PERSPECTIVES AND PARADIGMS

Using network analysis to study and manage human-mediated dispersal of exotic species

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Abstract Human-mediated dispersal is a major contributor of biological invasions. To reduce impacts induced by the introduction and spread of exotic species, biosecurity interventions are put into place. These interventions often rely on risk-assessment

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procedures, whereby biosecurity practitioners (which includes researchers, stakeholders such as national park managers, and all other decision makers who determine when and how to protect biodiversity) attempt to preemptively identify and predict which exotic species could potentially become a threat to natural ecosystems. In theory, extensive field and experimental studies would be required to accurately and precisely determine the risks of biological invasion of a species or group of species. However, due to a lack of resources or knowledge, such critical studies are limited. As a result, biosecurity practitioners rarely have a full picture of the extent to which the exotic species has and will spread at the time of decision making. Hence, they instead opt for preventive measures such as identifying and managing potential target exotic species which are likely to be invasive or dispersal pathways through which exotic species are likely to be introduced and spread. As most of the uncertainties pertaining to biosecurity interventions lie in the resolution of data made available to practitioners at the time of decision making, we first present some of the different types of information which are readily available during the risk-assessment procedure. We then highlight how one could exploit these different resolutions of data during the risk-assessment procedure using network analysis to better understand human-mediated dispersal of exotic species. By doing so, our paper puts forward what network analysis has to offer practitioners in the context of biosecurity interventions.

Introduction

Human-mediated dispersal of exotic species is a major contributor to biological invasion and biodiversity loss (Clifford 1959; Lonsdale and Lane 1994; Mack et al. 2000; Mount and Pickering 2009; Seebens et al. 2013, 2018; Essl et al. 2020). It includes both intentional (e.g. exotic plants introduced for ornamental, horticultural or agricultural purposes Niemiera and Von Holle 2009; Hulme 2011a) and unintentional (e.g. hitchhiking species concealed in soil contaminants or infectious diseases and pathogens introduced via introduced animals for livestock Fèvre et al. 2006; Bram et al. 2002; Craft 2015) introduction of exotic species. Amongst the different dispersal pathways, international trade and transportation networks are recognised as the primary sources of exotic species introduction both at the global and local scales (McCullough et al. 2006; Hulme 2009; Essl et al. 2015). As a consequence of globalisation, studies have found that maritime, air and land transportation and trade networks are likely to facilitate the dispersal of existing and new exotic species over increasingly longer distances (Mack et al. 2000; Meyerson and Mooney 2007; Hulme 2009; Seebens et al. 2013, 2015; Banks et al. 2015; Seebens et al. 2018). Hence, understanding the spread of exotic species via the different human-mediated dispersal pathways is vital to manage and reduce the rate of biological invasion.

To prevent the introduction, establishment and spread of exotic species, biosecurity measures such as policies, sanitary and phytosanitary agreements, and management action plans are implemented (Thornsbury 2002; Froud et al. 2008; Hulme 2011b). However, due to the high cost associated to the management of exotic species, biosecurity practitioners prioritise preventive measures as they are the most cost effective (Eagles et al. 2002; Keller et al. 2007; McGeoch et al. 2016; da Rosa et al. 2018). Risk assessment involves: (1) Identifying whether the exotic species has entered, established and spread in the recipient site (see Table 2); (2) Characterising the environmental and economic impacts caused

by the exotic species; and (3) Finally evaluating and estimating the risk level of the exotic species (Smith et al. 2009). As a result, this preemptive assessment of risks associated with the potential introduction of exotic species at given sites is considered as the most effective tool amongst practitioners.

Ideally, to assess the risk of human-mediated dispersal of exotic species, biosecurity practitioners require specific information about: (1) The taxonomy and life-history traits of the *exotic species*, (2) The range of climatic and environmental conditions where the *exotic species* is likely to survive and reproduce, (3) The potential impact of the exotic species in the recipient *site*, (4) The magnitude at which the exotic species is being introduced—i.e. propagule pressure, and (5) The *dispersal pathways*—i.e. the processes which might result in the movement of the exotic species from one site to another (Hulme 2011b). However, the aforementioned information is not always available (McGeoch et al. 2016; Hulme 2020). Consequently, practitioners are often unable to accurately assess the extent of spread of a given exotic species when recommending biosecurity interventions (Reichard 2001; Hulme 2009; Sinclair et al. 2020). As collecting more data to preemptively monitor when and where any given exotic species can become a threat would be time consuming, labour intensive and expensive, it is particularly vital to develop predictive tools.

