the considered habitat	Indirect impact potential of BCA on NTS[b,d]
9. Impacts	Evaluates whether the introduction of the BCA has an overall negative impact on the NTS population within the considered habitat	No input required, determined by other factors in the model

[a]Species abundance inputs will be directly informed by the "fact sheets" summarizing the identity and local abundance of the organisms considered in the assessment. It may take the form of a probability distribution to consider uncertainty. The outcome of the assessment will be more informative to the assessor if assumptions are made on these inputs under the form of "worst cases" or "what if" scenarios.
[b]Species ecological and biological inputs will be entered by the assessor under the form of a probability distribution based on the information provided by the applicant, eventually completed by additional information or knowledge gathered by the assessor. A "default" probability distribution can be used in case no information is available at all. This "default" distribution can be uniform or may depend on the type of organism investigated.
[c]The temporal match between the NTS and the BCA can be directly informed by the user or estimated from the known seasonal activity patterns of both the NTS and BCA.
[d]Evaluating the outcome of indirect interactions between a BCA and an NTS can be complex. It is therefore recommended that, first, assumptions of no possible indirect impacts, and second, assumptions of realization of the most severe impact from all possible outcomes are tested. This is equivalent to testing best and worst-case scenarios for indirect interactions.

NTS will be assumed present in the habitat under evaluation (as the reason for assessing NTS impact in this habitat), while the TS can be present or absent. Available information on the BCA can be provided but is not required as an input to the model. In a situation where biologically or ecologically distinct NTS have been identified as "at risk" (for instance using tools such as host range tests), these will each be evaluated in successive model runs.

Here, we retrospectively assessed the impact of *M. aethiopoides* on the native weevils in the genus *Nicaeana* (Curculionidae: Entiminae) in low grazing intensity pastures and mid-altitude native tussock grassland. Permanent populations of *M. aethiopoides* are generally established in pasture habitats, where they successfully control the target *S. discoideus*. In low grazing intensity pastures (hereafter referred to as pastures), *S. discoideus* (and *M. aethiopoides*) coexist with resident populations of native weevils, including species in the genus *Nicaeana*, such as *N. cinerea* and *N. cervina*. *Sitona discoideus* and these endemic *Nicaeana* weevils are also established in native tussock grassland (hereafter referred to as native grassland). These are distant from pasture environments and considered a "refuge" habitat for native weevils in the genus *Nicaeana*. Additional knowledge required as user input in BAIPA is provided in Table S2.

4.4. Results of Running BAIPA for the Case Study

Fig. 3 shows the BAIPA BN for the described case study, simplified to show only the key variable components.[1] The BN calculates the probability that the parasitic wasp *M. aethiopoides* (the BCA) will have an impact on populations of native weevils in the genus *Nicaeana* (the NTS), given the set of inputs (Table S2). For this case study example, the BAIPA BN predicts there will be a 10% probability of *BCA impact on NTS population* (i.e., an arguably substantial population reduction of *Nicaeana* weevils) in native grassland, denoting the results as a 6% probability of *BCA direct impact on NTS population* and a 5% probability of *BCA indirect impact on NTS population*.

Fig. 4(a) is a sensitivity tornado plot for the case study BN (Fig. 3), showing the sensitivity of the output variable probability (*BCA impact on NTS population* = *Yes*) to the observations on the key intermediate and input (indicated by asterisk in Fig. 4(a)) variables. Using the case study inputs as baseline,[2] the tornado plot shows the range of output probabilities (i.e., BCA impact on NTS population) that result when specifying each possible state for each individual node. For example, *BCA impact on NTS population* = *Yes* varies between 5% and 75%, as different states of the intermediate variable *NTS/BCA encounters* are tested. On the other hand, the model is almost completely insensitive to the *NTS non-lethal fitness impact after attack* variable[3] because successful attacks with this particular BCA will most likely cause mortality of this particular NTS as indicated by the *NTS mortality after successful attack* variable (65% probability of a successful attack eventually killing the host).

Next, we ran sensitivity analyses for the direct and indirect impact intermediate output variables. As shown in Figs. 4b and c, the *BCA direct impact on NTS population* value is primarily driven by *NTS/BCA encounters*, and the *BCA indirect Impact on NTS population* value is primarily driven by the *BCA population in habitat input*. In addition to providing insight into the key driving influences on the variable of interest, these sensitivity analyses can be used to indicate where input value refinement would be most beneficial, that is, for variables that may be least well known (greatest uncertainty) but having the highest potential influence on outcomes. A replicated analysis, addressing pastures, is presented in Figs. S1 and S2 (Figs. S3 and S4 are for the native grassland case).

5. DISCUSSION

5.1. Ecological Risk Assessments for Species Introduced into New Environments

Risk is defined as the product of the magnitude of an undesirable outcome and the probability of that outcome occurring. More specifically, and in the context of using BCAs, risk is the intersection of hazard (potential adverse impacts on NTS), exposure (overlap of BCA and NTS), and vulnerability (probability and uncertainty of impacts) (Füssel, 2007). Performing a quantitative risk assessment for a species moving into a novel environment requires a prospective evaluation of the probability and consequences

[1]For the detailed model components, see Table S1.

[2]All bars are centred on 10%, which is the base value for *BCA Impact on NTS*.

[3]This includes its parent variables, which have been omitted from the results here.

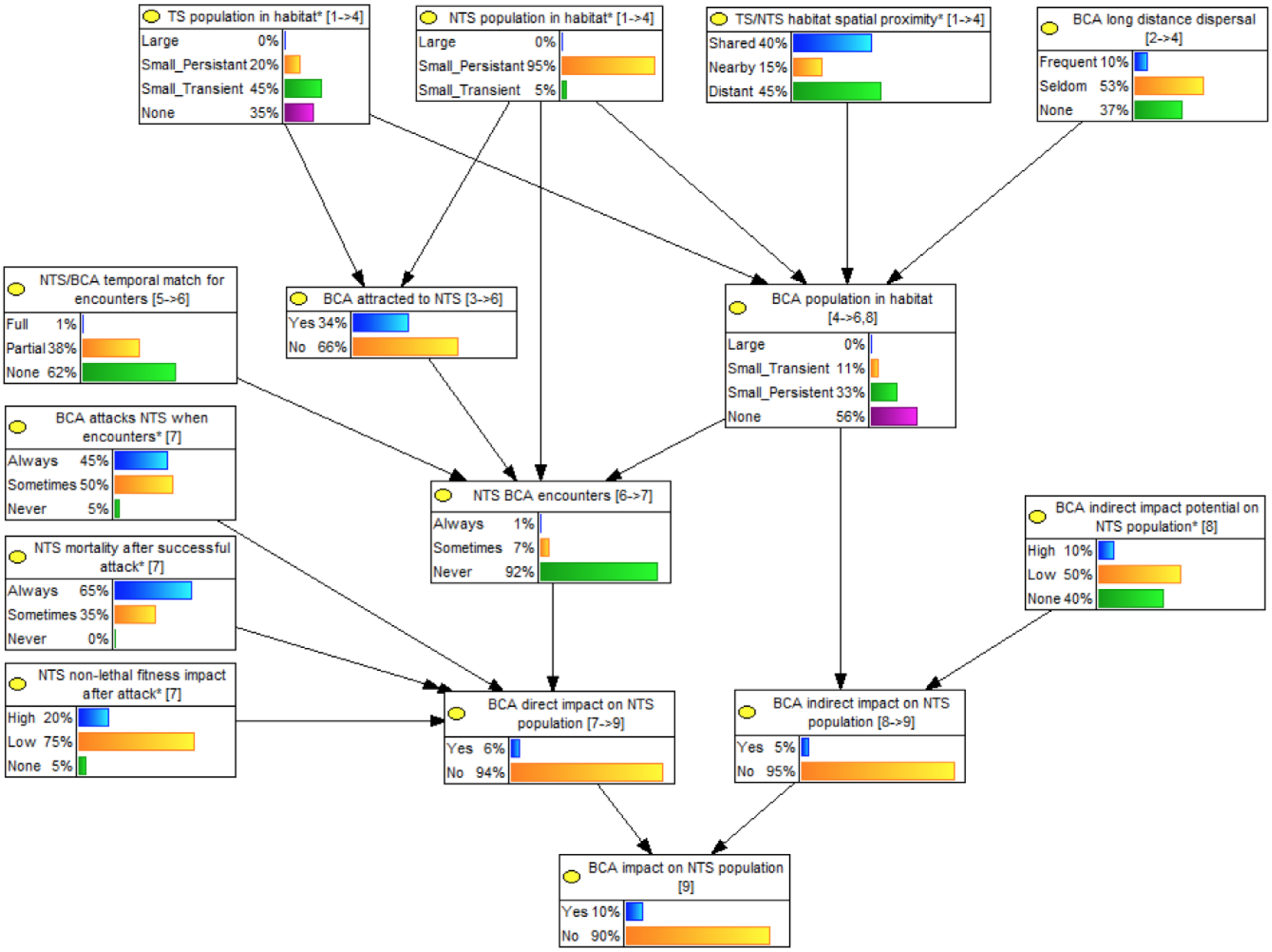

Fig 3. BAIPA BN model: Case study of the BCA *Microctonus aethiopoides* impact on NTS, native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in mid-altitude native tussock grassland. The BN predicts there will be a 10% probability of *BCA impact on NTS population*, divided between a 6% probability of *direct impact on NTS population* and a 5% probability of *indirect impact on NTS population*. Data on the TS, *Sitona discoideus*, is also used. The numbers in square brackets associated with the model nodes (each individual box) refer to the model components that use them (see Fig. 2 and Table I). Key input variables shown in the diagram are indicated by an asterisk. A complete description of the model structure and definitions of all variables and states are provided in Table S1.

of a series of events that have yet to occur. For any introduced species, this series of events can be broadly characterized by the different phases of the invasion process: entry, establishment, growth, and spread, along with the probabilities and uncertainties of each event occurring. For pests and other species that might become a nuisance in areas of introductions, a risk assessment typically is based on an in-depth evaluation of all invasion phases, as well as on an evaluation of the negative economic and/or environmental impacts in potentially invaded areas (Andersen, Adams, Hope, & Powell, 2004). For BCAs and other intentionally introduced species, organisms are selected based on their ability to successfully establish, increase population size, and spread in the introduction area. Risk assessments of these organisms, therefore, put emphasis on a comparison of the potential benefits (usually economic) with the potential adverse effects (usually environmental) (Heimpel & Cock, 2018). A difficulty in performing full risk assessments of introduced species resides in the lack of knowledge about novel ecological interactions. No two receiving environments are the same, and a risk assessment is a forecast that can be made only with the best data available, which does not include every eventuality that might not be predicted in the new environment. For instance, many species-to-species interactions may not exist anywhere else.

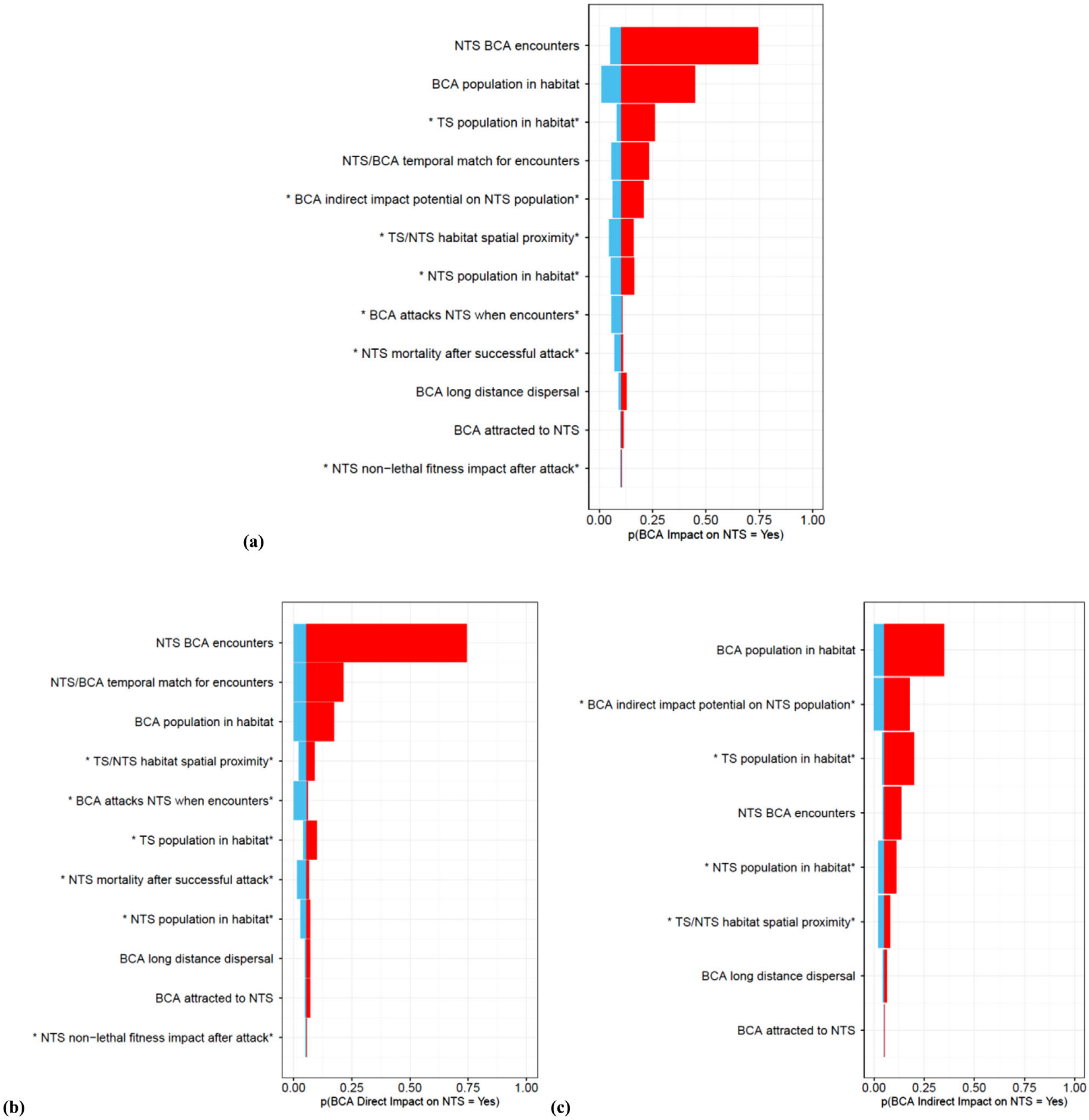

Fig 4. (a) Sensitivity tornado plot for the case study BN network (native grassland), showing the sensitivity of the output variable probability (*BCA impact on NTS population* = *Yes*) to the observations on the key intermediate and input (indicated by asterisks) variables. Each plot indicates the range of output probabilities that result when specifying each possible state for each individual node. The blue component of each plot shows the reduction in probability achievable, and the red component shows the increase. The *BCA impact on NTS population* is most sensitive to the intermediate variables *NTS/BCA encounters* and *BCA population in habitat*. Of the input variables, *BCA impact on NTS population* is most sensitive to the *TS population in habitat* and *BCA indirect impact potential on NTS population*. (b) and (c) Sensitivity tornado plot for the case study BN network (native grassland), showing the sensitivity of (b) the direct impact p(*BCA direct impact on NTS population* = *Yes*) and (c) the indirect impact p(*BCA indirect impact on NTS population* = *Yes*) probabilities to the observations on the key intermediate and input (indicated by asterisks) variables. The direct impact is most sensitive to the *NTS/BCA encounters* and *NTS/BCA temporal match for encounters*. The indirect impact is most sensitive to the *BCA population in habitat* and *BCA indirect impact potential on NTS population*. Note that variables with zero sensitivity have no causal relationship with the target variable. The corresponding sensitivity tornado plots for low grazing intensity pastures are presented in Figs. S2 and S4.
Note: In some cases, variables may be sensitive through a common cause. For example, NTS/BCA encounter rate and indirect impact have the active BCA population size as a common cause.

BCAs for instance, besides their assumed beneficial roles, may negatively affect native species and other valued nontarget organisms in multiple ways. They may directly feed on the local flora and fauna or affect other species' populations through cascading indirect interactions via the food web (Louda et al., 2003; Messing, Roitberg, & Brodeur, 2006). Potential indirect interactions between BCAs and other organisms can be identified from actual knowledge of the ecological community, including many interactions that could lead to negative impacts (Todd et al, 2020). Despite increasing efforts to monitor actual ecological impacts of BCA introductions, most of these interactions remain more hypothetical than realized, and the number of historical biological control cases that have had reportedly harmful ecological impacts remains small (Heimpel, & Cock, 2018).

5.2. BAIPA, a New Tool to Support Release Decisions of BCAs

Current models and tools support the selection of appropriate BCAs based on their potential to suppress the target and predicted safety to NTS based on quarantine screening. They help to prioritize at-risk NTS for further assessment, often in quarantine laboratory trials to evaluate the BCA host attraction and physiological host range. We propose here a new tool, BAIPA, that complements these existing tools by incorporating all gathered knowledge on the BCA and NTS interactions and enabling for a comprehensive assessment of the adverse impact of a BCA on populations of at-risk NTS. BAIPA explicitly denotes probability distributions of all linked events, thereby providing vital information on the degree of certainty and uncertainty of outcomes throughout the causal network of events. We aim for BAIPA to assist risk-management decision making for the release of BCAs by providing:

- reproducible evaluations of the ecological host range of a BCA, including the probability of *in situ* encounters with NTS in different habitats, and an evaluation of the BCAs impact at the population level;
- a method to incorporate information from various sources, including quantitative, qualitative, and expert knowledge;
- a display of the order of events that result in potential impacts on the NTS, including their quantification (conditional probabilities) and the propagation of uncertainties (variability, errors, etc.) associated with the model structure and parameter estimates; and
- a transparent and consistent decision-support tool, to help visualization of all input factors, intermediate calculations, and outcome probabilities in the model, with capacity for sensitivity analysis and scenario testing.

