Applying Fault Tree Analysis to biological invasions identifies optimal targets for effective biosecurity

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Abstract

1. The management of invasive species requires analytical tools that can synthesise the increasing and complex information generated through risk assessment protocols. To that end, Fault Tree Analysis (FTA) provides a means to conceptually map all of the events leading to a particular undesired scenario with associated probabilities and uncertainty.
2. We used a peer-reviewed dataset (the GB Non-Native Species Risk Assessments) to build and quantify a FT of all the events leading to the transport, introduction, establishment and spread of harmful aquatic invasive species in Great Britain.We also simulated management scenarios.
3. Individual barriers to invasion, either natural or human, were largely unsuccessful in hindering invasion (42-91% probability of failure in a 5-year period); yet the high interdependence of events in the tree resulted in an overall probability of harmful invasion of about 3%. This figure is much greater than that estimated by the tens rule, which posits that 10% of non-native species manage to colonise a new area, and only 10% of those become invasive, resulting in a 1% overall probability of harmful invasion.
4. We used the FTA to explore different management intervention scenarios and found that pre-border management reduced the overall risk of invasion by 86%, followed in importance by early action after introduction (85%), and detection at the border (81%). In contrast, post-establishment management techniques, such as eradication and containment, had a limited impact on the probability of widespread invasion (18-24%).
5. *Synthesis and application*s. While prevention has been long recognized as the most cost-effective action against biological invasions, here we were able to quantify the reduction in invasion risk under a range of management scenarios. Optimising all

management elements included in the FT reduced the overall probability of invasion by three orders of magnitude.

6. We conclude that FTA provides a baseline to capitalise on a growing source of peer-reviewed risk assessments, which allows systematic assessment of the effectiveness of future actions to prevent and manage invasive species at the national and international levels. The analytical framework can be extended to other biological threats (e.g. pests, pathogens, diseases) and scenarios (e.g. climate change, war), so that breach and leverage points in biosecurity can be identified.

Keywords: aquatic invasive species, biosecurity, cost-effectiveness, failure, fault-tree, invasion scenario, risk assessment, prevention.

Resumen

1. La gestión de las invasiones biológicas requiere de herramientas analíticas que permitan sintetizar la creciente y compleja información generada a través de protocolos de análisis de riesgos. Para ello, los árboles de fallas (*Fault Tree Analysis, FTA*) permiten mapear conceptualmente todos los eventos que tienen que suceder para alcanzar un determinado escenario de catástrofe, incluyendo sus probabilidades e incertidumbre.

2. Utilizamos una base de datos revisada por expertos (*GB No-Native Species Risk Assessments*) para construir y cuantificar un árbol de fallas con todos los eventos que conducen al transporte, introducción, establecimiento y dispersión de especies invasoras acuáticas con impacto en Gran Bretaña. También simulamos escenarios de manejo.

3. Las barreras individuales frente a la invasión, tanto las naturales como las artificiales, se revelaron como muy ineficaces a la hora de frenar el riesgo de invasión (42-91% probabilidad de fallo en un rango de 5 años); y sin embargo la elevada interdependencia de los eventos en el árbol resultó en una probabilidad total de invasión de tan solo el 3%. Este dato es mucho

mayor que el predicho por la regla de los 10, que anticipa que solo el 10% de las especies no nativas introducidas llegan a colonizar un nuevo área, y de ellas tan solo el 10% se vuelven invasoras, por lo que la probabilidad de una invasión biológica dañina quedaría en un 1%.

4. Utilizamos el árbol de fallas para explorar escenarios alternativos de gestión y confirmamos que el manejo en origen reduce el riesgo total de invasión en un 86%, seguido en importancia por la erradicación inmediata tras la introducción (85%) y la detección en la frontera (81%). En comparación, la gestión reactiva, como la erradicación y contención a largo plazo, tienen un impacto muy bajo en la probabilidad de invasión (18-24%).

5. Síntesis y aplicaciones. Siempre hemos considerado la prevención como la actuación más coste-eficiente frente a las invasiones biológicas. En este estudio hemos sido capaces de cuantificar la reducción en la probabilidad de invasión dañina que supone la prevención proactiva bajo un amplio rango de escenarios de manejo. Optimizar todas las barreras de manejo en el árbol de fallas redujo la probabilidad de invasión dañina en tres órdenes de magnitud.

6. Concluimos que los árboles de fallas proporcionan una herramienta óptima para aprovechar la información de experto recogida de forma sistemática en los análisis de riesgo, permitiendo estudiar la efectividad de actuaciones de prevención y gestión a escala nacional e internacional. El marco de trabajo se podría extender a otros riesgos biológicos (por ej. pestes, patógenos, enfermedades) y escenarios (por ej. cambio climático, guerra), de modo que podamos identificar los puntos débiles y fuertes de cada estrategia en bioseguridad.