Here we put forward the extent to which network analysis can assist practitioners in understanding and predicting human-mediated dispersal of exotic species during the risk-assessment process. More specifically, rather than attempting to understand the spread of an exotic species along the traditional invasion continuum (Fig. 1), in this paper we consider the introduction and subsequent spread of the given exotic species from a management perspective—i.e. the risk-assessment procedures required before (which we refer to as the pre-border) or after an exotic species arrives (which we refer to as the post-border) at a given site. We first summarise traditional risk-assessment procedures. As most of the uncertainties about biosecurity intervention lie in the resolution of data made available to practitioners at the time of decision making, we further summarise the typical information which are often provided to them both during pre- and post-border risk assessment. Finally, we introduce network analysis in the context of biosecurity interventions.

To do so, we specifically used examples from the literature to highlight how practitioners can exploit low resolution data using network analysis to evaluate the potential risk of introduction of exotic species by human-mediated dispersal both before and after an exotic species arrives, establishes and spreads at a site. As such, we hope that this contribution paves the way for practitioners to adopt network analysis as a complementary tool for risk-assessment procedures in the future.

Risk assessment of human-mediated dispersal of exotic species

Biological invasion is a multi-stage process (Fig. 1). The exotic species is first introduced in a new area, then it establishes, increases its abundance and/or expands its range to finally become invasive (Williamson 1996; Richardson et al. 2000; Frost et al. 2019). Similarly, risk-assessment (RA) procedures and management actions can be considered as a multi-stage process: pre-border RA—before an exotic species enters a site and post-border RA—after an exotic has entered a site. The aim of *pre-border* risk assessments is to prevent the entry and establishment of exotic species at a given recipient site. Hence pre-border RA mainly focuses on developing preemptive strategies to identify the potential risks posed by the exotic species if they were to enter a recipient site. On the other hand, *post-border* risk assessments focus on evaluating the invasion stage of the exotic species and the subsequent management actions depend on the extent to which the species has spread (Fig. 1).
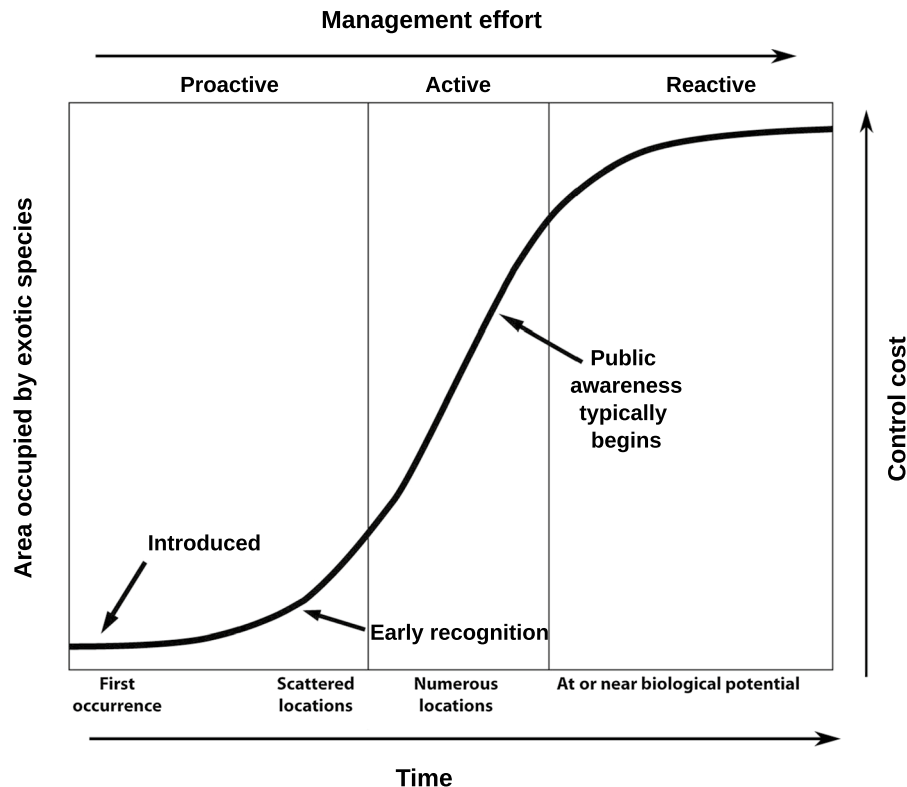