Thus, BAIPA can be seen as an additional tool to help decisionmakers assess the risk of releasing BCAs into new environments. As with other risk assessment tools, BAIPA can be used as a component of more complete biocontrol risk assessment frameworks (e.g., Fig. 1; Paula, Andow, Barratt, Pfannenstiel, & van Lenteren, 2019; Paula et al., 2021). Further discussion of the important attributes offered by BAIPA are given below.

5.3. Ecological Host Range Evaluation

Current risk assessment frameworks for BCAs put very little emphasis on the ecological host range of the BCA and often do not consider ecological barriers that occur in field conditions and that might restrict host accessibility or that might reduce the success rates of attacks toward nontargets. Instead, there is a focus on physiological host range testing to provide laboratory-based quantified predictions of the injurious potential of a BCA on each NTS. Physiological compatibility is a key prerequisite for a BCA to have an impact on an NTS population, and this can be tested in quarantine conditions, prerelease. If one bases predictions too strictly on physiological host testing data to estimate the outcome of direct interactions between BCAs and NTS in the field, there is the potential to overestimate or, perhaps more grievously, underestimate the risk (Barratt et al., 2010; Heimpel & Cock, 2018; Simberloff & Stiling, 1996).

On the one hand, for some BCAs, the ecological host range tends to be narrower than the physiological host range because of ecological barriers reducing exposure for NTS (Haye, Goulet, Mason, & Kuhlmann, 2005; Heimpel & Mills, 2017). For example, limitations in spatial and temporal co-occurrence have been shown by Wyckhuys, Koch, Kula, and Heimpel (2009) to reduce the exposure of native aphids to the braconid *Binodoxys communis* (a parasitoid released for control of the soybean aphid pest, *Aphis glycines*). "No release" decisions based solely on physiological matches between a BCA and NTS denote a somewhat precautionary approach in biological control programs. However, they might constitute false positive errors, that is, falsely assuming a potential, salient negative impact of the BCA on the NTS, when the impact could be minor or insignificant. In certain cases, more detrimental environmental consequences could result from this precautionary approach relative to a small risk of nontarget impact, for instance as effective BCA releases may have allowed a substantial reduction of pesticide use.

On the other hand, one cannot always assume the physiological host testing has properly tested all "exposure" situations that could occur in the field. For instance, encounter conditions and attack behaviors may be induced by specific conditions that could not always be reproduced in quarantine conditions (especially with a limited budget); that is, to test all combinations of life stages, physiological states, environmental cues, and other factors is usually not possible. For example, following relatively extensive laboratory tests showing no native gall-makers were suitable hosts for *Torymus sinensis* (a hymenopteran BCA released in Italy against the chestnut gall wasp *Dryocosmus kuriphilus*), postrelease surveys showed occasional, unexpected parasitism in the oak gall-maker, *Biorhiza pallida* (Ferracini et al., 2015). Another example is the beneficial weevil *Rhinocyllus conicus* (as a BCA of exotic thistles), which was tested in quarantine in New Zealand as a potential NTS for *M. aethiopoides*. Tests were carried out with *R. conicus* adults that were in diapause and nonactive, and no attacks were observed on the species. In the field, some attacks were observed post release, later confirmed by records of successful attack behaviors in the laboratory when mobile and active *R. conicus* adults were used (Barratt, 2004). This would constitute a false negative error, that is, the prediction made at the time was for no impact when the actual impact could have been substantial.

A "release" decision based solely on evidence of a physiological mismatch between a BCA and NTS, usually based on limited, or sometimes disparate and contradictory results, cannot, therefore, be necessarily considered the most prudent and efficacious approach. To avoid such errors, BAIPA uses a single, integrated, ecological model to consider how a BCA could disperse to field environments beyond those used by the TS, whether it may encounter NTS, and whether it may attack and potentially impact NTS population levels. It does so following the recommendations of Kaufman and Wright (2017), by integrating quantitative estimates of the probability of "exposure" of the NTS to the BCA, with estimates of the probability of "effects" on the NTS population conditional on exposure. Probability distributions of events are provided for every ecological interaction assessed in the model, down to the final evaluation of a population-level negative or positive impact on the NTS.

5.4. Management and Implications of Uncertainties

BAIPA provides a risk analysis framework that decisionmakers can use in risk management by helping to articulate decision criteria expressed as probabilities of negative impact outcomes that would be acceptable or unacceptable in comparison to benefits (Heimpel & Cock, 2018). Outcomes from the BAIPA BN are not intended to dictate decisions on BCA introductions but instead help inform a science-based decision. It is a matter of policy, management, and communication to define acceptable probability levels of BCA impacts on NTS (Ehlers, 2011; Lonsdale et al., 2001). Instead, the BN model serves to document current knowledge, to illustrate the key causal factors leading to the outcomes, and to depict the implications of how variations or uncertainties in the inputs propagate throughout the causal web of conditions and relations. BAIPA considers uncertainties associated with quantitative predictions, addressing general guidelines for biosecurity risk assessment (e.g., International Standard for Phytosanitary Measures 2, 3, 11), and other expert recommendations (e.g., Kaufman & Wright, 2017, for biological control). In this respect, BAIPA complements existing tools developed under international guidelines and codes of conduct relevant to the introduction of BCAs. Other examples of international and national organizations that regulate or advise on the release of BCAs are documented in Lockwood, Howarth, and Purcell (2001), van Lenteren et al. (2006), and Barratt and Ehlers (2017).

BAIPA coupled with sensitivity and scenario testing provides the user with the capability to determine which factors are the most influential, that is, could most affect outcomes of BCA impacts on NTS populations and that are least understood. Such information can be invaluable for prioritizing future field monitoring and targeted research effort.

5.5. Case Study

Generally, traits that contribute to the success of BCAs, such as a capacity for establishment, survival, population increase, and dispersal, are traits that enhance the likelihood of adverse ecological impacts (Barratt et al., 2010; Louda et al., 2003), and these will generally be identified to have the greatest influence on the BAIPA model output. The parasitoid *M. aethiopoides* has been shown to attack many weevil species, both in laboratory quarantine trials and during field assessments in productive and natural ecosystems (Barratt & Johnstone, 2001; Barratt et al., 1997, 2007). These include the target pest species, *S. discoideus*, and several native weevils including those in the genus *Nicaeana*. In our case study, we retrospectively investigated the actual risk for *Nicaeana* weevil populations being impacted by *M. aethiopoides* in a full ecological context not just considering them as physiological hosts but also considering their risk of exposure to the parasitoid.

The model showed that encounters between *M. aethiopoides* and *Nicaeana* weevils are principally driven by the abundance of the BCA and NTS in the habitat. Given the relatively small sizes of the populations for both species, encounters should be uncommon in both pastures and native grassland (87% and 92% probability that the nontarget weevils never[4] encounter the parasitoid). Thus, although the BCA has high rates of attack success[5] with these NTS, the low probability of encounters resulted in predictions of low parasitism levels.

For pastures, the model predicted an 87% probability of no or low levels of weevil parasitism and a 12% probability of occasional weevil parasitism[6]. These results concur with observations from Barratt, Ferguson, Evans, McNeill, and Addison (2000), where averages of 4–5% parasitism of *Nicaeana* spp. by *M. aethiopoides* were recorded in old pastures in the South Island of New Zealand. The highest recorded level of *Nicaeana* spp. parasitism was 51% at one of the Otago survey sites. For native grassland, the model predicted a 92% probability of no or low levels of weevil parasitism and a 7% probability of occasional weevil parasitism[8]. Ferguson et al. (2016), working in native grassland sites in the South Island of New Zealand, reported 7.8% parasitism of *Nicaeana* species by *M. aethiopoides*, with no noticeable impact on the population level over a period of more than 10 years. At one site, a middle altitude (780 m ASL) lightly grazed native grassland, parasitism rates peaked at 23.5% in summer (Barratt et al., 2007). This site was also the site with the highest recorded weevil abundance out of the nine survey locations. Our results suggest that the probability of encounters between this parasitoid and these NTS is the most influential factor conducive to population impact, in either native grassland or pastures. Results of the sensitivity analysis (Fig. 4) show these encounters are largely influenced by the possibility of a temporal match and the respective abundances of all three species (BCA, NTS, and TS) in the habitat. The abundance of the NTS and the TS are model inputs (both are present in most grassland and pasture habitats), whereas the abundance of the BCA and the spatial and temporal matches with the BCA, and the probability of encounters, are predicted by the model based on several factors such as the BCA's dispersal and host-finding capability. Consequently, predicting the likelihood that populations of *Nicaeana* weevils would be parasitized by *M. aethiopoides* relied on accurate abundance data for both the target and NTS in the habitat(s) of interest and information on the dispersal and host-finding capability of the BCA. In this case study, long-distance dispersal of the BCA does not appear to be a key influential factor because the target is present in a majority of New Zealand native grasslands and pastures, and therefore the BCA is expected to be present too.

Once the ecological constraint of an encounter between the two species is removed (as shown by a sensitivity analysis or conducting a what-if scenario), high parasitism levels are predicted (a 95% overall probability that more than 20% of NTS individuals are attacked, in both habitats[6]), and a direct impact at the population level is expected (77% and 83% probability of a reduction of the nontarget population, in pastures and native grassland, respectively,

[4]From predictions for the "NTS BCA encounters" node (Figs. 3 and S1). The state "never" corresponds to less than 5% of NTS individuals encounter the BCA (Table S1).

[5]From user input for the "BCA attacks NTS when encounters" node (Table S2). Attacks are considered to occur frequently within the population with an overall 95% probability, divided between a 45% probability for the state "always" (defined as a situation where more than 80% of susceptible individuals in the NTS population are attacked by the attacking stage of the BCA, Table S1), and a 50% probability for the state "sometimes" (defined as a situation where between 20% and 80% of susceptible individuals in the NTS population are attacked by the attacking stage of the BCA).

[6]From predictions for the "BCA attacks NTS" node (in component 7 "direct impacts", not shown in Figs. 3 and S1 but described in Table S1). The state "never", predicted at 87% probability of occurrence for pastures and at 92% for native grassland, corresponds to less than 20% of NTS individuals attacked by the BCA. The state "sometimes", predicted at 12% probability of occurrence for pastures and at 7% for native grassland, corresponds to between 20% and 80% of NTS individuals attacked by the BCA.

Figs. 4b and S2a). Ferguson et al. (2016) performed field trials for parasitism of *Nicaeana spp*. caged with *M. aethiopoides* and observed an average 40.6% parasitism rate. These slightly lower than expected parasitism rates may have been driven by a low propensity for *M. aethiopoides* to search microhabitats occupied by *Nicaeana* weevils (i.e., short-range attraction), hence low levels of actual exposures occurred despite the cages (i.e., 160 × 180 mm x 75 mm deep). Another explanation might be due to lower attack rates or parasitism success than those expected from laboratory host testing.

Overall, our model predictions matched the field observations, while erring on the side of caution. Nonetheless, these results pertain specifically to our current understanding of the *Microctonus–Sitona–Nicaeana* system in New Zealand. They may differ somewhat for the same species when the BN model parameters are updated with empirical evidence or further expert knowledge elicitation. Results are likely to differ for other species with different biological and ecological attributes.

The relationship between individual-level impact (the proportion of the population that is attacked) and population-level impact (the proportion of reduction in the population over multiple generations) is particularly difficult to evaluate. A rule of thumb derived from the meta-analysis by Hawkins and Cornell (1994) analyzing 787 parasitoid introductions suggests little impact is expected to arise from parasitoids unless parasitism rates exceed 32%.

Our own results predicted that direct impacts on *Nicaeana* populations are unlikely (91% and 94% probability that the BCA does not directly impact the NTS population[7] in pastures and native grassland, respectively). Kean and Barlow (2000, 2001) showed that the intrinsic rate of increase of the hosts is critical to determining the population impact of *Microctonus* on weevils. For the TS, *S. discoideus*, field sampling in South Australia showed no measurable impact on the TS at the population level even with 50–60% parasitism (Hopkins, 1989). In contrast to *Sitona* weevils, which produce hundreds of eggs, *Nicaeana* species have a low reproductive potential estimated to less than 50 eggs (number of eggs produced by fecund females ranged from 3.5 to 6 per five-day period during the reproductive season, Barratt et al., 2016) and are more likely to be affected at such parasitism levels.

Population dynamic mechanisms are difficult to evaluate when a parasitoid and at least two potential host populations coexist. BN models do not allow incorporation of feedback loops (e.g., to model population interactions) but can set dynamic processes based on time steps (e.g., considering rates of increase). The complexity of space and time interactions with multiple species in a dynamic BN framework requires a much more complex model structure that would make the model more difficult to parameterize and navigate. Instead, we suggest the user trials a series of "what-if" scenarios, by setting different habitat-relative abundances for the target and NTS (and possibly the BCA). This would allow, for instance, estimations of levels of attack and impacts realized in the field by BCAs either introduced via spill-over from distant populations or via permanent cycling locally. Tools such as BAIPA are well-suited for extensive model experimentations of this type.

5.6. Limitations and Possible Improvements

With the Bayesian approach used in BAIPA, predictions rely on the quality of the model structure, on the underlying conditional probabilities propagating the outcome and associated uncertainty throughout the model, and on the prior probability distributions on the input variables, as they can be used in place of missing data (Marcot et al. 2019).

BAIPA comes as a decision-support tool based on multiple sources of information, including quantitative scientific data, technical expert reports, and views from stakeholders and the public. When information for some input variables is lacking, prior probability distributions can be used as the default, as estimated from other BCA systems. In the current version of BAIPA, we have estimated all prior probability distributions and parameters of the CPTs based on our knowledge of ecological interactions between parasitoid wasps attacking defoliating insects (Table S2). These parameters pertain to the configuration of the model as an "alpha-level" model (in the sense used by Marcot, Steventon, Sutherland, & McCann, 2006) and use a parasitoid-host system as a guide.

To ensure that the model is rigorously developed, and therefore credible, one would require other subject-matter domain experts to perform a formal peer review and potentially recommend revisions of the prior probability distributions and the parameters of all CPTs and potentially of the model

[7]From predictions for the "BCA direct impact on NTS populations" node (Figs. 3 and S1). The state "no direct impact" corresponds to no substantial reduction of the NTS population in the habitat through direct interactions (parasitism in this case, Table S1).

structure itself. The use of BAIPA for the prediction of other trophic interactions may provide limited assurance of reliability and accuracy if built solely on the basis of parasitoid–host interactions. Several sets of model parameters should be developed, and the structures of some of the submodels could be altered, such as to accommodate predator–prey or herbivore–host plant systems. Following peer review, additional next steps in the model-building process are necessary to ensure rigorous expert-based construction of the "beta-level" model to warrant its credibility. Guidelines to transition from a "beta-level" to a "gamma-level" model are provided in Marcot et al. (2006) and include testing the model with case data (so that the prediction accuracy of the current model can be estimated) and its recalibration with these case data (allowing the model to better fit known examples and to handle missing data).

This testing and calibration process can be empirically expensive, that is, needing extensive data such as laboratory testing or field observations. The lack of specific field studies of BCA impacts and nontarget population-level outcomes, in particular, can prevent estimates of false negative and false positive model predictions. Pre- and postrelease population data are rarely available, in particular when long time-series data from multiple sites are needed to balance temporal and spatial differences in population dynamics. Lynch et al. (2001) reported that only 4.5% of arthropod BCAs released worldwide were evaluated for population impacts on NTS and were properly studied for impacts on TS.

For both target and NTS, alternative ways of estimating BCA impacts have been developed based on population models (Barlow, Barratt, Ferguson, & Barron, 2004; Barron, 2007), or based on models combined with experimental data obtained in containment (Raghu, Dhileepan, & Scanlan, 2007; Raghu, Dhileepan, & Treviño, 2006) and in the field (Boettner, Elkinton, & Boettner, 2000; Carvalheiro et al., 2008). As other input variables or intermediate outcomes might be lacking for the case data, these can be estimated based on demographic modeling (e.g., Raghu et al., 2007), dispersal modeling (e.g., Kimberling, 2004), parasitoid–host (or predator–prey, or herbivore–plant) dynamics (e.g., Grasman, van Herwaarden, Hemerik, & van Lenteren, 2001), or indirect effects estimation (e.g., Todd, Pearce, & Barratt, 2020). Such approaches provide an improvement, but certain relationships remain difficult to capture, such as the functional relationship between attack and population effects (affected by the intrinsic growth rates of the populations; Mills & Kean, 2010). Our probabilistic modeling approach provides a flexible framework by which such additional considerations and biological effects can be layered into the dynamics and calculations of BCA-NTS impacts.

6. CONCLUSION

For the purpose of risk assessment of potential impacts of BCAs on NTS, we found that the BN modeling approach provides the following significant advantages: (1) it displays outcomes as probabilities that work well in a risk management framework; (2) it explicitly shows the propagation of uncertainties and their implications for predictions; (3) through sensitivity and influence analysis, it provides an easy way to determine the relative influence of potential alternative management actions and prior conditions on outcomes; and (4) models can be run efficiently for sets of scenarios of alternative environmental and management conditions. The new BAIPA currently incorporates a BN model that assesses the risk for NTS to be negatively affected by the release of a BCA.

BAIPA has been developed with the potential to be turned into a designed-for-purpose web tool available for risk assessors and may support national regulatory authorities, such as the Environmental Protection Authority in New Zealand or the Animal and Plant Health Inspection Service in the United States, in their decision making to release BCAs. Eventually, model outcomes from BAIPA can be incorporated into a structured decision-making framework that may include a formal comparison between multiple risks and benefits associated with the potential or planned release of the BCA. It is important that such decisions are based on risk assessments that incorporate the most relevant ecological information within a logical, coherent, and transparent ecological framework. Hence, the accuracy of predictions will primarily depend on the veracity of assumptions of how BCAs respond to their new environments.

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AUTHOR CONTRIBUTIONS

Nicolas Meurisse, Bruce G. Marcot, Barbara I. P. Barratt, and Jacqui H. Todd contributed to the evaluation of the current risk assessment frameworks for biological control agents. Nicolas Meurisse, Owen Woodberry, and Bruce G. Marcot conceptualized the Bayesian network model. Nicolas Meurisse and Owen Woodberry developed the Bayesian network model in GeNIe. Owen Woodberry and Bruce G. Marcot supported the general interpretation of the model. All authors contributed to the writing, review, and editing.