Palabras clave: especies invasoras acuáticas, bioseguridad, coste-efectividad, fallo, árbol de fallas, escenario de invasión, prevención,

Introduction

The worldwide spread of invasive alien species is accelerating (Seebens et al., 2017), negatively affecting human, animal, and plant health (Vilà et al., 2021), damaging infrastructure (Pimentel et al., 2005), and threatening native biodiversity (Brondizio et al., 2019; Pyšek et al., 2020), costing the global economy US$26.8 billion each year (Diagne et al., 2021). As a result of these growing threats, strategies to deliver biological security have become a global priority in order to protect economies, society and the environment (Kemp et al., 2021). At a national scale, the UK's biological security strategy (2018) incorporates the need to reduce the risk of spreading invasive species, pests, pathogens and diseases. In particular, it highlights the need to learn from previous incidents and build scientific capabilities to respond to biological risks.

One method of learning from previous incidents is through Fault Tree Analysis (FTA). This is a systematic and deductive approach that allows for estimation of the likelihood of an undesired "Top Event" happening based upon the probability of failure of natural and management barriers, thereby identifying the events and pathways that are most likely to cause breaches in biosecurity (Ruijters & Stoelinga, 2015). Invasive alien species go through five major stages – transport, introduction, establishment, spread and impact—that result in severe impacts on biodiversity such as the displacement and ultimately extinction of native species, as well as impacts on socio-economic interests such as agriculture yields, tourism or human health; this is what we call the "Top Event". As represented in Figure 1, a series of barriers hinder whether a species becomes invasive. Some barriers are natural and therefore intrinsic to the system such as biogeographic barriers (mountain ranges, oceans), survival during transportation from native to invaded ranges, founder effects, environmental filtering or physical barriers to dispersal (Blackburn et al., 2011). Other barriers are related to the management of either species or the environment they invade, such as pre-border pathway management, disinfection in transit, secure keeping, early eradication or long-term containment (Robertson et al., 2020).

The application of FTA to complex ecological systems such as biological invasions has so far been limited to a few examples. Two decades ago, Hayes (2002a) built a comprehensive, yet descriptive, fault-tree for ballast water introductions; a similar exercise was later applied to recreational boating (Acosta & Forrest, 2009). These two conceptual trees demonstrated the value of FTA to guide decision-making by detailing all of the elements leading to the introduction of unwanted organisms through very specific pathways. Subsequent exercises populated the different elements in the tree with probabilities of failure obtained through expert elicitation. For instance Hayes (2002b) identified 286 combinations of vessel components and infection modes that were then scored through a series of nine workshops with different water users and authorities. This extraordinary effort allowed identifying water retention and internal fouling as the most hazardous for the introduction of marine alien invaders. Similarly, Acosta et al. (2010) used expert elicitation and a fuzzy logic system to quantify the risk associated with 72 different scenarios of vessel infection; they identified hull fouling, deck, internal space, anchor and fishing gear as high-risk invasion mechanisms. These initial works focused on the first steps of the invasion process (i.e. transport and introduction into the invaded area), but, to date, no FTA has covered the full invasion curve (Fig. 1), including establishment and secondary spread. In addition, expert elicitation is time and resources intensive and provides a snapshot of the scientific evidence that is difficult to update unless the exercise is repeated periodically.

Recently, a variety of risk assessment protocols have been developed to systematically evaluate and synthesise the scientific evidence available from other invaded regions about the likelihood of transport, introduction, establishment, spread and impact of invaders (González-Moreno et al., 2019). The results of risk assessments are commonly used to rank established or prospective invasive species in a given area so that management resources can be focused on the biggest risks (e.g. Gallardo et al., 2016; Peyton et al., 2019; Roy, Bacher, et al., 2018). However, simply ranking invasive species is of limited use for management because it fails to identify the strategic management actions that are more likely to reduce the probability of the worst invasion scenario (Booy et al., 2020). Since their initial development in the early 2010s, hundreds of invasive alien species have been systematically evaluated using risk assessment protocols (e.g. 116 in Great Britain, 135 by the European Commission, 2614 by the COST Action AlienChallenge (González-Moreno et al., 2019; Roy, Bacher, et al., 2018)), and will continue to be evaluated each year, offering a unique opportunity to use hazard identification techniques, such as FTA, to analyse the natural barriers and failures in management that have contributed to their widespread invasion.

Here we build an FTA to investigate the chain of events that leads to biological invasions in Great Britain. We assembled a descriptive FTA and then use data from the GB-Non Native Species Risk Assessment (GB-NNRA, www.nonnativespecies.org) to calculate the probability and uncertainty associated with the basic events leading to an invasion scenario. We further use FTA to simulate management scenarios, under the basic hypothesis that proactive intervention before or at the border is more effective at reducing the overall risk of invasion than reactive post-border interventions. This can be tested by simulating a reduction in the probability of failure of the different management barriers. The novelty of our FTA relies in that we build a fully quantitative tree that covers the initial four stages of the invasion process leading to widespread negative impacts (transport, introduction, establishment and spread), and simulate management scenarios. The result is a powerful analytical tool that can synthesise the increasing and complex information generated through risk assessment protocols and can be easily updated as new species and new information are evaluated. The FTA framework can be extended and stress-tested for other biological threats (e.g. pests, pathogens, diseases), scenarios (e.g. climate change) and contexts, so that the riskiest points in the Fault Tree can be identified and the cost-effectiveness of improved biosecurity at different stages quantified accordingly. More generally, we discuss the application of FTA to ecological systems and suggest ways of improvement.