Fig. 1 Invasion curve shows the stages of exotic species management from the first occurrence of the exotic species (proactive) to long-term control (Figure adapted from Department of Environment and Primary Industries Victoria (2010)). If the exotic species is detected when it is first introduced or is still in the early phase where abundance is relatively low and is only present at a few locations, the opportunity for successful eradication of the exotic species is higher. However, if the exotic species is not detected and is spread across numerous sites—either due to high propagule pressure or due to the ideal environmental conditions—more effort is required for managing the impact of the exotic species. As a result, constant management (active and reactive) might be required, causing an increase in the cost of control

Whether RA is carried out at pre- or post-border, the main goal of practitioners is to reduce the impacts induced by potential invasive species. Any delays in managing the introduced exotic species can further increase the cost associated to control and management options (Eiswerth et al. 2001). Hence, biosecurity practitioners strive to develop early warning risk-assessment tools to detect any introduction or spread of exotic species. Management actions usually vary according to the invasion stage of the exotic species. For instance, if the species is still at an early stage—i.e. has not yet established—active management of the individuals could eradicate it. However, the presence of the exotic species at several sites suggests that it has either just established some populations or has reached its peak invasive stage. As a result, active monitoring and management would be required to prevent the species from spreading any further. In the following sections we provide a summary of the main risk assessment procedures and management options which are traditionally considered by biosecurity practitioners both at the pre- and post-border (Table 1).

Policies and regulations as preventive measures

To prevent exotic species from entering and establishing at a site, policies and precautionary measures are implemented at different spatial scales. At an international level, trade agreements are governed by the World Trade Organisation. Each member of the World Trade Organisation imposes a threshold of acceptable risk and threat standards linked to trade. Similarly, member countries of the World Health Organisation and the World Organisation for Animal Health are required to report disease outbreaks and risks due to the movement of people or disease vectors, and to set standards to ensure the sanitary safety of international trade in animals and their products, respectively (Dunn and Hatcher 2015). At a national level, countries have their own policies and mitigation plans (Early et al. 2016). For example, compared to other countries both Australia and New Zealand are considered to have high standards of pre-border measures (Hayden and Whyte 2003; Simberloff et al. 2013; Baquero et al. 2021; Black and Bartlett 2020).

Table 1 Comparison of the aims of risk assessment and management plans, and the type of information required or often gathered for pre- and post-border risk assessments by practitioners. (Information summarised from Burne (2019); Latombe et al. (2019))

	Pre-border level	Post-border level
Goal of practitioners	Identify potential risk of exotic species if they were to enter	Evaluate and minimise risk and impact of exotic species
Management action	Prevent entry and establishment of exotic species	Eradicate or prevent spread of exotic species
Type of information collected/available		
Exotic species	The biological attributes of the target exotic species to assess its probability of entry and likelihood to establish	The abundance of the exotic species at identified site(s)
Occupancy of exotic species	Identify potential sites where exotic species could grow and thrive based on the site's climate and environment	Area of occupancy of population(s) of the exotic species: identify whether they exist in isolation or are spread out across surrounding sites; identify their likelihood to spread from identified recipient site
Impact of exotic species	Assess potential economic and environmental impacts of the exotic species, including on existing biota, human health and life style	Assess direct and indirect impacts in the recipient sites
Dispersal pathways	Identify main potential dispersal pathways through which the exotic species could enter	Identify main (or potential) dispersal pathways through which the exotic species are likely to spread