REFERENCES

Abram, P. K., & Moffat, C. E. (2018). Rethinking biological control programs as planned invasions. *Current Opinion in Insect Science*, *27*, 9–15.

Andersen, M. C., Adams, H., Hope, B., & Powell, M. (2004). Risk Assessment for Invasive Species. *Risk Analysis*, *24*(4), 787–793.

Askew, R. R. (1994) Parasitoids of leaf-mining Lepidoptera: what determines their host ranges? In B. Hawkins, & W. Sheehan (Eds.), *Parasitoid community ecology* (pp. 177–202). Oxford, UK: Oxford University Press.

Babendreier, D., Bigler, F., & Kuhlmann, U. (2005). Methods used to assess non-target effects of invertebrate biological control agents of arthropod pests. *Biocontrol*, *50*(6), 821–870.

Baker, J., & Stuckey, M. (2009). *Prioritising the impact of exotic pest threats using Bayes Net and MCDA Methods*. Melbourne, Australia: Australian Centre of Excellence for Risk Analysis, The University of Melbourne. Retrieved from https://protect-au.mimecast.com/s/J1qxCP7LAjt0P5EujyVc1?domain=acera.unimelb.edu.au

Barlow, N. D., Barratt, B. I. P., Ferguson, C. M., & Barron, M. C. (2004). Using models to estimate parasitoid impacts on non-target host abundance. *Environmental Entomology*, *33*(4), 941–948.

Barratt, B.I.P. (2004). *Microctonus* parasitoids and New Zealand weevils: comparing laboratory estimates of host ranges to realized host ranges. In R. Van Driesche, & R. Reardon (Eds.), *Assessing host ranges for parasitoids and predators used for classical biological control: A guide to best practice* (pp. 103–120). Morgantown, West Virginia: USDA Forest Service.

Barratt, B. I. P., Crook, K. E., Dickinson, K. J. M., Burritt, D. J. (2016). Cyanogenic white clover as a proxy for GM biosafety testing using two New Zealand native insects. *New Zealand Journal of Agricultural Research*, *59*(4), 377–388.

Barratt, B. I. P., & Ehlers, C. A. C. (2017). Impacts of Exotic biological control agents on non-target species and biodiversity. In M. Coll, & E. Wajnberg (Eds.), *Environmental pest management* (pp. 325–346). Oxford, UK: John Wiley & Sons, Ltd.

Barratt, B. I. P., Evans, A. A., Ferguson, C. M., Barker, G. M., McNeill, M. R., & Phillips, C. B. (1997). Laboratory nontarget host range of the introduced parasitoids *Microctonus aethiopoides* and *M. hyperodae* (Hymenoptera: Braconidae) compared with field parasitism in New Zealand. *Environmental Entomology*, *26*(3), 694–702.

Barratt, B. I. P., Ferguson, C. M., Bixley, A. S., Crook, K. E., Barton, D. M., & Johnstone, P. D. (2007). Field parasitism of nontarget weevil species (Coleoptera: Curculionidae) by the introduced biological control agent *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) over an altitude gradient. *Environmental Entomology*, *36*(4), 14.

Barratt, B. I. P., Ferguson, C. M., Evans, A. A., McNeill, M. R., & Addison, P. J. (2000). Phenology of native weevils (Coleoptera: Curculionidae) in New Zealand pastures and parasitism by the introduced braconid, *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae). *New Zealand Journal of Zoology*, *27*(2), 93–110.

Barratt, B. I. P., Howarth, F. G., Withers, T. M., Kean, J. M., & Ridley, G. S. (2010). Progress in risk assessment for classical biological control. *Biological Control*, *52*(3), 245–254.

Barratt, B. I. P., & Johnstone, P. D. (2001). Factors affecting parasitism by *Microctonus aethiopoides* (Hymenoptera: Braconidae) and parasitoid development in natural and novel host species. *Bulletin of Entomological Research*, *91*(4), 245–253.

Barron, M. C. (2007). Retrospective modelling indicates minimal impact of non-target parasitism by *Pteromalus puparum* on red admiral butterfly (*Bassaris gonerilla*) abundance. *Biological Control*, *41*(1), 53–63.

Boettner, G. H., Elkinton, J. S., & Boettner, C. J. (2000). Effects of a biological control introduction on three nontarget native species of Saturniid moths. *Conservation Biology*, *14*(6), 1798–1806.

Burgman, M. A., Wintle, B. A., Thompson, C. A., Moilanen, A., Runge, M. C., & Ben-Haim, Y. (2010). Reconciling uncertain costs and benefits in Bayes Nets for invasive species management. *Risk Analysis*, *30*(2), 277–284.

Carvalheiro, L. G., Buckley, Y. M., Ventim, R., Fowler, S. V., & Memmott, J. (2008). Apparent competition can compromise the safety of highly specific biocontrol agents. *Ecology Letters*, *11*(7), 690–700.

Dambacher, J. M., Shenton, W., Hayes, K. R., Hart, B. T. and Barry, S. (2008). *Qualitative modelling and Bayesian network analysis for risk-based biosecurity decision making in complex systems*. Melbourne, Australia: Australian Centre of Excellence for Risk Analysis, The University of Melbourne. Available from https://protect-au.mimecast.com/s/ZCYFCOMKzghNM2mTkbVs3?domain=acera.unimelb.edu.au

Davidson, A. D., Fusaro, A. J., Sturtevant, R. A., Rutherford, E. S., & Kashian, D. R. (2017). Development of a risk assessment framework to predict invasive species establishment for multiple taxonomic groups and vectors of introduction. *Management of Biological Invasions*, *8*(1), 25–36.

Dawid, A. P. (2015). Statistical causality from a decision-theoretic perspective. *Annual Review of Statistics and Its Application*, *2*, 273–303.

De Clercq, P., Mason, P. G., & Babendreier, D. (2011). Benefits and risks of exotic biological control agents. *BioControl*, *56*(4), 681–698.

Ehlers, R.-U. (2011). Regulation of biological control agents and the EU policy support action REBECA. In R. -U. Ehlers (Ed.), *Regulation of biological control agents* (pp. 2–23). Dordrecht, the Netherlands: Springer.

Eilenberg, J., Hajek, A., & Lomer, C. (2001). Suggestions for unifying the terminology in biological control. *BioControl*, *46*, 387–400.

European Food and Safety Agency Scientific Committee, Benford, D., Halldorsson, T., Jeger, M. J., Knutsen, H. K., More, S., … Hardy, A. (2018). The principles and methods behind EFSA's guidance on uncertainty analysis in scientific assessment. *EFSA Journal*, *16*(1), e05122.

European & Mediterranean Plant Protection Organization (2018). EPPO Standards on safe use of biological control–PM 6/04(1): Decision support scheme for import and release of biological control agents of plant pests. *OEPP/EPPO Bulletin*, *48*(3), 352–367

Ferracini, C., Ferrari, E., Saladini, M. A., Pontini, M., Corradetti, M., & Alma, A. (2015). Non-target host risk assessment for the parasitoid *Torymus sinensis*. *BioControl*, *60*(5), 583–594.

Ferguson, C. M., Kean, J. M., Barton, D. M., & Barratt, B. I. (2016). Ecological mechanisms for non-target parasitism by the Moroccan ecotype of *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) in native grassland. *Biological Control*, *96*, 28–38.

Füssel, H. -M. (2007). Vulnerability: A generally applicable conceptual framework for climate change research. *Global Environmental Change*, *17*(2), 155–167.

Goldson, S. L., Frampton, E. R., Barratt, B. I. P., & Ferguson, C. M. (1984). The seasonal biology of *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae), an introduced pest of New Zealand lucerne. *Bulletin of Entomological Research*, *74*(2), 249–259.

Goldson, S. L., McNeill, M. R., Proffitt, J. R., Barker, G. M., Addison, P. J., Barratt, B. I. P., & Ferguson, C. M. (1993). Systematic mass rearing and release of *Microctonus hyperodae* (Hym.: Braconidae, Euphorinae), a parasitoid of the argentine stem *weevil Listronotus bonariensis* (Col.: Curculionidae) and records of its establishment in New Zealand. *Entomophaga*, *38*(4), 527–536.

Grasman, J., Van Herwaarden, O. A., Hemerik, L., & Van Lenteren, J. C. (2001). A two-component model of host–parasitoid interactions: Determination of the size of inundative releases of parasitoids in biological pest control. *Mathematical Biosciences*, *169*(2), 207–216.

Grevstad, F. S. (1999). Factors influencing the chance of population establishment: implications for release strategies in biocontrol. *Ecological Applications*, *9*(4), 1439-1447.

Hajek, A. E., Hurley, B. P., Kenis, M., Garnas, J. R., Bush, S. J., Wingfield, M. J., … Cock, M. J. W. (2016). Exotic biological control agents: A solution or contribution to arthropod invasions? *Biological Invasions*, *18*(4), 953–969.

Hawkins, B. A., & Cornell, H. V. (1994). Maximum parasitism rates and successful biological control. *Science*, *266*(5192), 1886–1887.

Haye, T., Goulet, H., Mason, P. G., & Kuhlmann, U. (2005). Does fundamental host range match ecological host range? A retrospective case study of a *Lygus* plant bug parasitoid. *Biological Control*, *35*(1), 55–67.

Heimpel, G. E., & Cock, M. J. W. (2018). Shifting paradigms in the history of classical biological control. *Biocontrol*, *63*(1), 27–37.

Heimpel, G. E., & Mills, N. (2017). Ecological risk analysis in biological control. In G. Heimpel, & N. Mills (Eds.), *Biological control: Ecology and applications* (pp. 114–146). Cambridge, UK: Cambridge University Press.

Hinz, H. L., Schwarzländer, M., Gassmann, A., & Bourchier, R. S. (2014). Successes we may not have had: a retrospective analysis of selected weed biological control agents in the United States. *Invasive Plant Science and Management*, *7*(4), 565–579.

Holt, J., Leach, A. W., Johnson, S., Tu, D. M., Nhu, D. T., Anh, N. T., … Mumford, J. D. (2018). Bayesian networks to compare pest control interventions on commodities along agricultural production chains. *Risk Analysis*, *38*(2), 297–310.

Holt, J., Leach, A. W., Knight, J. D., Griessinger, D., MacLeod, A., van der Gaag, D. J., Schrader, G., & Mumford, J. D. (2012). Tools for visualizing and integrating pest risk assessment ratings and uncertainties. *EPPO Bulletin*, *42*(1), 35–41.

Hood, G. M., Barry, S. C., & Martin, P. A. J. (2009). Alternative methods for computing the sensitivity of complex surveillance systems. *Risk Analysis*, *29*(12), 1686–1698.

Hope, B. K. (2006). An examination of ecological risk assessment and management practices. *Environment International*, *32*(8), 983–995.

Hopkins, D. C. (1989). Widespread establishment of the Sitona weevil parasite, *Microctonus aethiopoides* and its effectiveness as a control agent in South Australia. In P. Stahle (Ed.), *Proceedings of the 5th Australasian conference on grassland invertebrate ecology* (pp. 49–53). Melbourne, Australia: University of Melbourne, D & D Printing.

Hopper, K. R. (2001). Research needs concerning non-target impacts of biological control introductions. In E. Wajnberg, J. Scott, & P. Quimby (Eds.), *Evaluating indirect ecological effects of biological control. Key papers from the symposium "Indirect ecological effects in biological control", Montpellier, France, 17–20 October 1999* (pp. 39–56). Wallingford: CABI Publishing. Retrieved from https://digitalcommons.unl.edu/usdaarsfacpub/478

Horton, B. J., Evans, D. L., James, P. J., & Campbell, N. J. (2009). Development of a model based on Bayesian networks to estimate the probability of sheep lice presence at shearing. *Animal Production Science*, *49*(1), 48–55.

Hosack, G. R., Hayes, K. R., & Dambacher, J. M. (2008). Assessing model structure uncertainty through an analysis of system feedback and Bayesian networks. *Ecological Applications*, *18*(4), 1070–1082.

Howarth, F. G. (1991). Environmental impacts of classical biological control. *Annual Review of Entomology*, *36*(1), 485–509.

Hunt, E. J., Kuhlmann, U., Sheppard, A., Qin, T. -K., Barratt, B. I. P., Harrison, L., Mason, P. G., Parker, D., Flanders, R. V., & Goolsby, J. (2008). Review of invertebrate biological control agent regulation in Australia, New Zealand, Canada and the USA: Recommendations for a harmonized European system. *Journal of Applied Entomology*, *132*(2), 89–123.

IPCC (International Plant Protection Convention) (2014). Summary for policymakers. In C. Field, V. Barros, D. Dokken, K. Mach, M. Mastrandrea, T. Bilir, … L. White (Eds.), Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change (pp. 1–32). Cambridge, UK and New York, NY: Cambridge University Press. Retrieved from https://www.ipcc.ch/site/assets/uploads/2018/02/ar5_wgII_spm_en.pdf

Jamieson, L. E., DeSilva, H. N., Worner, S. P., Rogers, D. J., Hill, M. G., & Walker, J. T. S. (2013). A review of methods for assessing and managing market access and biosecurity risks using systems approaches. *New Zealand Plant Protection 66*, 1–9.

Jamieson, L. E., Woodberry, O. G., McDonald, C., & Ormsby, M. (2016). Developing a generic biosecurity risk assessment model for imports. *New Zealand Plant Protection*, *69*, 186–199.

Kaufman, L. V., & Wright, M. G. (2017). Assessing probabilistic risk assessment approaches for insect biological control introductions. *Insects*, *8*(3), 67.

Kean, J. M., & Barlow, N. D. (2000). Long-term assessment of the biological control of *Sitona discoideus* by *Microctonus aethiopoides* and test of a model. *Biocontrol Science and Technology*, *10*(3), 215–221.

Kean, J. M., & Barlow, N. D. (2001). A spatial model for the successful biological control of *Sitona discoideus* by *Microctonus aethiopoides*. *Journal of Applied Ecology*, *38*(1), 162–169.

Kimberling, D. N. (2004). Lessons From History: Predicting Successes and Risks of Intentional Introductions for Arthropod Biological Control. *Biological Invasions*, *6*(3), 301–318.

Korb, K. B., & Nicholson, A. E. (2011). *Bayesian artificial intelligence* (2nd ed.). Boca Raton, FL: CRC/Chapman Hall.

Kenis, M., Bacher, S., Baker, R., Branquart, E., Brunel, S., Holt, J., … Schaffner, J. (2012). New protocols to assess the environmental impact of pests in the EPPO decision-support scheme for pest risk analysis. *EPPO Bulletin*, *42*(1), 21–27.

Lockwood, J. A., Howarth, F. G., & Purcell, M. F. (Eds.) (2001). *Balancing nature: assessing the impact of importing non-native biological control agents*. Langham, MD: Thomas Say Publications in Entomology.

Lonsdale, W. M., Briese, D. T., & Cullen, J. M. (2001). Evaluating indirect ecological effects of biological control. E. Wajnberg, J. K. Scott & P. C. Quimby, *Key papers from the symposium "Indirect ecological effects in biological control", Montpellier, France, 17-20 October 1999* (185–210). Wallingford, UK: CABI.

Louda, S. M., Pemberton, R. W., Johnson, M. T., & Follett, P. (2003). Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annual Review of Entomology*, *48*(1), 365–396.

Lynch, L. D., Hokkanen, H. M. T., Babendreier, D., Bigler, F., Burgio, G., Gao, Z. H., … Thomas, M. B. (2001). Insect biological control and non-target effects: a European perspective. In E. Wajnberg, J. Scott, & P. Quimby (Eds.), *Evaluating indirect ecological effects of biological control* (pp. 99–126). Wallingford, UK: CABI Publishing.

Marcot, B. G. (2012). Metrics for evaluating performance and uncertainty of Bayesian network models. *Ecological Modelling*, *230*, 50–62.

Marcot, B. G. (2021). *The science and management of uncertainty: dealing with doubt in natural resource management*. Oxfordshire, UK: Taylor & Francis a CRC Press Book.

Marcot, B. G., Hoff, M. H., Martin, C. D., Jewell, S. D., & Givens, C. E. (2019). A decision advisory system for identifying potentially invasive and injurious freshwater fishes. *Management of Biological Invasions*, *10*(2), 200–226.

Marcot, B. G., Steventon, J. D., Sutherland, G. D., & McCann, R. K. (2006). Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation. *Canadian Journal of Forest Research*, *36*(12), 3063–3074. http://doi.org/10.1139/x06-135

McDaniels, T., Axelrod, L. J., & Slovic, P. (1995). Characterizing Perception of Ecological Risk. *Risk Analysis*, *15*(5), 575–588.

McGeoch, M. A., Butchart, S. H. M., Spear, D., Marais, E., Kleynhans, E. J., Symes, A., … Hoffmann, M. (2010). Global indicators of biological invasion: Species numbers, biodiversity impact and policy responses. *Diversity and Distributions*, *16*(1), 95–108.

Mengersen, K., Quinlan, M. M., Whittle, P. J. L., Knight, J. D., Mumford, J. D., Wan Ismail, W. N., … Hermawan. (2012). Beyond compliance: Project on an integrated systems approach for pest risk management in South East Asia. *EPPO Bulletin*, *42*(1), 109–116.

Messing, R., Roitberg, B., Brodeur, J. (2006) Measuring and predicting indirect impacts of biological control: competition, displacement and secondary interactions. In F. Bigler, D. Babendreier, & U. Kuhlman (Eds.), *Environmental impact of invertebrates for biological control of arthropods: Methods and risk assessment* (pp. 64–77). Wallingford, UK: CABI Publishing.

Mills, N. J., & Kean, J. M. (2010). Behavioral studies, molecular approaches, and modeling: Methodological contributions to biological control success. *Biological Control*, *3*(52), 255–262.

Murphy, B., Jansen, C., Murray, J., & De Barro, P. (2010). *Risk analysis on the Australian release of Aedes aegypti (L.) (Diptera: Culicidae) containing Wolbachia*. Indooroopilly, Australia: CSIRO Entomology.