Material and Methods

We developed a Fault Tree to analyse the risk of biological invasions in Great Britain following six steps.

Step 1. Constructing the Fault Tree

FTA is a deductive technique where we start from the Top Event (i.e. invasion scenario) and work top-down to identify the specific chain of events that caused failure of the system. A Fault Tree is, therefore, a graphical model of all the parallel and sequential combinations of events that lead to the Top Event (Hayes, 2002a). A FTA consists of two types of nodes: events and gates. *Intermediate events* are caused by the combination of several *basic events,* which do not need or can't be subdivided further, because an appropriate level of resolution has been reached. We connected basic events into intermediate events using logical gates. Gates determine how failures propagate through the system: "AND" gates are used when all of the basic events have to occur for the intermediate event to take place. In the case of "OR" gates, the intermediate event occurs if at least one (or all) of the basic events occur.

The GB-NNRA was established in 2006 and up to 2020 has been used to systematically evaluate the risks associated with 116 invasive species. The scheme provides a structured framework with four modules for evaluating the potential for non-native organisms to Enter, Establish, Spread and cause significant Impacts in all or part of Great Britain. Assessments are carried out by independent specialists, peer-reviewed by both an external expert and a central panel of risk assessment professionals, and finally open to public feedback at the GB-Non-native Species Secretariat webpage (GB-NNSS, http://www.nonnativespecies.org). To build our FTA, we identified the basic events that can lead to the successful establishment and spread of invasive species using the 34 questions in the Entry, Establishment and Spread modules (Table S1). Intermediate events are not directly evaluated in the protocol, but combine multiple basic events that can be linked together. An example of this is the intermediate event "biotic filter"

(Event 10 in Table 1, Fig. 2) that combines biological aspects that may prevent establishment related to the invasive species (e.g. genetic bottlenecks, lack of adaptability to local conditions) and the invaded community (e.g. presence of competitors or natural enemies). These biological barriers are combined with an AND gate because all of them must fail for the species to continue with the invasion process. In contrast, the intermediate event "management fails" (Event 6 in Table 1, Fig 2) combines containment and eradication barriers connected in this case with an OR gate, because failure in just one of them would allow the species to continue spreading. We ignored the Impact module of the GB-NNRA because it describes the consequences rather than the causes of the "Top Event" i.e. the harmful and widespread colonisation of the study area by a non-native species.

Step 2. Obtaining probabilities from expert judgement

From the 116 species evaluated using GB-NNRA, we downloaded risk assessments for 28 aquatic species (Table S2) from the GB-NNSS webpage (http://www.nonnativespecies.org, last accessed 1st September 2019). We focused on the aquatic environment because, in comparison with terrestrial habitats, it is i) more *invasible* because of multiple vectors and pathways of invasions that are difficult to control, ii) particularly susceptible to the negative impacts of invasion, and iii) challenging to manage because of the low detectability of species, and high connectivity inherent to the aquatic environment (Moorhouse & Macdonald, 2015). The list included 19 freshwater and 9 marine organisms introduced through three major gateways: stowaway (N= 10), aquaculture (N= 10) and ornamental (N= 8), which correspond to the most important pathways of aquatic introduction in Europe (Nunes et al., 2015). These 28 species have been identified by the GB-NNSS as representing the greatest immediate risks to biosecurity in Great Britain and include high-profile invaders such as the water hyacinth (*Eichhornia crassipes*), the zebra and quagga mussels (*Dreissena polymorpha* and *D. r. bugensis*), the signal crayfish (*Pacifastacus leniusculus*) and the topmouth gudgeon (*Pseudorasbora parva*).

In traditional FTA, failure probabilities of system components are used to investigate the probability of the Top Event. This is because original Fault Trees were used in the chemical and safety industries where the probability of operational faults in valves and pumps can be quantitatively measured. In ecological systems, however, this kind of information is rarely available. In the case of the GB-NNRA, the assessor is required to answer questions choosing one of five levels that represent the probability of the event occurring over a 5-year period (very low= 0-10%, low= 11-33%, medium= 34-66%, high= 67-90%, and very high= 91-100%); justifying these with a written, referenced comment (Mumford et al., 2010). The scale is narrower at the extremes to allow more positive discrimination of both very rare and highly likely events. Histograms showing the frequency of each response are given in Figure S1. Here we used the mean value to represent each category (5, 22, 50, 78 and 95%). We replicated analyses using alternative transformations (e.g. 10-33-66-90-100%; 0-11-34-67-91%) but given that general patterns were similar, they are not shown for simplicity.

We calculated the mean probability of failure (Q) across the 28 species for each of the 34 questions in the GB-NNRA and used these values to populate the Fault Tree. Results using the median probability did not differ significantly, and are therefore not reported here.