Identifying and predicting potential invasive exotic species

Besides policies, risk assessment procedures are conducted at different spatial scales. Practitioners often assess the potential risk for the target exotic species to enter and establish in the recipient site based on the extent of information they were able to get on the species. Predicting invasive species spread is an important component of the risk-assessment procedure as it allows practitioners to prioritise sites where more effort is required for targeted surveillance, and early detection allows the implementation of eradication or other control strategies. Practitioners use traits and preferences of the exotic species to assess its likelihood of survival, establishment and being a threat at a site of interest (Pheloung et al. 1999; Pyšek and Richardson 2010; Pyšek et al. 2011a; Burne 2019). However, estimating the niche space of the potential invasive species can be inaccurate and highly criticised in absence of information (Soberón and Nakamura 2009; Gallagher et al. 2010). In such a case, practitioners often use surrogate data to obtain a rough estimation of the types of sites which are more likely to be vulnerable to the exotic species. Interceptions at the border might be especially critical for determining risk of entry and/or establishment (e.g. James et al. 2014; Turner et al. 2021; Robinson and McNeill 2022). Interception data can also include that of sympatric species of the potential invasive species (Barker et al. 1996). Using interception data, practitioners attempt to identify whether the environmental conditions of the exotic species at its different life stages match that of the recipient site to assess whether the exotic species is likely to survive, establish and spread (Pheloung et al. 1999; Molnar et al. 2008; Leung et al. 2012; Turner et al. 2021). Following the assessment of the given exotic species, it can be listed as a potential threat to a given site for future reference (also referred as "invasive species listing", e.g. Auckland Regional Council (2019)). Sometimes a score is also assigned to the species to indicate its level of threat (Pheloung et al. 1999; Leung et al. 2012; Kumschick et al. 2015a).

Assessing the impact of invasive exotic species

Once an exotic species is identified to have entered a given site, the main focus of practitioners is to assess its relative risks (Fig. 1). This involves distinguishing whether the exotic species is at its introduction phase (when the population of the exotic species is still localised and its abundance is still low), establishment phase (when the exotic species is established, its population is scattered, and its abundance is high and having negative environmental or economic impacts) or invasive phase (when the exotic species is widespread) (Ricciardi and MacIsaac 2008) (Fig. 1). Then, the spatial distribution of the exotic species within the area of interest (e.g. country) is first assessed at different sites while taking into account its seasonality.

During the assessment, both direct and indirect impacts of the potential invasive exotic species on the native species are measured. Direct impacts involve, for example, competition for resources between species occupying the same niche space (Levine and D'antonio 2003), while indirect impacts are related to, for instance, apparent competition induced by shared pathogens or parasites (Saggar et al. 1999; Meiners 2007). Moreover, practitioners attempt to identify the different dispersal routes and/or vectors through which the exotic species might spread or is spreading across ecosystems within the region or country of concern. This can include identifying and characterising the different transportation networks or the behaviour of the dispersers; determining whether the site at which the exotic species is found represents a reproductive population and therefore act as the main source for secondary dispersal. Practitioners can also assign a score as an indication of the relative risks of the potential invasive species to prioritise management plans (Pheloung et al. 1999; Pyšek and Richardson 2010; Jeschke et al. 2014; Kumschick et al. 2015b).

Usually, if the exotic species is considered as a serious threat impacting the native biota of the receiving area and/or causes economical impacts on the natural environment or primary industries, the main focus is to design a strategic management plan to

control and prevent further spread of the exotic species. The latest management effort, often referred as mitigation, is a continuous process of monitoring, controlling or managing the invasive species spread and their potential impacts. In some cases if the exotic species is detected at a sufficiently early stage, eradication is possible (Rejmánek et al. 2002; Vander Zanden et al. 2010; Phillips et al. 2020).

Identifying the potential dispersal pathways contributing to introduction and spread of invasive exotic species

Another important measure to monitor biological invasion is the propagule pressure of the exotic species. Propagule pressure refers to the number of individuals introduced at a site combined with the number of introduction attempts (Colautti et al. 2006; Simberloff 2009). Propagule pressure has been found to be a good indication of invasion success (Williamson 1996; Pyšek et al. 2011b; Lockwood et al. 2005). However, due to detection errors caused by low densities of some species, the identification of the exotic species which are likely to become invasive can sometimes be challenging, especially early in the establishment phase (Fig. 1). This often causes pinpointing the timing of an incursion and subsequent establishment of an exotic species to be inaccurate (Hulme et al. 2020), which can consequently result in higher control costs of those exotic species at a later stage (Eiswerth et al. 2001) (Fig. 1). Exotic species are often spread through transportation routes or via other vectors facilitating the movement of exotic species (Hulme 2009). Therefore, an alternative to gazetting potential invasive species is to identify the most likely routes through which exotic species could be introduced (Andersen et al. 2004) to determine potential establishment sites. This is often referred as pathway analysis (Hulme 2009; Yemshanov et al. 2009; Essl et al. 2015) and is listed as one of the strategic goals of the 2030 Aichi targets of the Convention on Biological Diversity (COP 2010; Convention On Biological Diversity 2016). During pathway analysis, practitioners assess the relative likelihood for target exotic species to be spread by different processes such as dispersal routes