Office of the Prime Minister's Chief Science Advisor (2016). *Making decisions in the face of uncertainty: Understanding risk*. Wellington, New Zealand: Office of the Prime Minister's Chief Science Advisor. Retrieved from https://www.pmcsa.org.nz/wp-content/uploads/PMCSA-Risk-Series-Paper-1_final_2.pdf

Paynter, Q., & D. Teulon. (2019). Laboratory tests to estimate the non-target impacts of four *Aphidius* spp. parasitoids in the field. *Biological Control*, *133*, 41–49.

Paynter, Q., Fowler, S. V., Gourlay, A. H., Peterson, P. G., Smith, L. A., & Winks, C. J. (2015). Relative performance on test and target plants in laboratory tests predicts the risk of non-target attack in the field for arthropod weed biocontrol agents. *Biological Control*, *80*, 133–142.

Pearl, J. (1988). *Probabilistic reasoning in intelligent systems: networks of plausible inference*. San Mateo, CA: Morgan Kaufmann.

Pearl, J. (2000). *Causality: models, reasoning, and inference*. Cambridge, UK: Cambridge University Press.

Peterson, D. P., Rieman, B. E., Dunham, J. B., Fausch, K. D., & Young, M. K. (2008). Analysis of trade-offs between threats of invasion by nonnative brook trout (*Salvelinus fontinalis*) and intentional isolation for native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(4), 557–573

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3), 273–288.

Paula, D. P., Andow, D. A., Barratt, B. I. P., Pfannenstiel, R. S., Gerard, P. J., Todd, J. H., … van Lenteren, J. C. (2021). Integrating adverse effect analysis into environmental risk assessment for exotic generalist arthropod biological control agents: a three-tiered framework. *BioControl 66*, 113–139.

Paula, D. P., Andow, D. A., Barratt, B. I. P., Pfannenstiel, R. S., van Lenteren, J. C. (2019, November). Revisiting the biosafety of exotic generalist biological control agents. In P. Pires, & D. Andow (Chairs), *Entomology 2019*. Entomological Society of America, St Louis, MO. Abstract retrieved from https://esa.confex.com/esa/2019/meetingapp.cgi/Paper/144845

Raghu, S., Dhileepan, K., & Scanlan, J. C. (2007). Predicting risk and benefit a priori in biological control of invasive plant species: A systems modelling approach. *Ecological Modelling*, *208*(2–4), 247–262.

Raghu, S., Dhileepan, K., & Treviño, M. (2006). Response of an invasive liana to simulated herbivory: Implications for its biological control. *Acta Oecologica*, *29*(3), 335–345.

Rees, M., & Hill, R. L. (2001). Large-scale disturbances, biological control and the dynamics of gorse populations. *Journal of Applied Ecology*, *38*(2), 364–377.

Roy, H., Wajnberg, E. (2008). From biological control to invasion: the ladybird *Harmonia axyridis* as a model species. *BioControl*, *53*, 1–4.

Sheehan, W. (1986). Response by specialist and generalist natural enemies to agroecosystem diversification: A selective review. *Environmental Entomology*, *15*(3), 456–461.

Simberloff, D., Martin, J. -L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., … Vilà, M. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution*, *28*(1), 58–66.

Simberloff, D., & Stiling, P. (1996). How risky is biological control? *Ecology*, *77*(7), 1965–1974.

Thomas, M. B., & Willis, A. J. (1998). Biocontrol – Risky but necessary? *Trends in Ecology & Evolution*, *13*(8), 325–329.

Todd, J. H., Barratt, B. I., Tooman, L., Beggs, J. R., & Malone, L. A. (2015). Selecting non-target species for risk assessment of entomophagous biological control agents: Evaluation of the PRONTI decision-support tool. *Biological Control*, *80*, 77–88.

Todd J. H., Pearce B. M., & Barratt B. I. P. (2020). Using qualitative food webs to predict species at risk of indirect effects from a proposed biological control agent. *BioControl*, *66*, 45–58. https://doi.org/10.1007/s10526-020-10038-7

Todd, J. H., Ramankutty, P., Barraclough, E. I., & Malone, L. A. (2008). A screening method for prioritizing non-target inverte-

brates for improved biosafety testing of transgenic crops. *Environmental Biosafety Research*, *7*, 35–56.
van Lenteren, J. C., Babendreier, D., Bigler, F., Burgio, G., Hokkanen, H. M. T., Kuske, S., Loomans, A. J. M., Menzler-Hokkanen, I., Van Rijn, P. C. J., & Thomas, M. B. (2003). Environmental risk assessment of exotic natural enemies used in inundative biological control. *BioControl*, *48*(1), 3–38.
van Lenteren, J. C., Bale, J., Bigler, F., Hokkanen, H., & Loomans, A. (2006). Assessing risks of releasing exotic biological control agents of arthropod pests. *Annual Review of Entomology*, *51*, 609–634.
van Lenteren, J. C., & Loomans, A. J. M. (2006). Environmental risk assessment: methods for comprehensive evaluation and quick scan. In F. Bigler, D. Babendreier, & U. Kuhlmann (Eds.), *Environmental impact of invertebrates for biological control of arthropods: methods and risk assessment* (pp. 254–272). Cambridge, MA: CAB International Publishing.
Varis, O. (1997). Bayesian decision analysis for environmental and resource management. *Environmental Modelling & Software*, *12*(2–3), 177–185.
Waage, J., & Mills, N. (1992). Biological control. In M. Crawley (Ed.), *Natural enemies: The population biology of predators, parasites and diseases* (pp. 412–430). Oxford, UK: Blackwell Scientific Publications.
Wapshere, A. J. (1974). A strategy for evaluating the safety of organisms for biological weed control. *Annals of Applied Biology*, *77*, 201–211.
Walshe, T., & Burgman, M. (2010). A Framework for assessing and managing risks posed by emerging diseases. *Risk Analysis*, *30*(2), 236–249.
Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience*, *48*(8), 607–615.
Wintle, B.C., & Nicholson, A.E. (2014). Exploring risk judgments in a trade dispute using Bayesian Networks. *Risk Analysis*, *34*(6), 1095–1111.
Withers, T. M., & Browne, L. B. (2004). Behavioral and physiological processes affecting outcomes of host range testing. In R. Van Driesche, T Murray, & R. Reardon (Eds.), *Assessing host ranges for parasitoids and predators used for classical biological control: A guide to best practice* (Vol. *3*, pp. 40–55). Morgantown, West Virginia: United States Department of Agriculture Forest Health Technology Enterprise Team.
Wright, M. G., Hoffmann, M. P., Kuhar, T. P., Gardner, J., & Pitcher, S. A. (2005). Evaluating risks of biological control introductions: A probabilistic risk-assessment approach. *Biological Control*, *35*(3), 338–347.
Wyckhuys, K. A. G., Koch, R. L., Kula, R. R., & Heimpel, G. E. (2009). Potential exposure of a classical biological control agent of the soybean aphid, *Aphis glycines*, on non-target aphids in North America. *Biological Invasions*, *11*(4), 857–871.
Wyman-Grothem, K. E., Popoff, N., Hoff, M., & Herbst, S. (2018). Evaluating risk of African longfin eel (*Anguilla mossambica*) aquaculture in Michigan, USA, using a Bayesian belief network of freshwater fish invasion. *Management of Biological Invasions*, *9*(4), 395–403.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. "Biocontrol Adverse Impact Probability Assessment" (BAIPA) Bayesian network (BN) model: Case study of the impact of the biological control agent (BCA), *Microctonus aethiopoides*, on non-target species (NTS), native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in low grazing intensity pastures.
Fig. S2. Sensitivity tornado plots for the case study BN of the impact of the BCA, *M. aethiopoides*, on NTS, native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in low grazing intensity pastures.
Fig. S3. BAIPA: Case study BN model of the impact of the BCA, *M. aethiopoides*, on NTS, native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in mid-altitude native tussock grassland.
Fig. S4. Sensitivity tornado plots for the case study BN of the impact of the BCA, *M. aethiopoides*, impact on NTS, native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in mid-altitude native tussock grassland.
Supporting Information
Table S1. Detailed structure of the nine components in the "Biocontrol Adverse Impact Probability Assessment" (BAIPA) Bayesian network (BN) model.
Table S2. Input probabilities for the *Microctonus*—*Siton–Nicaeana* case study in the different model components of the BAIPA BN model.

SUPPLEMENTAL FIGURES

Risk Analysis Frameworks Used in Biological Control and Introduction of a Novel Bayesian Network Tool

Low grazing intensity pastures

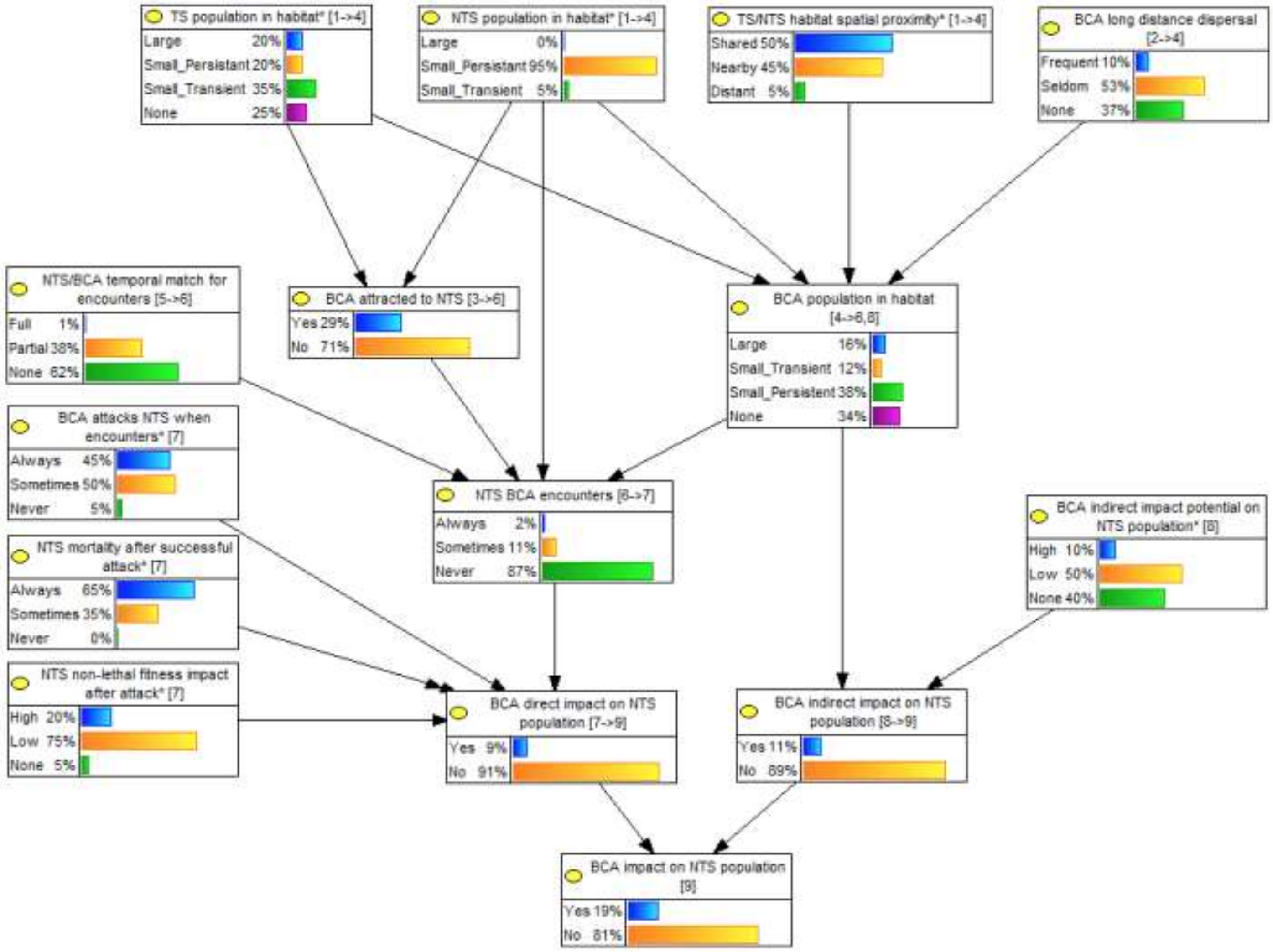


Fig. S1. "Biocontrol Adverse Impact Probability Assessment" (BAIPA) Bayesian network model: Case study of the impact of the biological control agent (BCA), *Microctonus aethiopoides,* on non-target species (NTS), native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in **low grazing intensity pastures**. Information on the target species (TS), *Sitona discoideus*, is included in the model. The numbers in square brackets in the model nodes (each individual box) refer to the model components that use those nodes (see Fig. 2 and Table I in the manuscript). Key input variables are indicated with an asterisk. A complete description of the model structure and definitions of all variables and states are provided in Table S1.

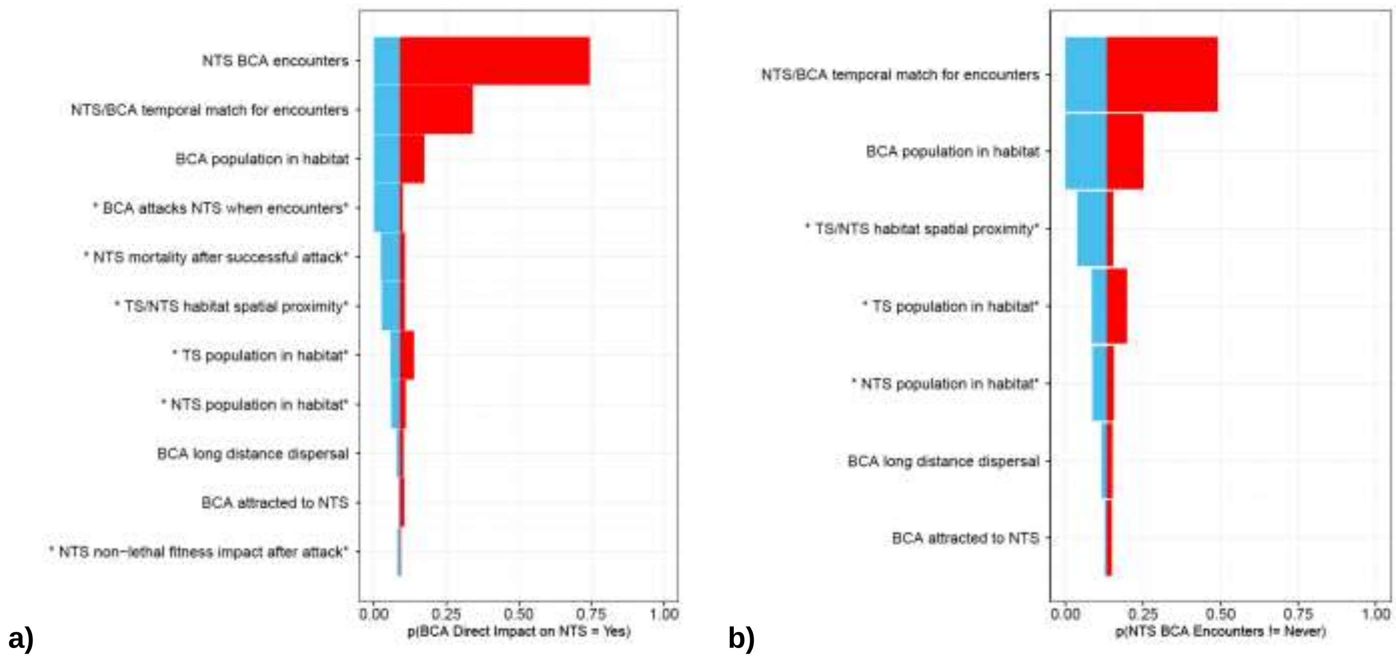


Fig. S2.
Sensitivity tornado plots for the case study Bayesian network of the impact of the biological control agent (BCA), *Microctonus aethiopoides,* on non-target species (NTS), native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in **low grazing intensity pastures**. Information on the target species (TS), *Sitona discoideus*, is included in the model. Plots compare the sensitivity of a) the direct impact p(BCA direct impact on NTS population = Yes) and b) the encounters p(NTS BCA encounters = Sometimes or Always) probabilities to the observations on the key intermediate and input (indicated by asterisk) variables. Each plot indicates the range of output probabilities that result when specifying each possible state for each individual node. The blue component of each plot shows the reduction in probability achievable and the red component shows the increase.