Step 3. Quantification of the Fault Tree: probability of the Top Event

To calculate the probability of the Top Event (i.e. the harmful and widespread colonisation of the study area by a non-native species that results in severe impacts on biodiversity and/or socio-economic interests), numerical probabilities (Q) assigned to the basic events were combined using boolean statistics depending on the gates that connect them: the probability of events linked with an OR gate is summed, whereas the probability of events linked with AND gates is multiplied. We calculated the probability of the Top Event for individual species using the R package FaultTree (Silkworth, 2017a), and also grouped them by pathway and region of origin.

Step 4. Quantification of the Fault Tree: importance of basic events

The importance of basic events provides information about their impact on the system. This analysis can be used to prioritise those management actions that could reduce the overall risk. There are multiple measures of importance, here we employed the following indicators, already implemented in the R package FaultTree.SCRAM (Silkworth, 2017b):

- *Marginal Importance Factor* (MIF) gives the increase in risk due to the failure of the event by measuring the difference between failed-event (Q_{event}=1) and non-failed event (Q_{event}=0).
- *Risk Reduction Worth* (RRW) indicates the maximum decrease in risk of the system if the event never fails; it measures the difference between the current level of risk (Q_{event}) and the risk if the component never fails (Q_{event}=0). RRW is useful for prioritising improvements that can most reduce the risk in the future.
- *Minimal Cut Sets* (MCS) is the minimum collection of basic events that would lead to the Top Event. MCS are used to understand the structural vulnerability of the system and identify weak points.

Importance measures take into account the position of the event in the FT, which means that those events with high MIF or RRW do not necessarily show the highest probability of failure (Q).

Step 5. Uncertainty of the Fault Tree

Confidence in question responses, registered in the GB-NNRA protocol, was transformed into a numerical measure of uncertainty (U) using the following scale: “Certain”= 0, “Low uncertainty”= 0.2, “Moderate uncertainty”= 0.4 and “High uncertainty”= 0.6. The maximum confidence level (Certain) is used for events that refer to intrinsic characteristics of the species that are well known, such as the ability to establish and reproduce. We used the package "propagate" in R (Spiess et al., 2018) to propagate the error of basic events towards the Top Event.

Step 6. Simulate management scenarios

We simulated a range of management scenarios by modifying the probability of failure of all management events, individually and collectively, from 5 to 100%. This allowed exploration of the effectiveness of investing in one single strategy, *versus* a more holistic approach to prevent invasions. Our options therefore range from an "ideal scenario", where the probability of failure of all management interventions is set to 5%, to the "worst case scenario" where all probabilities of failure are set to 100%.

Results

Our Fault Tree of aquatic invasions in Great Britain was composed of 26 basic and 12 intermediate events that correspond to the sequential and parallel barriers, both natural and related to management, which hinders biological invasions. Steps in the FT are fully described in Supplementary Information 2, and synthesised in Figure 2.

Quantification of the Fault Tree: probability of the Top Event

The fault probability of the invasion scenario, averaged across 28 aquatic species, was calculated as 3.14±0.05% for a 5-year period. Because the probability of the Top Event strongly depends on the number of events included in the tree, and the idiosyncrasies of the 28 species that have been assessed by the GB-NNRA, we must use this value with caution to compare across species and scenarios rather than as an absolute probability of invasion.

Barriers showing very high probability of failure (darker shading in Fig. 2) include propagule pressure (Event 38, Q=98±13%), transference from the pathway to the natural environment (Event 19, Q=95±6%), biotic filters (Events 26 and 30, Q= 99±1% and 92±6% respectively), and management post-establishment (Event 6, Q=97±5%). The probability of failure of the propagule pressure barrier is particularly high because basic events are connected with an OR gate and thus probabilities or failure are combined. This means that the propagule pressure barrier is expected to fail if any of the initial premises (concentration transported, frequency transported or volume transported) is high enough. This could occur through one single transportation event, albeit with a very high concentration of the invader, or through repeated events with a low concentration of the invader.

Species differed in their probability of reaching the Top Event (Fig. 3), and across pathways of introduction (ANOVA, $F_{2,25}$=3.77, P=0.04) (Fig. 4). Organisms that were introduced as stowaways were seven times more likely to reach the Top Event than organisms introduced by aquaculture, and four times more than organisms introduced through the ornamental trade. No significant differences in the probability of the Top Event were found among regions of origin or types of habitat. The probability of the Top Event was distinctively high for marine organisms originating in Australia and Asia, but differences were not statistically significant (Fig. 4).

Quantification of the Fault Tree: importance of Basic Events

Minimal Cut Sets were found with 19 degrees of freedom;this means that 19 (68%) of the 28 Basic Events included in the tree should happen for the system to fail completely (Table 1). Early detection at the border (Event 33), adaptability of the species to local conditions (Event 13), and the degree to which the pathway (as commodity, contaminant or stowaway; Event 34) is associated with source populations of potential invaders, were highlighted as the most important events in terms of Marginal Importance Factor, which calculates the increase in risk due to the failure of the event. Other events in order of importance were: suitable climate and habitat conditions for establishment (Events 23 and 24), and the absence of genetic bottlenecks preventing establishment (Event 14). Events achieving highest Risk Reduction Worth values (RRW, the maximum decrease in risk of the system if the event never fails) include pre-border management (Event 42), capacity of the species to spread (Event 16) and capacity to survive in transit (Event 31).