or vectors acting as pathways. This includes distinguishing whether the exotic species is more likely to be dispersed and spread by a given dispersal pathway or vectors acting as pathways such as tourists, vehicles, ships, aeroplanes, and trade and transportation of freight. Following the criteria of Hulme (2009), the potential human-mediated dispersal pathways are characterised as either intentional or unintentional. Furthermore, practitioners often also assign a relative score to rank the different dispersal pathways based on their likelihood of spreading the exotic species (Burne 2019).

Although pathway analysis informs practitioners about the potential sites where invasive species could be introduced and spread, to date such analysis is mostly used as a descriptive tool solely to identify the paths contributing to human-mediated dispersal of exotic species (Hulme 2009; Pyšek et al. 2011a; Essl et al. 2015). A key step moving forward is to develop more predictive tools. The main factors widely used to predict the presence of invasive species are the exotic species' traits, vector behaviour, different dispersal routes and how dynamic those routes might be, biotic and abiotic factors of the sites and habitat suitability (Banks et al. 2015). However, accounting for the intricate interactions between and amongst species, sites and dispersal pathways when prioritising the management of biological invasion can be challenging. Depending on the spatial scale of the study, the importance of the aforementioned factors will vary (Pyšek et al. 2011b). For example, at the regional scale, the likelihood of spread of invasive terrestrial plants will depend more on the dispersal pathway of introductions rather than their traits (Lloret et al. 2004).

In practice, it is challenging to accurately determine the invasion stage of an introduced exotic species and practitioners take management actions based on the resolution of available information at the time of decision making (Table 2) (Fig. 2). In the following sections, we present the different types of information often available to practitioners. Furthermore, we introduce how network approaches can be used on the different resolution types of information to get a better understanding of human-mediated dispersal of exotic species.

Table 2 Resolution of data collected when assessing the risk of biological invasion

| Foci	Surrogate data	Coarse grained data	Fine grained data
Species	Global distribution of species and/or presence of species in neighbouring countries. Taxonomic/Functional group of species	Presence-Absence at different sites	Inventory data at different time stamps. Abundance and distribution of species in invaded and non-invaded locations. Measured traits of species: morphometrics such as width, length and height, offspring size, body size of individuals. Biology of species: life stages, thermal development times, mobility, trophic or parasitic interactions
Sites	Spatial proximity of sites to facilities such as roads, trails, cities. Level of management carried out at site	Category of site: human settlement/ recreational site/ protected area/ agricultural areas	Geolocation, environmental parameters such as micro-climate of site determining its habitat suitability
Pathways	Proxy of frequency path use (e.g. trade, transport or tourism)	Transparency of dispersal pathway: intentional or unintentional	Identity: point of entry, source (contaminant or stowaway) or pathway; Frequency of use: identify species and the number of individuals introduced or relative population size of the introduced species
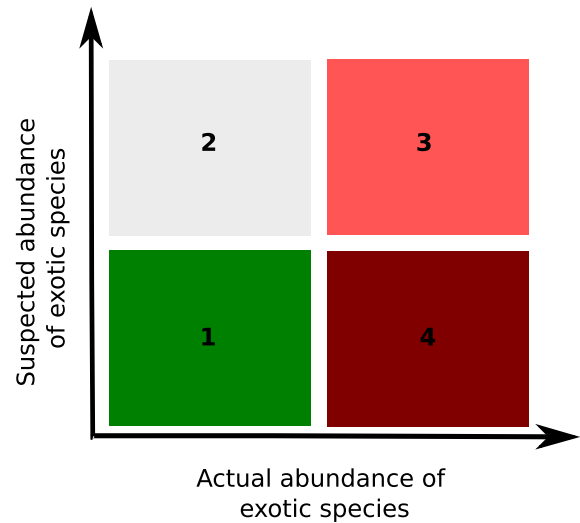
Fig. 2 Information available at the time of decision making. When data on the actual spread of the exotic species is available, practitioners take adequate measures to either eradicate the exotic species or actively manage it to prevent or mitigate further impacts (Case 1 and 3). When data on the actual spread of the given exotic species is fuzzy, practitioners *falsely* assume the exotic species to *be* a threat, hence overestimate its actual spread. This leads to disproportionate management actions being taken (Case 2). Eradication of the exotic species is possible in cases 1, 2 and 3. When data on the actual spread of the given exotic species is fuzzy, practitioners *falsely* assume the exotic species to *not* be a threat, hence underestimate its actual spread (Case 4). Incorrect management actions are taken. The exotic species is not detected until it spreads across numerous sites, reactive management might be required causing an increase in the cost of control (Case 4)

What current data are available for risk assessments?