Native tussock grassland

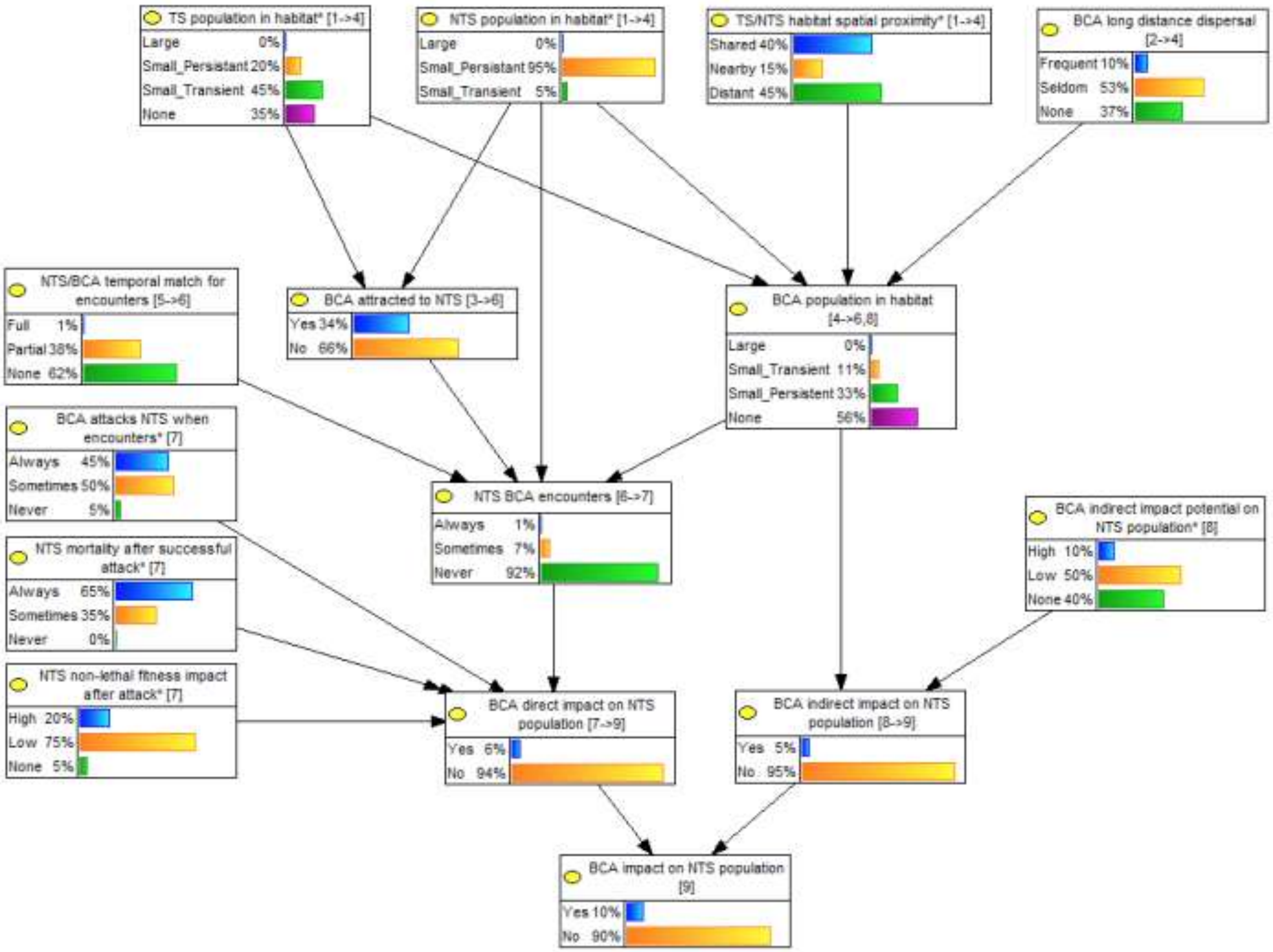
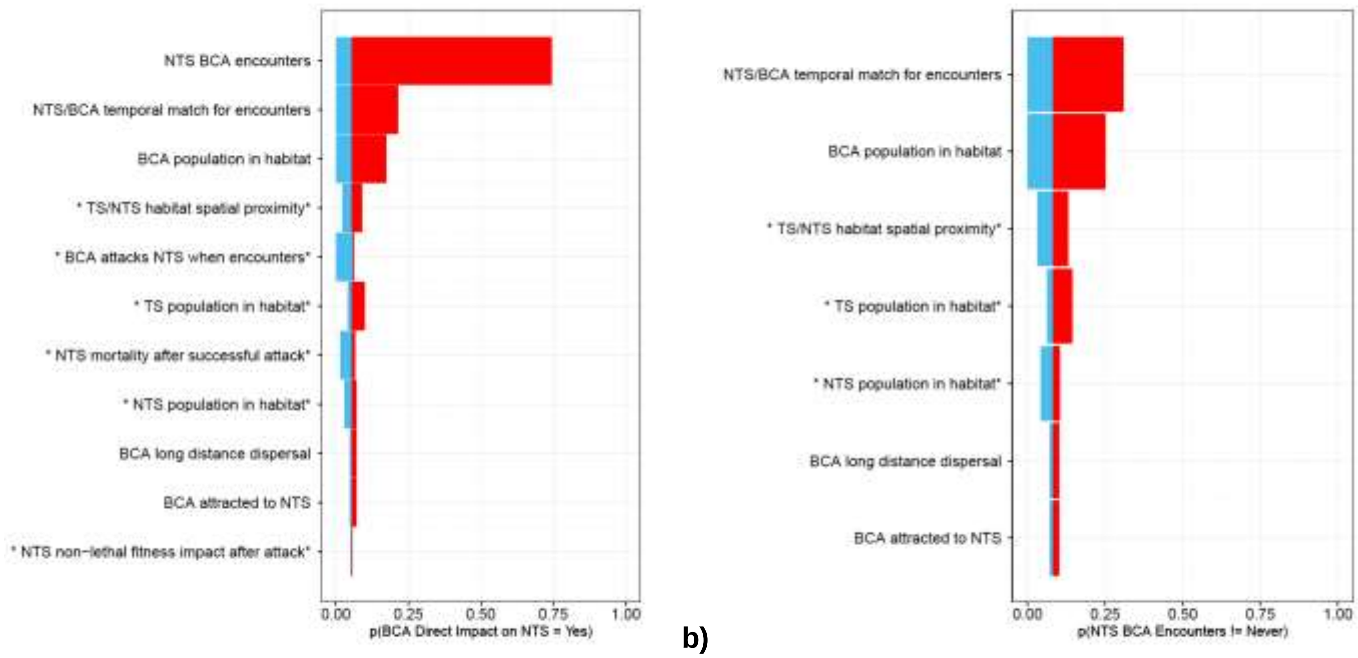


Fig. S3. "Biocontrol Adverse Impact Probability Assessment" (BAIPA): Case study Bayesian network model of the impact of the biological control agent (BCA), *Microctonus aethiopoides,* on non-target species (NTS), native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in **mid-altitude native tussock grassland**. Information on the target species (TS), *Sitona discoideus*, is included in the model. The numbers in square brackets in the model nodes (each individual box) refer to the model components that use those nodes (see Fig. 2 and Table I in the manuscript). Key input variables are indicated with an asterisk. A complete description of the model structure and definitions of all variables and states are provided in Table S1.



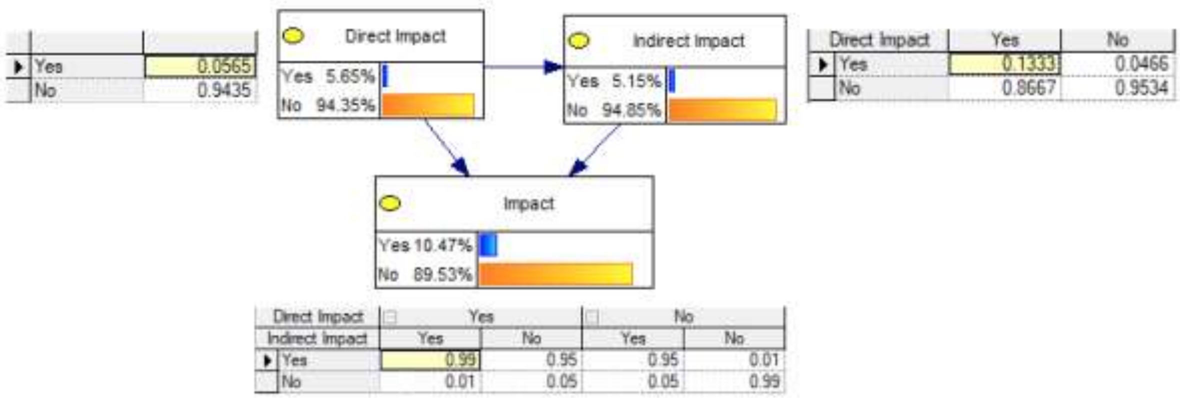
a) b)

Fig. S4.
Sensitivity tornado plots for the case study Bayesian network of the impact of the biological control agent (BCA), *Microctonus aethiopoides,* impact on non-target species (NTS), native weevils in the genus *Nicaeana* (Curculionidae: Entiminae), in **mid-altitude native tussock grassland**. Information on the target species (TS), *Sitona discoideus*, is included in the model. Plots compare the sensitivity of a) the direct impact p(BCA direct Impact on NTS population = Yes) and b) the encounters p(NTS BCA encounters = Sometimes or Always) probabilities to the observations on the key intermediate and input (indicated by asterisk) variables. Each plot indicates the range of output probabilities that result when specifying each possible state for each individual node. The blue component of each plot shows the reduction in probability achievable and the red component shows the increase.

SUPPLEMENTAL NOTE S1

Risk Analysis Frameworks Used in Biological Control and Introduction of a Novel Bayesian Network Tool

Here we provide an example of the posterior probability calculation for the final *Impact* node. For illustrative purposes, we have reduced the BN to three nodes: the *direct*, *indirect* and final *impact* nodes. Note that we have had to create an arc between *direct* and *indirect impacts* to capture the dependency between them – the direction of the arc is arbitrary, but necessary to create a directed acyclic graph.



The posterior belief for *BCA Impact* can be calculated by summing across the joint probability distribution, which can be generated from the BN CPTs via the chain rule:

$$p(Impact, Indirect, Direct) = p(Impact|Indirect, Direct)p(Indirect|Direct)p(Direct)$$

Calculating the joint probabilities where Impact = True:

$$p(impact, direct, indirect) = 0.99 * 0.1333 * 0.0565 \approx 0.0075$$

$$p(impact, direct, \sim indirect) = 0.95 * 0.0466 * 0.9485 \approx 0.0420$$

$$p(impact, \sim direct, indirect) = 0.95 * 0.8667 * 0.0565 \approx 0.0465$$

$$p(impact, \sim direct, \sim indirect) = 0.01 * 0.9534 * 0.9485 \approx 0.0090$$

And summing to get the posterior probability:

$$\begin{aligned} p(impact) = \ & p(impact, direct, indirect) + p(impact, direct, \sim indirect) \\ & + p(impact, \sim direct, indirect) + p(impact, \sim direct, \sim indirect) \\ & \approx 0.0075 + 0.0420 + 0.0465 + 0.0090 = 0.1050 \end{aligned}$$

$$\begin{aligned} p(\sim impact) &= 1 - p(impact) \\ &\approx 1 - 0.1050 = 0.895 \end{aligned}$$

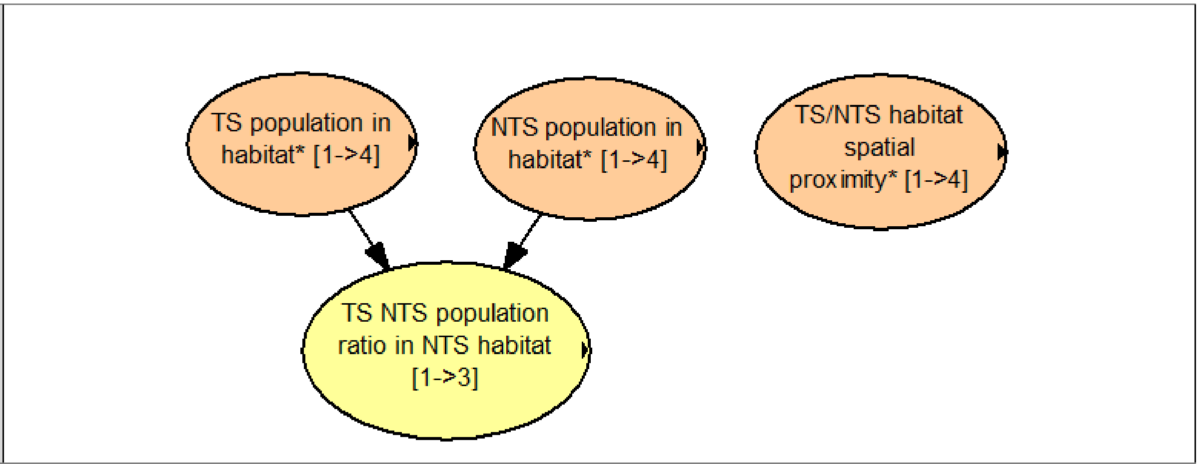
SUPPLEMENTAL TABLE S1

Risk Analysis Frameworks Used in Biological Control and Introduction of a Novel Bayesian Network Tool

Table S1. Detailed structure of the nine components in the “Biocontrol Adverse Impact Probability Assessment” (BAIPA) Bayesian network model. Input variables are indicated by orange ellipses and with an asterisk. Intermediate variables are indicated by yellow ellipses, and the output variable by a green ellipse. Definitions are also provided for all variables and for all states for each variable. In the following definitions, the term “biological control agent” (BCA) is defined as a living organism that is intentionally released with the expectation that it will multiply and control the target permanently (classical biological control), the term “target species” (TS) as a weed or pest of which population is intended to be reduced by the BCA, the term “non-target species” (NTS) as any organism of which population is not intended to be reduced by the BCA. BCAs can be predators, parasitoids or pathogens of invertebrate pests, herbivores or pathogens of weeds, or micro-organisms antagonistic of plant pathogens or inducing plant resistance. Some NTS could be endangered species, species that provide crucial ecosystem services, or economic benefits to the society (they can also be other weeds or pests, in which case attack by the BCA would be considered "fortuitous biological control"). Note: This table does not provide sufficient information to reconstruct the conditional probability tables for all nodes. However, the Bayesian network models described in the paper can be accessed in the original GeNIe format on the ABNMS BN repository (https://www.abnms.org/bnrepo/#).

Model Component 1:

TS/NTS Habitat & Abundance



<u>TS population in habitat</u>		**Definition**	**Comments**
		The size and temporal stability of the TS population within the considered habitat.	Node with unconditional prior probability table (input variable). No default prior probability distribution. Input probabilities must be assigned according to the expected distribution of abundances across all populations of the TS occupying the considered habitat in the area of interest to the assessor. The considered habitat must be defined by the assessor as a type of productive or natural environment in which he wants to investigate the threat of the BCA to the NTS. It can be a type of forest, crop, grassland, or any other considered land-uses that can be occupied by a breeding population of the NTS. Within the area of interest to the assessor, the habitat consists of multiple "patches" which vary in their characteristics (sizes, shapes, climates, etc.), and are likely to be occupied by organism populations of various sizes and stabilities. This variability is to be reflected in the distribution of input probabilities.
States	***None***	The TS is absent.	
	Small transient	The TS occurs in numbers and distribution not adequate for the population to use all available habitat and resources, or these are extremely fragmented or limited. The population is likely to be affected by environmental stressors resulting in a population with greatly reduced abundance and occupancy. The population is restricted to isolated pockets or may undergo temporary disappearances.	
	Small persistent	The TS occurs in numbers and distribution adequate for the population to use available habitat and resources, but these are not continuous and limited. The population can locally be affected by environmental stressors leading to declines in abundance or occupancy.	
	Large	The TS occurs in numbers and distribution robust enough for the population to use available habitat and resources, which are abundant. The population can fully withstand environmental stressors without significant declines in abundance or distribution.	
Model component(s)		**1. TS/NTS Habitat and abundance (input variable)** **4. BCA Habitat & Abundance**	

<table>
<tr><td colspan="2" rowspan="2"><u>NTS population in habitat</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The size and temporal stability of the NTS population within the considered habitat.</td><td rowspan="4">Node with unconditional prior probability table (input variable). No default prior probability distribution.

Input probabilities must be assigned according to the expected distribution of abundances across all populations of the NTS occupying the considered habitat in the area of interest to the assessor. The considered habitat must be defined by the assessor as a type of productive or natural environment in which he wants to investigate the threat of the BCA to the NTS. It can be a type of forest, crop, grassland, or any other considered land-uses that can be occupied by a breeding population of the NTS.

Within the area of interest to the assessor, the habitat consists of multiple "patches" which vary in their characteristics (sizes, shapes, climates, etc.), and are likely to be occupied by organism populations of various sizes and stabilities. This variability is to be reflected in the distribution of input probabilities.</td></tr>
<tr><td rowspan="3">States</td><td>Small transient</td><td>The NTS occurs in numbers and distribution not adequate for the population to use all available habitat and resources, or these are extremely fragmented or limited. The population is likely to be affected by environmental stressors resulting in a population with greatly reduced abundance and occupancy. The population is restricted to isolated pockets or may undergo temporary disappearances.</td></tr>
<tr><td>Small persistent</td><td>The NTS occurs in numbers and distribution adequate for the population to use available habitat and resources, but these are not continuous and limited. The population can locally be affected by environmental stressors leading to declines in abundance or occupancy.</td></tr>
<tr><td>Large</td><td>The NTS occurs in numbers and distribution robust enough for the population to use available habitat and resources, which are abundant. The population can fully withstand environmental stressors without significant declines in abundance or distribution.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">1. TS/NTS Habitat and abundance (input variable)
4. BCA Habitat & Abundance</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>TS/NTS habitat spatial proximity</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The spatial proximity between the considered habitat (occupied by the NTS) and the habitat occupied by the TS.</td><td rowspan="4">Node with unconditional prior probability table (input variable). Default prior probability distribution: 100% shared

The considered habitat can be a type of forest, crop, grassland, or any other considered land-uses that can be occupied by a breeding population of the NTS.

In the case of a non-shared habitat, the expected distribution between distant and nearby can be based on inspection of land cover maps. When a TS occupies a wide range of habitats, the "nearby" state will be favoured. When a TS occupies a small range of habitats, the "distant" state will be favoured.</td></tr>
<tr><td rowspan="3">States</td><td>Shared</td><td>The considered habitat is also a habitat for the TS.</td></tr>
<tr><td>Nearby</td><td>The considered habitat is within the dispersal range of the BCA. Distances <10km between the considered habitat and the nearest TS habitat (assumed to be also occupied by the BCA) are compatible with typical active and passive dispersal distances for insects.</td></tr>
<tr><td>Distant</td><td>The considered habitat is not within the dispersal range of the BCA. Distances >10km between the considered habitat and the nearest TS habitat (assumed to be also occupied by the BCA) are not compatible with typical active dispersal distances for insects. Important dilution effects are also to be expected for insects dispersing passively over distances >10 km.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">1. TS/NTS Habitat and abundance (input variable)

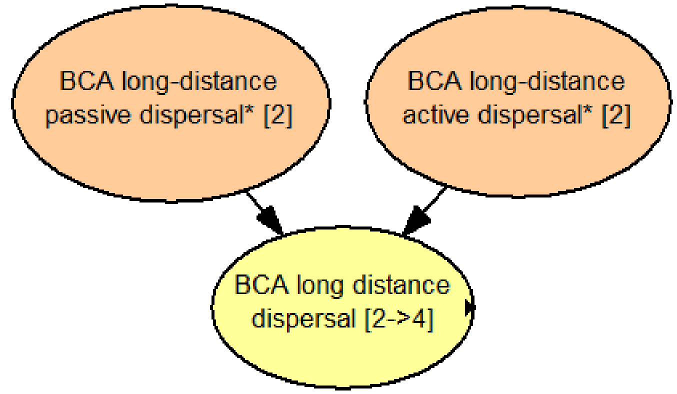
4. BCA Habitat & Abundance</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>TS/NTS population ratio in habitat</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The abundance ratio comparing the population levels of the TS and the NTS in the considered habitat.</td><td rowspan="4">Node with conditional prior probability table. Integration of the parent nodes: “TS population in habitat” and “NTS population in habitat”.