Simulation of management scenarios

The average probability of failure across the five management barriers included in the FT is 79±8%. This means that management is typically considered highly probable to fail by assessors. Here, we simulated values of management failure between 5 and 100% to find the ideal allocation of resources to avert widespread harmful invasions (Fig. 5). In accordance with our expectations, proactive management, such as reducing the failure of pre-border management (Event 42), early detection (Event 33) or rapid response (Event 17), were able to reduce 17-fold the probability of the Top Event in comparison with the current scenario (Fig. 5A). In contrast, reactive measures such as eradication (Event 8) and long-term containment (Event 7) had little to no impact on the overall probability of invasion (Fig. 5A). Despite these figures, it is important to note that control and eradication can still be important to mitigate the harmful effects of the invaders at local or regional scales.

Under an ideal management scenario, strong support of management interventions across all stages of the invasion process (probability of failure Q= 5% for all management events) is able to reduce the probability of the top event considerably with respect to the current scenario (from Q=3.14% to 0.000087%, Fig. 5B). Simply decreasing the probability of failure of management actions currently calculated at 79% (High) to a modest target of 50% (Medium), would achieve a 5-fold decrease in the chances of the invasion scenario (from Q=3.14% to Q=0.67%).

In contrast, under the worst case scenario of no management (probability of failure Q=100% for all management events), the probability of harmful widespread invasion doubles in comparison with the current situation (from Q=3.14% to Q= 7.12%), further evidencing the benefits of the ideal management scenario.

Discussion

Applying FTA to assess the risk of biological invasions

In this study, we built the first quantitative Fault Tree Analysis that incorporates the four major stages of the invasion process that lead to widespread harmful invasions: transport, introduction, establishment and spread. We were able to do so by capitalising on the vast amount of information generated by the GB-NNSS after 15 years of systematic risk assessment of invasive species. Across the 28 species we investigated, the probability of failure of natural and management barriers to invasion was high, ranging from 42 to 91% in a 5-year period. As such, most barriers were moderately to very unlikely to avert invasion, at least individually. Yet, because many of them need to fail simultaneously at each major invasion stage and in subsequent stages, the overall probability of widespread and harmful invasion drops to 3% in a 5-year period.

The probability of the top event can be compared with the "tens-rule", which states that about 10% of introduced species take all the consecutive steps of the invasion process, and that 10% of them (that is, 1% of all initial introductions) become invasive and cause "significant detrimental impacts" (sensu Williamson & Brown, 1986); a concept that is equivalent to our Top Event. The tens rule gained popularity in the 1990s even if it had little empirical or theoretical basis, but later evidence suggested that the actual rate of successful introduction may be 4-times higher, with large variations across taxonomic groups (Jeschke & Heger, 2018). This is more in line with the rough 3% that we obtained through a quantitative FTA. This apparently low figure should not be underestimated since the propagule and colonisation pressure of aquatic habitats is enormous: one study estimated that 7–10,000 aquatic species are being transported with ballast water globally at any one time (Endresen et al., 2004); aquaculture is responsible of >5,600 introductions globally (FAO 2019); focusing in Great

Britain, there are approximately 560,000 registered boats that can transport invasive species within and towards the country (Ashton et al., 2006).

Top event probabilities varied considerably among species, and were highest for those transported as stowaways, one of the most important gateways of aquatic invasion into Great Britain (Gallardo et al., 2016; Gallardo & Aldridge, 2015). The Japanese skeleton shrimp (*Caprella mutica*) and New Zealand Mudsnail (*Potamopyrgus antipodarum*) stand out as the invasive species with the highest probability of widespread invasion in Great Britain. Indeed, *C. mutica* (probability of Top Event, Q=39%) has been present in Great Britain since 2000 and is distributed from the English Channel to the Celtic Sea coast (Ashton et al., 2006, 2007; Cook et al., 2007). Likewise, *P. antipodarum* (Q= 24%) is an extremely tolerant species that is common and widespread across freshwater and brackish habitats in Great Britain with a very small body size that is difficult to detect during biosecurity screening (Alonso & Castro-Diez, 2008; Gallardo et al., 2020). Only one of the species investigated, the marbled crayfish (*Procambarus fallax f. virginalis*), is not yet established in Great Britain. The probability of the Top Event (Q=0.004%) is one of the lowest, which makes sense because its sale and keeping is regulated in Great Britain, it cannot be imported from non-EU countries, it is adapted to warm subtropical climates, subject to a high competition and predation by resident species, and not known to be able to spread naturally, only through human intervention (Holdich, 2011).

In this study, FTA was applied to an ecological system, and this application differs substantially from their typical use in industrial settings. First, basic events are not necessarily accidents or failures but rather aspects related to the species' biology or ecology (e.g. adaptability, traits, survival capacity), or to the environment (e.g. climate and habitat suitability) that cannot be modified but definitely contribute to the process of invasion. The probability of failure of such ecological basic events is difficult to quantify and subject to high uncertainty. Another important difference is the high interdependence between events in ecological systems, which is reflected in the prevalence of AND gates, as opposed to OR gates. This makes it more difficult to find alternative cut sets (the minimum collection of basic events that would lead to the Top Event) but has the practical advantage that minimising the probability of failure of key events can dramatically affect the overall risk of invasion. This can be clearly seen in the management scenarios, where reducing to 10% the probability of failure of just one basic event "detection at the border" resulted in a reduction of >80% in the probability of the Top Event.

How can we optimise the allocation of resources for management?

Beyond the Top Event, FTA allowed quantification of the maximum reduction in total risk that could be achieved focusing resources on different stages of the invasion process. Based on the evidence collected, we confirm that even small improvements in proactive management can have major repercussion in the overall probability of invasion; whereas the effectiveness of reactive management is rather limited. According to our analysis, eradication programs for aquatic invasive species of established, reproducing populations are very likely (for 68% of species) or likely (25%) to fail (Fig S1A). To illustrate the enormous challenge posed by biological invasions, only nine of the 3,163 non-native species known to have established in Great Britain (0.002%) have been eradicated, and even then only locally (NNSIP scorecard 2017). Our study therefore adds to the mounting calls that prevention is far more cost-effective than control for invasive species (Leung et al., 2002). According to Cuthbert et al. (2022), prioritising investment at early invasion stages for prevention and rapid eradication could save trillions in economic costs over the long-term.

We can also confirm that investing in one single strategy has limited capacity to reduce the overall risk of invasion (Robertson et al., 2020; Vander Zanden et al., 2010). Considering the current state of invasion of aquatic habitats in Great Britain, with the south-east of England considered one of Europe's hotspots (Gallardo & Aldridge, 2015; Jackson & Grey, 2013; Zieritz et al., 2014), biosecurity strategies should tackle all stages of the invasion process simultaneously, with a focus on proactive prevention and rapid eradication. National biosecurity campaigns, like Check Clean Dry (www.nonnativespecies.org/checkcleandry) and Be Plant Wise (www.nonnativespecies.org/beplantwise) share such a holistic vision and are fundamental to protect aquatic ecosystems, but their actual efficacy is difficult to quantify (Sutcliffe et al., 2018). An FTA focused on the cascade of human actions and decisions that facilitate the Top Event would best reveal breach and leverage points, and help optimise management of aquatic invasions. For instance, reducing the probability of failure of management barriers affected by the check-clean-dry strategy to a mere 50/50 chance reduces the probability of widespread invasion of *P. antipodarum* from 24% to 0.03%. The GB Risk Management scheme (GB-NNRM) can be further used to qualify basic events in the FT by addressing the feasibility of eradicating invasive species according to their effectiveness, practicality, cost, impact, acceptability, window of opportunity and likelihood of re-invasion (Booy et al., 2017). To that end, it is important that risk assessment and risk management protocols are applied to the same species (which was not always the case), so that we can integrate information about how an invasion may unfold in Great Britain with information about how best to respond to it.

Once the FT is built, is it easy to modify and run multiple scenarios, allowing a rapid yet rigorous evaluation of the effectiveness of intervention scenarios that is fundamental to prioritise investment. Another possibility, not explored here, is to simulate climate change scenarios by modifying the probability of events likely to be affected, such as propagule pressure, climate suitability, natural spread (e.g. because of a higher frequency of climatic events such as storms and floods), and the effectiveness of control measures. As such, FTA can be used to set up a baseline and track progress towards reducing the probability of the Top Event.

Limitations and suggestion for improvement

The FTA has several advantages over other traditional statistical techniques that call for further application to biological invasions. Failure space, albeit initially counterintuitive for an invasion ecologist, was particularly useful to identify all of the management interventions that must fail for the worst case scenario to materialise. This process should be ideally undertaken by a multidisciplinary group of researchers and stakeholders, in order to incorporate different perceptions on what constitutes failure as well as their respective responsibilities. However, this approach is very time and resource intensive (Acosta & Forrest, 2009; as in Hayes, 2002a), which is why we limited the construction of the FT to a predefined set of questions from the GB-NNRA. We considered three major pathways of introduction: aquaculture, ornamental trade and stowaway; but other secondary pathways such as intentional release (as fish bait, or as food source) and natural spread from invaded locations, should be ideally incorporated. For instance, waterfowl can be a vector for a broad spectrum of invertebrates that attach to feathers or are eaten (Frisch et al., 2007). Pre-border intervention could be broken down to the different treatments that may fail such as quarantine, ballast water treatment, hull cleaning or disinfection. Likewise, rapid response could distinguish between rapid detection and immediate eradication. However, it must be noted that to build a FT, it is crucial to obtain quantitative information that enables calculation of the probability of failure of these additional barriers. Otherwise, the application of FTA to biological invasions would continue to be limited by the evidence and data available.