These parent nodes are equally weighted.A population rated as "large" is always considered more abundant than a population rated as "small transient" (with a 100% probability). A population rated as "small persistent" is generally considered more abundant than a population rated as "small transient" (90% probability). A population rated as "large" is generally considered more abundant than a population rated as "small persistent (90% probability). Two populations rated the same ("small transient", "small persistent" or "large" are generally considered balanced (90% probability).</td></tr>
<tr><td rowspan="3">States</td><td>More TS</td><td>The TS is more abundant than the NTS in the considered habitat.</td></tr>
<tr><td>Balanced</td><td>The TS is about equally as abundant as the NTS in the considered habitat.</td></tr>
<tr><td>More NTS</td><td>The NTS is more abundant than the TS in the considered habitat.</td></tr>
<tr><td colspan="2">Model component</td><td colspan="2">1. TS/NTS Habitat and abundance (intermediate variable)
3. Short & Medium-range Attraction</td></tr>
</table>

Model Component 2:

BCA Long-distance Dispersal



<table>
<tr><th colspan="2" rowspan="2"><u>BCA long-distance passive dispersal</u></th><th>Definition</th><th>Comments</th></tr>
<tr><td>The frequency at which BCAs disperse outside their habitat of introduction by means other than active, directed movement.</td><td rowspan="4">Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 30% None, 40% Seldom, 30% Frequent.

The habitat of introduction of the BCA can be a type of forest, crop, grassland, or any other land uses occupied by a population of the TS. Within the area of interest to the assessor, the habitat consists of multiple "patches" which vary in their characteristics (sizes, shapes, climates, etc.) and proximity to other habitat types. These characteristics are likely to affect the dispersal of BCA individuals to other habitats, and this is to be reflected in the distribution of input probabilities.

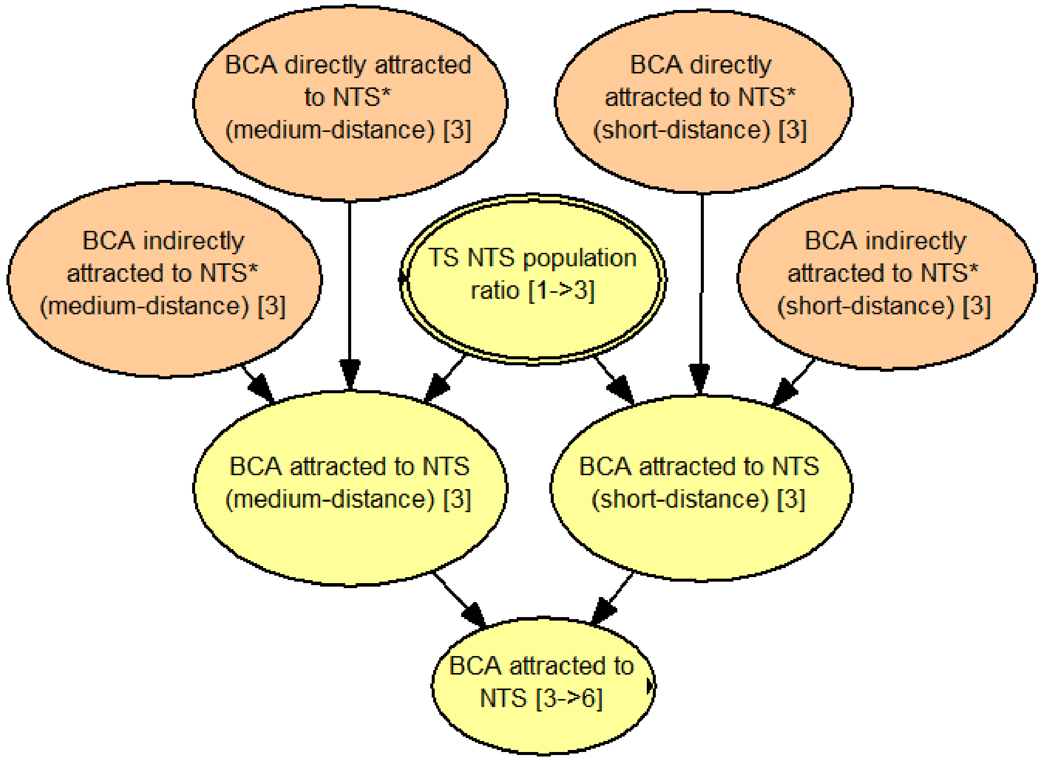
Examples of long-distance passive dispersal include insects blown in high elevation air currents, transported as immature stages via birds or other insects (e.g. mites on moths), or moved by vehicles or other human activities (including via transport of plant material). Immature stages of parasitoids can also be vectored by their hosts as such parasitised hosts can still perform dispersal or migration flights. Insects typically disperse greater distances when they are passively transported, but also experience high dilution rates and mortalities.</td></tr>
<tr><td rowspan="3">States</td><td>None</td><td>A negligible proportion of BCA individuals (<1 in a million) disperse passively out of their habitat of introduction, by means of air or water currents or vectors, to another habitat.</td></tr>
<tr><td>Seldom</td><td>A small proportion of BCA individuals (1 in a million to 1 in a hundred) disperse passively out of their habitat of introduction, by means of air or water currents or vectors, to another habitat.</td></tr>
<tr><td>Frequent</td><td>A relatively high proportion of BCA individuals (>1 in a hundred) disperse passively out of their habitat of introduction, by means of air or water currents or vectors, to another habitat.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">2. BCA Long-distance Dispersal (input variable)</td></tr>
</table>

BCA long-distance active dispersal		**Definition**	**Comments**
		The frequency at which BCAs disperse outside their habitat of introduction by use of active, directed movement.	Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 50% None, 30% Seldom, 20% Frequent.
States	***None***	A negligible proportion of BCA individuals (<1 in a million) disperse actively out of their habitat of introduction by means of walking or flying.	The habitat of introduction of the BCA can be a type of forest, crop, grassland, or any other land uses occupied by a population of the TS. Within the area of interest to the assessor, the habitat consists of multiple "patches" which vary in their characteristics (sizes, shapes, climates, etc.) and proximity to other habitat types. These characteristics are likely to affect the dispersal of BCA individuals to other habitats, and this is to be reflected in the distribution of input probabilities.
	Seldom	A small proportion of BCA individuals (1 in a million to 1 in a hundred) disperse actively out of their habitat of introduction by means of walking or flying.	
	Frequent	A relatively high proportion of BCA individuals (>1 in a hundred) disperse actively out their habitat of introduction by means of walking or flying.	
Model component		**2. BCA Long-distance Dispersal (input variable)**	

<table>
<tr><td colspan="2" rowspan="2"><u>BCA long-distance dispersal</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The frequency at which BCAs disperse outside the habitat of introduction and have the potential to establish a viable population in the new habitat.</td><td rowspan="4">Node with conditional prior probability table. Integration of the parent nodes: “BCA long-distance active dispersal” and “BCA long-distance passive dispersal”.

These parent nodes are unequally weighted to account for a higher probability of actively dispersing BCAs to establish a new viable population in a new habitat. For instance, BCA characterised by “Frequent” long-distance active dispersal but no ability for long-distance passive dispersal will be rated equally (each with a 50% probability) for “Frequent” and “Seldom” for the likelihood of long-distance dispersal. Conversely, BCAs characterised by “Frequent” long-distance passive dispersal but no ability for long-distance active dispersal will be rated with a 40% probability for “Frequent” and with a 60% probability for “Seldom”, for the likelihood of long-distance dispersal.</td></tr>
<tr><td rowspan="3">States</td><td>None</td><td>A negligible proportion of BCA individuals disperse out of their habitat of introduction and establish a viable population in the new habitat.</td></tr>
<tr><td>Seldom</td><td>A small proportion of BCA individuals disperse out of their habitat of introduction and establish a viable population in the new habitat.</td></tr>
<tr><td>Frequent</td><td>A relatively high proportion of BCA individuals disperse out of their habitat of introduction and establish a viable population in the new habitat.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">2. BCA Long-distance Dispersal (intermediate variable)

4. BCA Habitat and abundance</td></tr>
</table>

Model Component 3: **Short & Medium-range Attraction**	 *Note. The variable with a double border has been defined in Model Component 1.*

BCA directly attracted to NTS (medium-distance)		Definition	Comments
		BCAs are directly attracted at medium-distance to individuals of the NTS within the considered habitat.	Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 75% never, 20% not preferentially, 5% preferentially.
States	***Never***	At medium range (1-100m), the BCA does not have an ability to locate NTS individuals and move directly towards them.	
	Not preferentially	At medium range (1-100m), the BCA has an ability to locate NTS individuals and move directly towards them. The BCA exhibits a stronger response to the TS than the NTS.	Cues perceived by a BCA to locate a NTS can be visual (e.g. seeing the NTS), chemical (e.g., perceiving odours emitted by the NTS, or for insect NTS host plant volatiles associated with their feeding activity), or aural (e.g. perceiving noises emitted by the NTS).
	Preferentially	At medium range (1-100m), the BCA has an ability to locate NTS individuals and move directly towards them. The BCA exhibits a stronger response in the presence of the NTS as opposed to the TS.	When possible, input probabilities must be assigned based on experimental testing of the attraction behaviour of the BCA in presence of the NTS (in the laboratory or in the field). It is recommended that these tests standardise factors such as host age, mating and feeding history, and include the TS as a positive control to confirm that the experimental protocol is appropriate. When incomplete information is available on the impact of the BCA on the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.
Model component		**3. Short & Medium-range Attraction (input variable)**	

<table>
<tr><th colspan="2" rowspan="2"><u>BCA indirectly attracted to NTS (medium-distance)</u></th><th>Definition</th><th>Comments</th></tr>
<tr><td>BCAs are not attracted at medium-distance to individuals of the NTS, but to other organisms and certain microhabitats associated with the NTS in the considered habitat.</td><td>Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 50% no, 50% yes.</td></tr>
<tr><td rowspan="2">States</td><td>No</td><td>At medium range (1-100m), the BCA does not tend to move towards plants where NTS individuals could be present.</td><td rowspan="2">Cues perceived by a BCA to locate organisms and microhabitats associated with the NTS can be visual (e.g. seeing a host plant, or an insect host or prey), chemical (e.g., perceiving odours emitted by a host plant, or an insect host or prey, or the plant on which an insect host or prey is living), or aural (e.g. perceiving a noise emitted by an insect host or prey).

When possible, input probabilities must be assigned based on experimental testing of the behaviour of the BCA in presence of organisms and microhabitats associated with the NTS (in the laboratory or in the field). It is recommended that these tests include the TS as a positive control to confirm that the experimental protocol is appropriate.

When incomplete information is available on the impact of the BCA on the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.</td></tr>
<tr><td>Yes</td><td>At medium range (1-100m), the BCA does tend to move towards plants where NTS individuals could be present.</td></tr>
<tr><td colspan="2">Model component</td><td colspan="2">3. Short & Medium-range Attraction (input variable)</td></tr>
</table>

<table>
<tr><th colspan="2" rowspan="2"><u>BCA directly attracted to NTS (short-distance)</u></th><th>Definition</th><th>Comments</th></tr>
<tr><td>BCAs are directly attracted at short-distance to individuals of the NTS within the considered habitat.</td><td rowspan="2">Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 5% never, 90% not preferentially, 5% preferentially.</td></tr>
<tr><td rowspan="3">States</td><td>Never</td><td>At short range (<1m), the BCA does not have an ability to locate NTS individuals and move towards them.</td></tr>
<tr><td>Not preferentially</td><td>At short range (<1m), the BCA has an ability to locate NTS individuals and move towards them. The BCA exhibits a stronger response in the presence of the TS as opposed to the NTS.</td><td rowspan="2">Cues perceived by a BCA to locate a NTS can be visual (e.g. seeing the NTS), chemical (e.g., perceiving odours emitted by the NTS, or for insect NTS host plant volatiles associated with their feeding activity), or aural (e.g. perceiving noises emitted by the NTS).

When possible, input probabilities must be assigned based on experimental testing of the attraction behaviour of the BCA in presence of the NTS (in the laboratory or in the field). It is recommended that these tests standardise factors such as host age, mating and feeding history, and include the TS as a positive control to confirm that the experimental protocol is appropriate.

When incomplete information is available on the impact of the BCA on the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.</td></tr>
<tr><td>Preferentially</td><td>At short range (<1m), the BCA has an ability to locate NTS individuals and move towards them. The BCA exhibits a stronger response in presence of the NTS as opposed to the TS.</td></tr>
<tr><td colspan="2">Model component</td><td colspan="2">3. Short & Medium-range Attraction (input variable)</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>BCA indirectly attracted to NTS (short-distance)</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>BCAs are indirectly attracted at short-distance to individuals of the NTS within the considered habitat.</td><td rowspan="3">Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 50% no, 50% yes.

Cues perceived by a BCA to locate organisms and microhabitats associated with the NTS can be visual (e.g. seeing a host plant, or an insect host or prey), chemical (e.g., perceiving odours emitted by a host plant, or an insect host or prey, or the plant on which an insect host or prey is living), or aural (e.g. perceiving a noise emitted by an insect host or prey).

When possible, input probabilities must be assigned based on experimental testing of the behaviour of the BCA in presence of organisms and microhabitats associated with the NTS (in the laboratory or in the field). It is recommended that these tests include the TS as a positive control to confirm that the experimental protocol is appropriate.

When incomplete information is available on the impact of the BCA on the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.</td></tr>
<tr><td rowspan="2">States</td><td>No</td><td>At short range (<1m), the BCA does not tend to move towards microhabitats where NTS individuals could be present.</td></tr>
<tr><td>Yes</td><td>At short range (<1m), the BCA does tend to move towards microhabitats where NTS individuals could be present.</td></tr>
<tr><td colspan="2">Model component</td><td colspan="2">3. Short & Medium-range Attraction (input variable)</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>BCA attracted to NTS (medium-distance)</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>BCAs are attracted at medium-distance to individuals of the NTS within the considered habitat.</td><td rowspan="3">Node with conditional prior probability table. Integration of the parent nodes: “BCA directly attracted to NTS (medium-distance)”, “BCA indirectly attracted to NTS (medium-distance)” and “TS/NTS population ratio in habitat”.

These parent nodes are unequally weighted. For balanced populations of the TS and the NTS, the probability of a non-preferential medium-distance direct attraction to the NTS is rated as 50% in the absence of an indirect attraction mechanism, and 90% if a mechanism is present. The probability of a preferential direct attraction is rated as 90% in the absence of an indirect attraction mechanism, and 99% if a mechanism is present.

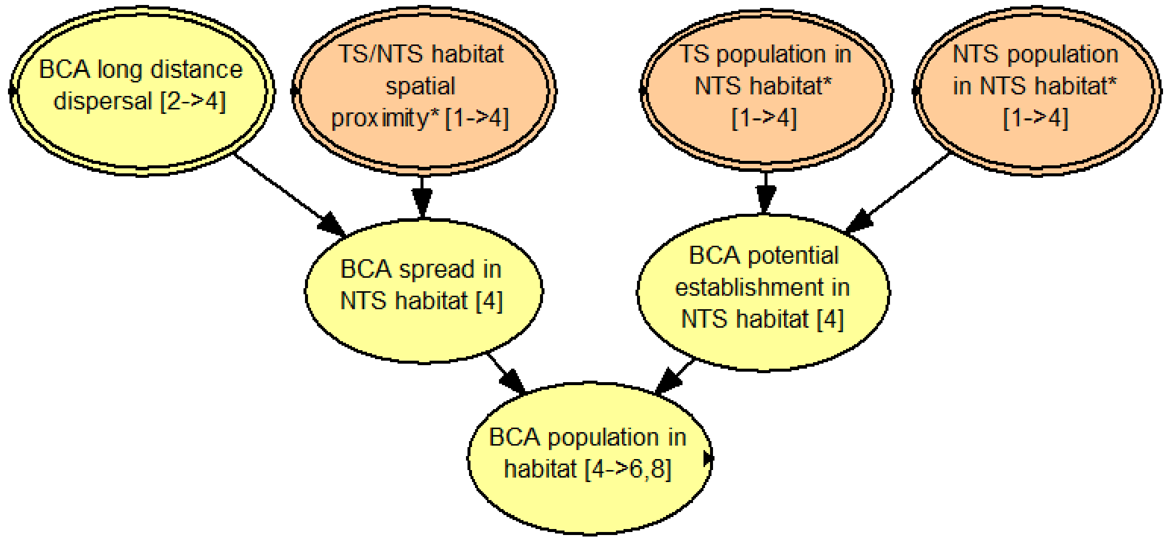
These ratings are altered when the TS and NTS populations are unbalanced. For instance, in the absence of an indirect attraction mechanism, the 50% probability of a non-preferential attraction to the NTS is reduced to 10% if the TS is more abundant, or increased to 90% if the NTS is more abundant.</td></tr>
<tr><td rowspan="2">States</td><td>No</td><td>At medium range (1-100m), the BCA does not move towards NTS individuals.</td></tr>
<tr><td>Yes</td><td>At medium range (1-100m), the BCA does move towards NTS individuals.</td></tr>
<tr><td colspan="2">Model component</td><td colspan="2">3. Short & Medium-range Attraction (intermediate variable)</td></tr>
</table>

BCA attracted to NTS (short-distance)		Definition	Comments
		BCAs are attracted at short-distance to individuals of the NTS within the considered habitat.	Node with conditional prior probability table. Integration of the parent nodes: “BCA directly attracted to NTS (short-distance)” and “BCA indirectly attracted to NTS (short-distance)”. These parent nodes are unequally weighted. For balanced populations of the TS and NTS, the probability of a non-preferential short-distance direct attraction to the NTS is rated as 50% in the absence of indirect attraction mechanism, and 70% if the mechanism is present. The probability of a preferential direct attraction is rated as 90% in the absence of an indirect attraction mechanism, and 99% if the mechanism is present. These ratings are altered in the presence of unbalanced populations of the two species. For instance, in the absence of an indirect attraction mechanism, the 50% probability of a non-preferential attraction to the NTS is reduced to 10% if the TS is more abundant, or increased to 90% if the NTS is more abundant.
States	***No***	At short range (<1m), the BCA does not move towards NTS individuals.	
	Yes	At short range (<1m), the BCA does move towards NTS individuals.	
Model component		**3. Short & Medium-range Attraction (intermediate variable)**	

<table>
<tr><td colspan="2" rowspan="2"><u>BCA attracted to NTS</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>BCAs are attracted to individuals of the NTS within the considered habitat.</td><td rowspan="3">Node with conditional prior probability table. Integration of the parent nodes: “BCA attracted to NTS (medium-distance)” and “BCA attracted to NTS (short-distance)”.

These parent nodes are equally weighted. The probability of attraction to the NTS is very low (1%) in the absence of short and medium-range attraction. Conversely, the probability is very high (99%) in the presence of short and medium-range attraction. BCA with only short, or only medium-range attraction to the NTS rate as an overall low probability (10%).</td></tr>
<tr><td rowspan="2">States</td><td>No</td><td>The BCA does not move towards NTS individuals.</td></tr>
<tr><td>Yes</td><td>The BCA does move towards NTS individuals.</td></tr>
<tr><td colspan="2">Model component</td><td colspan="2">3. Short & Medium-range Attraction (intermediate variable)

6. NTS-BCA Encounters</td></tr>
</table>

Model Component 4: **BCA Habitat & Abundance**	 *Note. The variables with a double border have been defined in Model Component 1.*

<table>
<tr><td colspan="2" rowspan="2"><u>BCA spread in habitat</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The potential for the BCA, on a long-term horizon, to spread in the habitat occupied by the NTS.</td><td rowspan="4">Node with conditional prior probability table. Integration of the parent nodes: “BCA long-distance dispersal” and “TS/NTS habitat spatial proximity”.

These parent nodes are unequally weighted. The BCA is assumed present in all habitats occupied by the TS, including in habitats shared by the TS and the NTS.

When the BCA has no capability for long-distance dispersal, the potential for the BCA to spread to NTS habitats distant from target habitats is rated low with a 90% probability. For nearby NTS habitats, the BCA has medium (with a 50% probability) or high potential (with a 40% probability) for spread. The BCA is rated with a higher probability of spread when it has a capability for long-distance dispersal. For a BCA with “Frequent” long-distance dispersal for instance, spread to distant habitats is rated medium (with a 60% probability) or high potential (with a 30% probability), and spread to nearby habitats has high potential (100% probability).</td></tr>
<tr><td rowspan="3">States</td><td>Low potential</td><td>The TS is not present in the habitat, and the habitat is out of reach of the BCA given its current dispersal capabilities, even on a long-term horizon (10+ years).</td></tr>
<tr><td>Medium potential</td><td>The TS is not present in the habitat, but the habitat is within reach of the BCA on a long-term horizon, given its current dispersal capability.</td></tr>
<tr><td>High potential or present</td><td>The TS is either present in the habitat, in which case the BCA is assumed to eventually spread in this habitat, or the habitat is within reach of the BCA given its current dispersal capability.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">4. BCA Habitat & Abundance (intermediate variable)</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>BCA potential establishment in NTS habitat</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The potential for the BCA, given the local food resources, to establish in the habitat considered.</td><td rowspan="5">Node with conditional prior probability table. Integration of the parent nodes: “TS population in NTS habitat”, “NTS population in NTS habitat”.

These parent nodes are unequally weighted. The BCA is assumed present in all habitats with a transient or persistent population of the TS. Conversely, the model does not assume that a population of the BCA, even transient, can breed in habitats occupied by the NTS alone.

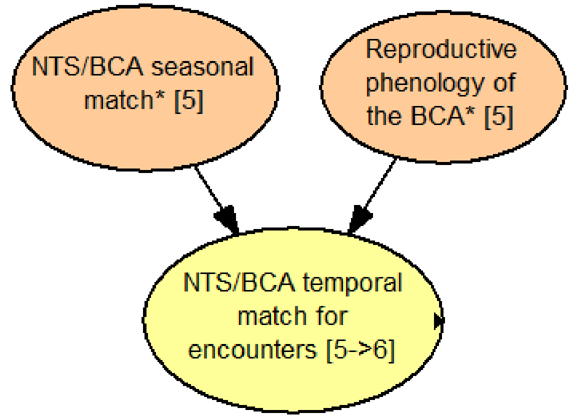
When the TS is absent, there is always a 50% probability for absence of the BCA, and a 50% probability for presence (either small transient, small persistent, or large, aligned with the population of the NTS). When the TS population is small, there is usually a 100% probability for a small BCA population (either 50% small transient, 50% small persistent, or 100% for one of these two states). Except with a large NTS population, in which case the size of the BCA population is more uncertain (rated with a 50% probability for small and 50% for large). When the TS population is large, there is a 100% probability for a large BCA population.</td></tr>
<tr><td rowspan="4">States</td><td>None</td><td>The BCA does not have the potential to establish a local population given the absence of the TS and NTS.</td></tr>
<tr><td>Small transient</td><td>The BCA has the potential to establish a local population given the local presence of the TS and/or the NTS. These hosts are in numbers and distribution not adequate for the BCA population, which is likely to be affected by environmental stressors resulting in a population with greatly reduced abundance and occupancy.</td></tr>
<tr><td>Small persistent</td><td>The BCA has the potential to establish a local population given the local presence of the TS and/or the NTS. These hosts are in limited numbers and distribution, and the BCA population can locally be affected by environmental stressors leading to declines in abundance or occupancy.</td></tr>
<tr><td>Large</td><td>The BCA has the potential to establish a local population given the local presence of the TS and/or the NTS. These hosts are abundant, and the BCA population can fully withstand environmental stressors without significant declines in abundance or distribution.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">4. BCA Habitat & Abundance (intermediate variable)</td></tr>
</table>

<table>
<tr><th colspan="2" rowspan="2"><u>BCA population in habitat</u></th><th>Definition</th><th>Comments</th></tr>
<tr><td>The size and temporal stability of the BCA population within the considered habitat.</td><td rowspan="5">Node with conditional prior probability table. Integration of the parent nodes: “BCA spread in NTS habitat” and “BCA potential establishment in NTS habitat”.
These parent nodes are unequally weighted. The distribution of predictions for the BCA population is primarily governed by the distribution of states from the BCA potential establishment. When the potential for establishment is rated as “None”, there is a 100% probability for absence of a BCA population in the habitat.
The BCA is also unlikely to be present when the spread of the BCA is rated “Low potential” (with a 5 to 10% presence probability), or “Medium potential” (with a 20 to 30% presence probability). Conversely, the BCA is more likely to be present when its spread is rated “High potential or present” (with a 70 to 90% presence probability). For possible BCA populations, the ranking for the size and stability of the population is the same estimate as for potential establishment. For instance, a BCA with “High potential” for spread and a “Small transient” potential for establishment will be rated a 70% probability to establish a small transient population (and a 30% probability not to establish).</td></tr>
<tr><td rowspan="4">States</td><td>None</td><td>The BCA is absent.</td></tr>
<tr><td>Small transient</td><td>The BCA occurs in numbers and distribution not adequate for the population to use all available habitat and resources, or these are extremely fragmented or limited. The BCA population is likely to be affected by environmental stressors and fluctuations in abundance of hosts, resulting in a population with greatly reduced abundance and occupancy. The population is restricted to isolated pockets or temporary disappearances.</td></tr>
<tr><td>Small persistent</td><td>The BCA occurs in numbers and distribution adequate for the population to use available habitat and resources, but these are not continuous and limited. The population can locally be affected by environmental stressors and fluctuations in abundance of hosts, leading to declines in abundance or occupancy.</td></tr>
<tr><td>Large</td><td>The BCA occurs in numbers and distribution robust enough for the population to use available habitat and resources, which are abundant. The population can fully withstand environmental stressors and fluctuations in abundance of hosts, without significant declines in abundance or distribution.</td></tr>
</table>

Model component(s)	**4. BCA Habitat & Abundance (intermediate variable)** **6. NTS-BCA Encounters** **8. indirect Impacts**

Model Component 5:

Temporal Window



<table>
<tr><td colspan="2" rowspan="2"><u>NTS/BCA seasonal match</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The overlap between the seasonal appearance of the susceptible life stage of the NTS and the attacking life stage of the BCA.</td><td rowspan="4">Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 10% None, 50% Partial, 40% Complete.

The seasonal appearance of the susceptible life stage of the NTS, and of the appearance of the attacking life stage of the BCA, must be evaluated in the habitat considered by the assessor. The phenology of both species must be considered, as well as periods of time when the NTS is possibly sheltered from the BCA (e.g. underground) or not attractive (e.g. resting stage). Migratory processes must also be considered.

A dedicated companion BN has been designed to facilitate the estimation of this variable, taking into account the seasons of observations of the NTS and the BCA (for instance from databases or collections).</td></tr>
<tr><td rowspan="3">States</td><td>None</td><td>The attacking life stage of the BCA is present and active at a completely different period of the year than the period of activity of the susceptible life stage(s) of the NTS.</td></tr>
<tr><td>Partial</td><td>The attacking life stage of the BCA is present and active during a period of the year that partially overlaps with the period of activity of the susceptible life stage(s) of the NTS.</td></tr>
<tr><td>Complete</td><td>The attacking life stage of the BCA is present and active during a period of the year that includes the full period of activity of the susceptible life stage(s) of the NTS.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">5. Temporal Window (input variable)</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>Reproductive phenology of the BCA</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The reproductive activity of the BCA during the period of seasonal appearance of the attacking life stage of the BCA and the susceptible life stage of the NTS.</td><td rowspan="4">Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 30% Low, 40% Moderate, 30% High.

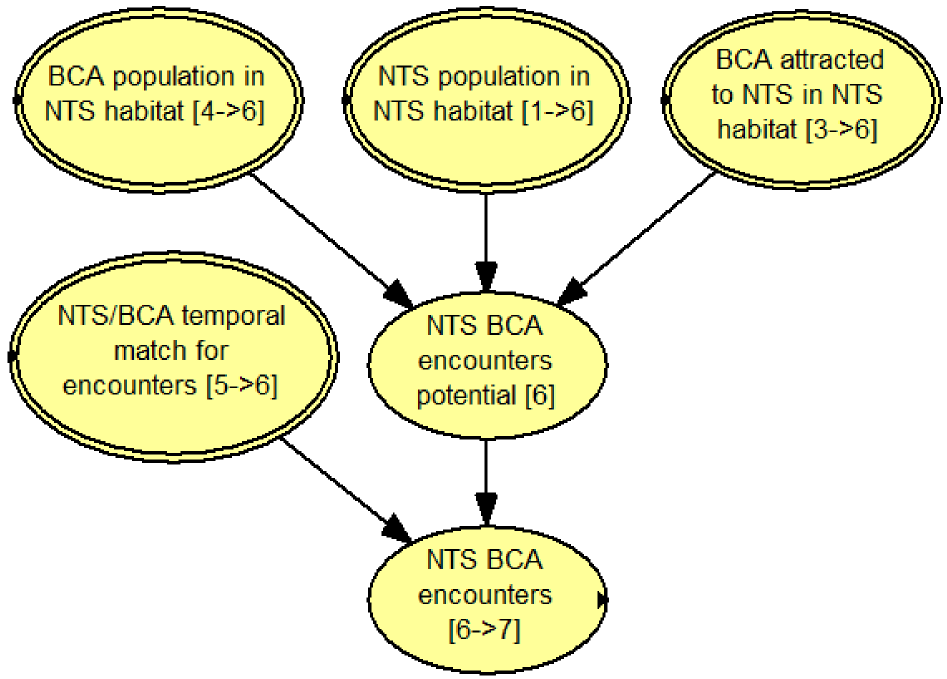
A low reproductive potential can be considered for a BCA with 1 or 2 generations per year and a potential fecundity below 30 progeny per female. A moderate reproductive potential can be considered for a BCA with 1 or 2 generations per year and a potential fecundity above 30 progeny per female, or at least 3 generations per year but a potential fecundity below 30 progeny per female. A high reproductive potential can be considered for a BCA with at least 3 generations per year and a potential fecundity above 30 progeny per female.</td></tr>
<tr><td rowspan="3">States</td><td>Low</td><td>The attacking life stage of the BCA is only active for a fraction of the time that the susceptible life stages of the NTS are present in the habitat. The BCA is characterised by a low reproductive potential. Encounters between the attacking life stage of the BCA and the susceptible life stage of the NTS can be restricted by an inadequate match of their daily cycles of activity.</td></tr>
<tr><td>Moderate</td><td>The attacking life stage of the BCA is active for most of the time that the susceptible life stages of the NTS are present in the habitat. The BCA is characterised by a moderate reproductive potential. Encounters between the attacking life stage of the BCA and the susceptible life stage of the NTS are not restricted by an inadequate match of their daily cycles of activity.</td></tr>
<tr><td>High</td><td>The attacking life stage of the BCA is active for most of the time that the susceptible life stages of the NTS are present in the habitat. The BCA is characterised by a high reproductive potential. Encounters between the attacking life stage of the BCA and the susceptible life stage of the NTS are not restricted by an inadequate match of their daily cycles of activity.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">5. Temporal Window (input variable)</td></tr>
</table>

<table>
<tr><th colspan="2" rowspan="2"><u>NTS/BCA temporal match for encounters</u></th><th>Definition</th><th>Comments</th></tr>
<tr><td>The overlap between the period of presence of susceptible NTS individuals and the period of activity of attacking individuals of the BCA.</td><td rowspan="4">Node with conditional prior probability table. Integration of the parent nodes: “NTS/BCA seasonal match” and “Reproductive phenology of the BCA”.

These parent nodes are unequally weighted. The distribution of predictions for the NTS/BCA temporal match for encounters is primarily governed by the distribution of states from their seasonal match. When the seasonal match is rated as “None”, there is a 100% probability for no temporal match for encounters.

A “Partial” seasonal match yields at best a “Partial” temporal match for encounters, with 40%, 70%, and 90% probability associated with “Low”, “Moderate” or “High” reproductive rates, respectively (otherwise no match). A “Complete” seasonal match yields at best a “Full” temporal match for encounters, with 10%, 70%, and 80% probability associated with “Low”, “Moderate” or “High” reproductive rates, respectively (otherwise a partial match or no match).</td></tr>
<tr><td rowspan="3">States</td><td>None</td><td>Susceptible individuals in the NTS population will not be present when attacking individuals the BCA population are likely to be present.</td></tr>
<tr><td>Partial</td><td>Only a portion of the susceptible individuals in the NTS population will be present at the time attacking individuals the BCA population are likely to be present.</td></tr>
<tr><td>Complete</td><td>All the susceptible individuals in the NTS population will be present at the time attacking individuals the BCA population are likely to be present.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">5. Temporal Window (intermediate variable)

6. NTS-BCA Encounters</td></tr>
</table>

Model Component 6: NTS-BCA Encounters	 *Note. The variables with a double border have been defined in Model Components 1,3, 4 and 5.*

NTS BCA encounters potential		Definition	Comments
		The frequency at which susceptible NTS individuals may be exposed to attacking BCA individuals if there was no temporal constraint for encounters.	Node with conditional prior probability table. Integration of the parent nodes: “BCA population in NTS habitat”, “NTS population in NTS habitat”, and “BCA attracted to NTS in NTS habitat”. These parent nodes are unequally weighted. No encounters can occur in absence of the BCA, and these are rated “Never”. For small populations of the NTS, encounters are primarily driven by the size of the BCA population and whether the BCA is attracted to the NTS. When the BCA is not attracted to the NTS, the most probable states are “Never” for small transient populations of the BCA (75-95%), and “Sometimes” for small persistent populations of the BCA (70-75%). When the BCA is attracted to the NTS, the most probable states are “Sometimes” or “Always” for small transient populations of the BCA (95% for these two states combined), and “Always” for small persistent of the BCA populations (60-80%). For large populations of the NTS, when the BCA is not attracted to the NTS the most probable states is “Sometimes” in presence of small populations of the BCA (80-89%), and “Always” when both populations are large (70%). When the BCA is attracted to the NTS, the most probable states is “Sometimes” or
States	***Never***	Less than 20% of susceptible individuals in the NTS population would be exposed to attacking individuals of the BCA if there was no temporal constraint.	
	Sometimes	Between 20% and 80% of susceptible individuals in the NTS population would be exposed to attacking individuals of the BCA if there was no temporal constraint.	
	Always	More than 80% of susceptible individuals in the NTS population would be exposed to attacking individuals of the BCA if there was no temporal constraint.	