One important limitation of FTA is the lack of temporal variation in the probability of failure. In FTA, the basic components either occur or they do not (Hayes, 2002a), yet the window of opportunity for controlling invasive species may vary between months to decades (Booy et al., 2017), which means that a particular management measure applied at the wrong time may increase the likelihood of failure considerably. In addition, the tree is based on data from actual aquatic invasions (equivalent to past accidents in the industry), which means that it is biased towards successful invaders. The difficulty of finding equivalent information for failed introductions is a pervasive problem for invasion studies (Zenni & Nuñez, 2013), which in this case means that the probability of failure of the various filters may be overestimated.

Conclusions

Beyond Great Britain, hundreds if not thousands of species have been evaluated using over 30 different risk assessment protocols available in the literature (González-Moreno et al., 2019; Roy, Rabitsch, et al., 2018). The information generated therein has been primarily used to rank current and future invaders so that funds are focused on the most immediate risks (Gallardo et al., 2016; McGeoch et al., 2012; Peyton et al., 2019; Roy, Bacher, et al., 2018). Beyond rankings, FTA provides a systematic and rigorous tool to synthesise this increasing body of information, thereby allowing practitioners to optimise resources on the events offering the biggest wins to risk reduction. FTA could further allow identifying breaches in biosecurity across different biological threats (e.g. GMO, plant pests, and human diseases) so that common challenges are approached jointly.

FTA has had little application to ecological systems to date, but could be useful to tackle other problems such as species extinction, pollution events (e.g. oil spill), food security or the spread of human diseases. Results of this study clearly show the broad applicability of FTA in risk analysis to identify breach points in biological invasions. Given the current understanding and awareness of biosecurity issues globally, we conclude that FTA provides a baseline to systematically assess the effectiveness of future actions to prevent and manage biosecurity threats at the national and international levels.

Authors' contributions

Belinda Gallardo, William Sutherland and David C. Aldridge conceived the ideas and designed methodology; Belinda Gallardo collected and analysed the data with the support of

Phillip Martin. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of Interest

The authors declare no conflicts of interest in relation with this publication.

Data availability statement

Data used to construct the Fault Tree is available through Figshare (DOI: 10.6084/m9.figshare.20283339).

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Tables

Table1. Characteristics of events considered in the Fault Tree of invasion in Great Britain (GB). A description of events can be found in Table 1 and Supplementary Material 2. Type: Top Event (TP), Intermediate Event (IE) or Basic Event (BE). MCS: inclusion in Minimal Cut Sets, the minimum collection of basic events that would lead to the Top Event (yes/no). Q: probability of failure in 0-100% scale. Uncertainty: standard deviation of the probability of failure. The importance of events, measured through the Marginal Importance Factor (MIF, increase in risk due to the failure of the event) and the Risk Reduction Worth (RRW, maximum decrease in risk of the system if the event never fails), is only calculated by the program for Basic Events.

Event Num.	**Name**	**Description**	**Type**	**MCS**	**Q (%)**	**Uncertainty (%)**	**MIF (x1000)**	**RRW**
1	INVASION SCENARIO	Harmful and widespread colonisation of the study area by a non-native species, also called Top Event	TP	no	3.14	0.05		
2	ESTABLISHED	Non-native species is established in GB	IE	no	4.09	0.14		
3	Spreads	Secondary spread of the non-native species in GB	IE	no	79	9		
4	By Natural Means	Likelihood the non-native species is not able to spread naturally	BE	no	50	6	0.52	1.85
5	By Human Means	Likelihood the non-native species is not able to spread by human assistance	BE	yes	59	6	0.52	2.18
6	Management Fails	Reactive measures to halt the secondary spread of the non-native species fail	IE	no	97	5		
7	Containment	Likelihood the non-native species cannot be contained within the invaded area	BE	no	85	4	0.35	2.08
8	Eradication	Likelihood the non-native species survives eradication campaigns	BE	yes	79	3	0.35	1.92
9	INTRODUCED	Non-native species is introduced in GB	IE	no	18	1		
10	Biotic Filter	Biotic characteristics of the non-native species or the invaded habitat that prevent establishment	IE	no	28	4		
11	Competitors	Likelihood that competition will prevent establishment of the non-native species	BE	yes	81	5	0.71	-1.02x10^{15}
12	Natural Enemies	Likelihood that natural enemies will prevent establishment of the non-native species	BE	yes	81	5	0.71	-1.02x10^{15}
13	Adaptability	Likelihood the non-native species is not able to adapt to local conditions	BE	yes	73	7	0.78	0

14	Genetic bottlenecks	Likelihood genetic diversity in the founder populations prevent establishment	BE	yes	77	6	0.74	-1.71x10^{15}
15	Traits	Likelihood the non-native species lacks biological characteristics that facilitate its establishment	BE	yes	90	2	0.63	-5.14x10^{15}
16	Spread	Likelihood the capacity of the non-native species to spread limits establishment	BE	yes	85	4	0.67	2.57x10^{15}
17	Management Fails: Rapid Response	Likelihood that the non-native species establishes despite existing management practices	BE	yes	83	3	0.69	-5.14x10^{15}
18	ENTERS GREAT BRITAIN	Non-native species enters GB	IE	no	35	4		
19	Transferred	Non-native species is transferred from pathway to natural habitat in GB	IE	no	95	6		
20	By Natural Means	Likelihood the non-native species is able to transfer from pathway to suitable habitat or host naturally	BE	yes	78	4	0.37	2.00
21	By Human Means	Likelihood the intended use of the commodity or other material with which the non-native species is associated aids transfer to a suitable habitat	BE	no	78	4	0.37	2.00
22	Abiotic Filter	Abiotic characteristics of the habitat preventing establishment in GB	IE	no	53	2		
23	Suitable Climate	Likelihood climate conditions will allow the establishment of the non-native species	BE	yes	77	3	0.74	-1.71x10^{15}
24	Suitable Habitat	Likelihood the abiotic conditions will prevent the establishment of the non-native species	BE	yes	81	3	0.71	-1.03 x10^{15}
25	Timing	Likelihood the non-native species arrives during months of the year most appropriate for establishment	BE	yes	86	2	0.66	-5.14 x10^{15}
26	Biotic Filter	Biotic characteristics of the invaded habitat that prevent introduction into GB	IE	no	99	1		
27	Key species	Likelihood that species or habitats key for the survival, development and multiplication of the non-native species are absent	BE	no	87	0.38	0.32	1.96
28	Widespread	Likelihood that species or habitats key for the survival, development and multiplication of the non-native	BE	no	91	1	0.32	2.05

		species are rare						
29	TRANSPORTED TO GB	Non-native species is transported to GB	IE	no	58	7		
30	Biotic Filter	Biotic characteristics of the non-native species that prevents successful transportation into GB	IE	no	92	6		
31	Survives Transit	Likelihood to survive during transport/storage	BE	yes	86	3	0.44	2.91
32	Reproduces in Transit	Likelihood that the non-native species multiplies or increases in prevalence during transport/storage	BE	no	45	5	0.44	1.52
33	Management Fails: Detection at border	Likelihood that the non-native species enters GB undetected	BE	yes	66	3	0.87	0
34	Associated to Pathway	Likelihood that the non-native species is associated to the pathway at origin	IE	no	76	6	0.75	-5.10×10^{15}
35	Aquaculture	Likelihood that the non-native species is associated to aquaculture	BE	yes	57	6	0.28	1.08
36	Ornamental	Likelihood that the non-native species is associated to ornamental trade	BE	no	62	2	0.32	1.11
37	Stowaway	Likelihood that the non-native species is transported accidentally	BE	no	66	6	0.36	1.13
38	Propagule Pressure	Characteristics that increase propagule pressure	IE	no	92	13		
39	Frequency Transported	Likelihood the frequency of the pathway allows transportation	BE	yes	62	7	0.34	1.60
40	Volume Transported	Likelihood the volume of movement along the pathway allows transportation	BE	no	42	10	0.34	1.34
41	High Concentration	Concentration of the non-native species on the pathway at origin	BE	no	62	6	0.34	1.60
42	Management Fails: pre-border intervention	Likelihood that the non-native species survives existing management practices during passage along the pathway	BE	yes	84	4	0.68	2.57×10^{15}

Figures

Figure 1. Barriers to invasion along the invasion curve. Invasive alien species go through five different stages of invasion from being absent to widespread and causing negative ecological and socioeconomic impacts in a particular area. Stages are separated by natural (green) and management (red) barriers that must fail for the species to pass on to the next stage. The costs of managing the invasion accumulate over time, while the probabilities of controlling it decline. The invasion curve sets the conceptual failure space for the development of a Fault Tree Analysis. Curve adapted from Harvey and Mazzotti (2014).

Figure 2. Fault-tree of aquatic invasions in Great Britain. Probabilities of failure (Q) refer to a 5-year period. Events are colour-coded according to their probability of failure (see legend at the top-right corner). In brackets, the uncertainty associated with the event. Stages of the invasion process are represented along the left side of the tree. A description of events can be found in Table 1 and Supplementary Material 2.

Figure 3. Probability of harmful widespread invasion (Top Event) of 28 aquatic species calculated using Fault Tree Analysis (FTA). The vertical line represents the probability of the Top Event using data from all species (3.14%). Values represent the probability that all natural and management barriers against the colonisation of the species fail over a 5-year period.

Figure 4: Differences in the probability of harmful widespread invasion (Top Event) of aquatic species in Great Britain across major habitats (ANOVA, $F_{1,26}$=1.72, P> 0.05), origins (ANOVA, $F_{4,23}$= 1.88, P>0.05) and pathways of invasion (ANOVA, $F_{2,25}$= 3.77, P=0.04).

Figure 4. Simulated changes in the likelihood of invasion at increasing probabilities of failure of individual management actions (A), or all management actions simultaneously (B). The probability of the Top Event refers to the probability of a non-native species passing through all of the natural and management barriers to invasion included in the fault-tree over a 5-year period. A probability of failure of Q=5% for all management interventions simultaneously represents an “ideal scenario”, whereas the “worst scenario” represents a situation where no management of invaders is implemented at all (Q=100%).