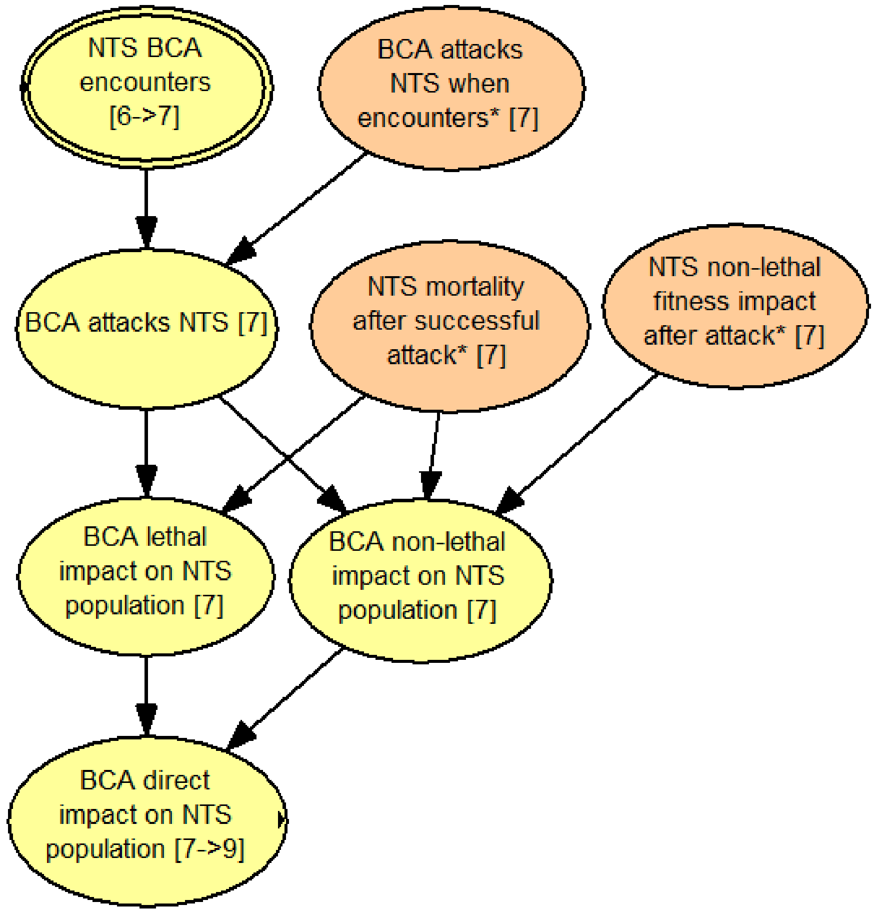
			"Always" in presence of small populations of the BCA (89-95% for these two states combined), and "Always" when both populations are large (90%).
Model component(s)		**6. NTS-BCA Encounters (intermediate variable)**	

NTS BCA encounters		**Definition**	**Comments**
		The frequency at which susceptible NTS individuals are exposed to the attacking life stage of the BCA in the habitat.	Node with conditional prior probability table. Integration of the parent nodes: "NTS/BCA temporal match for encounters" and "NTS BCA encounters potential". These parent nodes are unequally weighted. The distribution of predictions for the NTS BCA encounters is primarily governed by the distribution of states from their encounters potential. When the encounters potential is rated as "Never", or when there is the temporal match is rated as "None", there is a 100% probability for no encounters. An encounters potential rated as "Sometimes" associates a higher probability of "Sometimes" for encounters (50% with partial temporal match, or 80% with full temporal match). An encounters potential rated as "Always" associates a higher probability of "Sometimes" and "Always" for encounters (50% and 20, respectively, with partial temporal
States	***Never***	Less than 20% of susceptible individuals in the NTS population are exposed to attacking individuals of the BCA.	
	Sometimes	Between 20% and 80% of susceptible individuals in the NTS population are exposed to attacking individuals of the BCA.	
	Always	More than 80% of susceptible individuals in the NTS population are exposed to attacking individuals of the BCA.	

			match, or 40% “and 50% “Always”, respectively, with full temporal match).
Model component(s)		**6. NTS-BCA Encounters (intermediate variable)** **7. Direct impacts**	

Model Component 7:

Direct impacts



Note. The variable with a double border has been defined in Model Component 6.

BCA attacks NTS when encounters		Definition	Comments
		The frequency at which a susceptible NTS individual is attacked in a situation of exposure to the attacking life stage of the BCA.	Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 33% Never, 34% Sometimes, 33% Always. When possible, input probabilities must be assigned based on experimental testing of the behaviour of the BCA in presence of the NTS. For instance, starvation and oviposition tests on plants for herbivore insects, oviposition tests towards hosts for parasitoids, predation tests towards prey for predators. It is recommended that these tests standardise factors such as host age, mating and feeding history, and include the TS as a positive control to confirm that the experimental protocol is appropriate. This information can be summarised from laboratory choice and non-choice tests. When incomplete information is available on the attacking behaviour of the BCA towards the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.
States	***Never***	In a situation of close contact exposure (<10 cm), less than 20% of susceptible NTS individuals are attacked by the attacking life stage of the BCA.	
	Sometimes	In a situation of close contact exposure (<10 cm), between 20% and 80% of susceptible individuals in the NTS population are attacked by the attacking stage of the BCA.	
	Always	In a situation of close contact exposure (<10 cm), more than 80% of susceptible individuals in the NTS population are attacked by the attacking stage of the BCA.	

Model component(s)	7. Direct impacts (input variable)

<u>NTS mortality after successful attack</u>		**Definition**	**Comments**
		The frequency at which an NTS individual attacked by the BCA dies before it can reproduce.	Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 33% Never, 34% Sometimes, 33% Always. When possible, input probabilities must be assigned based on experimental testing of the behaviour of the BCA in presence of the NTS. For instance, laboratory or field studies on BCA attacks and impact on NTS plants for herbivore insects, on NTS insect hosts for parasitoids, on NTS prey for predators. It is recommended that these tests standardise factors such as host age, mating and feeding history, and include the TS as a positive control to confirm that the experimental protocol is appropriate. When incomplete information is available on the impact of the BCA on the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.
States	***Never***	Less than 20% of NTS individuals die before they can reproduce as the result of an attack by the BCA.	
	Sometimes	Between 20% and 80% of NTS individuals die before they can reproduce as the result of an attack by the BCA.	
	Always	More than 80% of NTS individuals die before they can reproduce as the result of an attack by the BCA.	
Model component(s)		**7. Direct impacts (input variable)**	

<u>NTS non-lethal fitness impact after attack</u>		**Definition**	**Comments**
		The frequency at which a NTS individual attacked by the BCA survives the attack and reproduces, but has reduced reproductive potential.	Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 33% Never, 34% Sometimes, 33% Always. When possible, input probabilities must be assigned based on experimental testing of the behaviour of the BCA in presence of the NTS. For instance, laboratory or field studies on BCA attacks and impact on NTS plants for herbivore insects, on NTS insect hosts for parasitoids, on NTS prey for predators. It is recommended that these tests standardise factors such as host age, mating and feeding history, and include the TS as a positive control to confirm that the experimental protocol is appropriate. When incomplete information is available on the impact of the BCA on the NTS, information can be obtained from close relatives (e.g. NTS in the same subfamily). The estimation of input probabilities obtained from such surrogate species must reflect additional uncertainty, notably by considering morphological and ecological differences between species.
States	***Never***	Less than 20% of NTS individuals experience a reduction in their reproductive potential as the result of an attack by the BCA.	
	Sometimes	Between 20% and 80% of NTS individuals experience a reduction in their reproductive potential as the result of an attack by the BCA.	
	Always	More than 80% of NTS individuals experience a reduction in their reproductive potential as the result of an attack by the BCA.	
Model component(s)		**7. Direct impacts (input variable)**	

BCA attacks NTS		Definition	Comments
		The frequency at which susceptible NTS individuals in the population are attacked by the BCA.	Node with conditional prior probability table. Integration of the parent nodes: “NTS BCA encounters” and “BCA attacks NTS when encounters”. These parent nodes are equally weighted. When no encounters occur, or when no attacks occur when there are encounters, the variable BCA attacks on NTS rate as “Never” with a 100% probability. It rates as 100% “Always” when encounters always occur and when attacks always occur when there are encounters, and as “Sometimes” in all other situations.
States	***Never***	Less than 20% of the NTS individuals in the population are attacked by the BCA.	
	Sometimes	Between 20% and 80% of the NTS individuals in the population are attacked by the BCA.	
	Always	More than 80% of the NTS individuals in the population are attacked by the BCA.	
Model component(s)		**7. Direct impacts (intermediate variable)**	

		Definition	Comments
BCA lethal impact on NTS population		**The proportion of NTS individuals in the population that die before they can reproduce because they have been attacked by the BCA.**	Node with conditional prior probability table. Integration of the parent nodes: “BCA attacks NTS” and “NTS mortality after successful attacks”. These parent nodes are equally weighted. When no attacks occur, or when no attacks are not associated with mortality, the variable BCA lethal impact on NTS rate as “None” with a 100% probability. It rates as 95% “High” when attacks always occur and when these attacks are lethal (reduced to 80% when attacks occur sometimes). Attacks that are only sometimes lethal yield intermediate values, for instance a 80 % probability of “Low” lethal impact on the NTS population.
States	***None***	Less than 20% of the NTS individuals in the population die before they can reproduce because they have been attacked by the BCA.	
	Low	Between 20% and 80% of the NTS individuals in the population die before they can reproduce because they have been attacked by the BCA.	
	High	More than 80% of the NTS individuals in the population die before they can reproduce because they have been attacked by the BCA.	
Model component(s)		**7. Direct impacts (intermediate variable)**	

<table>
<tr><td colspan="2" rowspan="2"><u>BCA non-lethal impact on NTS population</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The proportion of NTS individuals in the population that experience non-lethal impact affecting their reproductive fitness because they have been attacked by the BCA.</td><td rowspan="4">Node with conditional prior probability table. Integration of the parent nodes: “BCA attacks NTS”, “BCA non-lethal fitness impact after attacks” and “NTS mortality after successful attacks”.

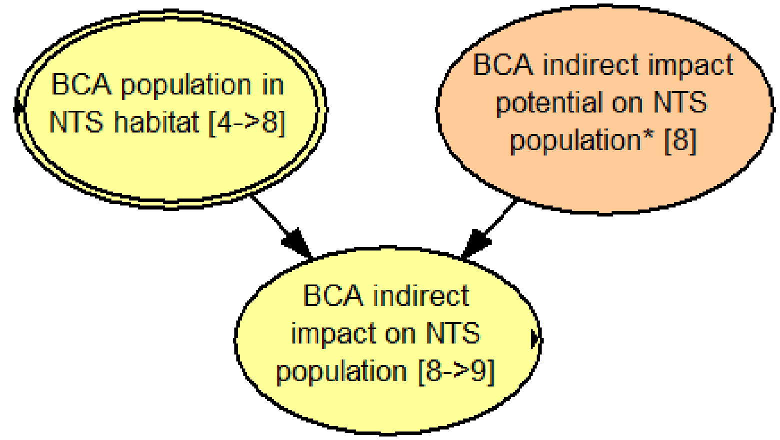
These parent nodes are unequally weighted. A non-lethal impact on NTS population requires attacks that are successful but non-lethal. It is rated with a “High” rating only in situations where there are always attacks, the non-lethal fitness impact is high and, there is no mortality (100% probability of a non-lethal impact) or occasional mortality (10% probability).</td></tr>
<tr><td rowspan="3">States</td><td>None</td><td>Less than 20% of the NTS individuals in the population experience non-lethal fitness impact because they have been attacked by the BCA.</td></tr>
<tr><td>Low</td><td>Between 20% and 80% of the NTS individuals in the population experience non-lethal fitness impact because they have been attacked by the BCA.</td></tr>
<tr><td>High</td><td>More than 80% of the NTS individuals in the population experience non-lethal fitness impact because they have been attacked by the BCA.</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">7. Direct impacts (intermediate variable)</td></tr>
</table>

<table>
<tr><td colspan="2" rowspan="2"><u>BCA direct impact on NTS population</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The introduction of the BCA causes a reduction in abundance of the NTS in the considered habitat, through direct interactions.</td><td rowspan="3">Node with conditional prior probability table. Integration of the parent nodes: “BCA lethal impact on NTS population” and “NTS non-lethal impact on NTS population”.

These parent nodes are unequally weighted. A lethal impact implies the death of the NTS before age of reproduction, hence any “High” rating for lethal impact yields a 100% probability of an overall direct impact.

A non-lethal impact has a lower impact on the overall direct impact. In absence of lethal impact, a “High” non-lethal impact only yields a 50% probability of impact. This rating increases to 80% with a “Low” lethal impact.</td></tr>
<tr><td rowspan="2">States</td><td>No</td><td>Direct interactions between the BCA and the NTS, such as predation, parasitism or herbivory, do not result in a reduction in abundance of the NTS population. There are no interactions between the two species, or if such interactions exist, they only cause short-term fluctuations in the local abundance of the NTS. No substantial population reduction of the NTS, e.g. a more than 10% decrease, is considered likely to occur over the long term (10+ years).</td></tr>
<tr><td>Yes</td><td>Direct interactions between the BCA and the NTS, such as predation, parasitism or herbivory, result in a reduction in abundance of the NTS population. A substantial population reduction of the NTS, e.g. a more than 10% decrease, is considered likely to occur over the long term (e.g. 10+ years).</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">7. Direct Impacts (intermediate variable)

9. Impacts</td></tr>
</table>

Model Component 8: Indirect Impacts	 *Note. The variable with a double border has been defined in Model Component 4.*

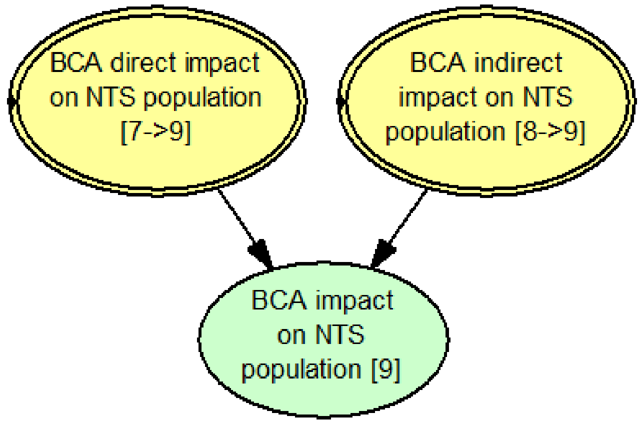
Potential for BCA to have indirect impact on NTS population		Definition	Comments
		The co-occurrence of the BCA, the NTS, and other organisms in the considered habitat, may cause a reduction in abundance of the NTS, through indirect interactions.	Node with unconditional prior probability table (input variable). Default prior probability distribution for parasitoid-host systems: 50% No, 45% Low, 5% High. Input probabilities must be assigned based on the best available information on abundances and feeding relationships between the BCA, the TS and NTS, as well as their prey/hosts and natural enemies. Food webs for instance, can be drawn to identify the species with which the BCA can be directly interacting, the proportion of that population affected, and identify how the NTS is connected to those populations in ways that can result in indirect effects.
States	***None***	No indirect interactions between the BCA and the NTS, defined as population feedbacks mediated through the interaction of two or more biotic agents, have been identified to have a negative effect on individuals of the NTS.	
	Low	One or several indirect interactions between the BCA and the NTS, defined as population feedbacks mediated through the interaction of two or more biotic agents, have been identified, with the potential to have a negative effect on individuals of the NTS. However, if such interactions exist, they will only cause short-term fluctuations in the local abundance of the NTS. No substantial population reduction of the NTS, e.g. a more than 10% decrease, is expected over the long term (10+ years).	
	High	One or several indirect interactions between the BCA and the NTS, defined as population feedbacks mediated through the interaction of two or more biotic agents, have been identified, with the potential to have a negative effect on individuals of the NTS. These may result in an irreversible decline in the population of the NTS, rather than just short-term fluctuations in local abundance. A substantial population reduction of the NTS, e.g. a more than 10% decrease, is expected over the long term (10+ years).	
Model component(s)		**8. Indirect Impacts (input variable)**	

<table>
<tr><td colspan="2" rowspan="2"><u>BCA indirect impact on NTS population</u></td><td>Definition</td><td>Comments</td></tr>
<tr><td>The introduction of the BCA causes a reduction in the abundance of the NTS in the considered habitat, through indirect interactions.</td><td rowspan="3">Node with conditional prior probability table. Integration of the parent nodes: “BCA population in NTS habitat” and “Indirect impact potential on NTS population”.

These parent nodes are unequally weighted. When there is no BCA in the considered habitat, or when there the BCA indirect impact potential is rated as “None”, there is a 100% probability for the indirect impact being rated as “No”.

There is also a high probability, ≥ 90%, of “No” indirect impact in presence of “Small transitional” BCA populations. Conversely, the probability of indirect impact is affected by the potential for indirect impact for “Small persistent” (up to 50% probability) or “Large” populations of the BCA (up to 99% probability).</td></tr>
<tr><td rowspan="2">States</td><td>No</td><td>Indirect interactions between the BCA and the NTS, defined as population feedbacks mediated through the interaction of two or more biotic agents, do not result in a reduction in abundance of the NTS population. There are no indirect interactions between the two species, or if such interactions exist, they only cause short-term fluctuations in the local abundance of the NTS (or an increase of the population of the NTS). No substantial population reduction of the NTS, e.g. a more than 10% decrease, is considered likely to occur over the long term (10+ years).</td></tr>
<tr><td>Yes</td><td>Indirect interactions between the BCA and the NTS, defined as population feedbacks mediated through the interaction of two or more biotic agents, result in a reduction in abundance of the NTS population. A substantial population reduction of the NTS, e.g. a more than 10% decrease, is considered likely to occur over the long term (10+ years).</td></tr>
<tr><td colspan="2">Model component(s)</td><td colspan="2">8. Indirect Impacts (intermediate variable)

9. Impacts</td></tr>
</table>

Model Component 9: Impacts	 *Note. The variables with a double border have been defined in Model Component 7 and 8.*

BCA impact on NTS population		Definition	Comments
		The introduction of the BCA causes a reduction in the abundance of the NTS in the considered habitat, through direct and/or indirect interactions.	Node with conditional prior probability table. Integration of the parent nodes: “BCA direct impact on NTS population” and “BCA indirect impact on NTS population”. These parent nodes are equally weighted. In absence of direct and indirect impact, there is a 100% probability of no impact. In presence of both direct and indirect impact, there is a 100% probability of an impact. The presence of only direct or indirect impact yields a 95% probability of an impact.
States	***No***	The introduction of the BCA has no negative impacts on the population of the NTS (or has a positive impact through indirect interactions). No substantial population reduction of the NTS, e.g. a more than 10% decrease, is considered likely to occur over the long term (10+ years).	
	Yes	The introduction of the BCA negatively impacts the population of the NTS. A substantial population reduction of the NTS, e.g. a more than 10% decrease, is considered likely to occur on the long term (10+ years).	
Model component(s)		**9. Impacts (output variable)**	