Ideally, if we had information on the true occupancy of the exotic species and its mode of dispersion, or the human-mediated paths through which it is spread, we would be able to both make an accurate assessment of the invasion stage and predict the likelihood for the species to spread. However, such information is not always available. Hence, practitioners focus on assessing the area the exotic species occupies by collecting information on the *exotic species*, the *sites* at which they were identified and the likely human-mediated *dispersal pathways* through which they might have been spread.

During pre-border RA, the exotic species is presumed to be absent from the given site, and there might be limited information about the exotic species. Therefore, the

main focus at the pre-border level is to extract information from relevant research literature, databases and reports from areas where the target species is native or has established to determine whether the exotic species could be a potential threat (Pheloung et al. 1999; Burne 2019). To further assess the likelihood of entry of the species at a given site, the global spatial distribution of the exotic species can also be extracted from global databases such as Global Biodiversity Information Facility (Global Biodiversity Information Facility 2020). To identify whether the target exotic species has been catalogued as invasive in neighbouring areas or worldwide, data can be extracted from the IUCN's Global Invasive Species Database (Lowe et al. 2000) or the Centre for Agriculture and Bioscience International (CABI 2020), among others.

However during post-border RA, the exotic species has been identified at a given recipient site, and we can thus assume that some information is available on the species. As a starting point, a taxonomic assessment is carried out to gather information on the biological attributes on the species. When the identity of the species is unknown, and limited information is available, it can be identified at the lowest taxonomic level. Following this, practitioners assess the potential impacts of the exotic species in the new area by assuming that the target exotic species will behave in a similar fashion to its closest relatives in the post-border site. For instance, they may assume that the target exotic species will have shared similarities in terms of its biological attributes, mode of reproduction and dispersal. On the other hand, if the identity of the species is known, further information of the species acting as an invasive species will be extracted from databases (e.g. CABI (CABI 2020) or Chinese National Knowledge Infrastructure (CNKI) (Chinese National Knowledge Infrastructure 2021)) to assess the potential impact of the target species on the native biota.

To monitor the presence of an exotic species at the site level, the most common data at this stage is inventory data. This includes presence–absence data, but in some cases, further information such as the exotic species' phenology—i.e. periodic biological phenomena in species life cycles—is also available. For a plant species, for example, this might include information about the successive stages of their ontogeny. Such information would include identifying whether the individual identified is a seedling, sapling or mature; or their reproductive state. Finally, the abundance of the population of the exotic species at that given site is recorded. To characterise local or regional site(s), environmental parameters defining the climatic condition such as the temperature, relative humidity, level nutrients in the soil are sometimes gathered. Such data are also often used to determine the suitability of the different sites to sustain a population of the exotic species using species distribution models and variants (Elith and Leathwick 2009; Pollock et al. 2014; Torres et al. 2018). In some cases, proxies of the suitability of a given site are determined by the level of environmental protection (e.g. recreational activities undertaken by tourists or agriculture).

If the exotic species was previously identified as a potential threat, as a result of a pre-border risk assessment, an initial risk score is already available for the different potential dispersal pathways. For example, practitioners could potentially distinguish whether it is likely to hitch-hike on commodities, as opposed to be dispersed via soil, vehicles or people, solely basing on the size, weight, or hairs on the seeds (Pickering and Mount 2010; Ansong and Pickering 2013; Anderson et al. 2014). Moreover, the rate or frequency of use of different pathways is sometimes recorded. Following this, interception data—information about the number of viable seeds, pathogens or other foreign material present in the soil—can also be collected along the high risk pathways as in McNeill et al. (2011). Conversely, if the exotic species is not listed as a potential threat in the recipient site, the identity of the human-mediated dispersal pathways will probably be unknown.

How can network analysis be used for risk assessments?

Network science (refer to Box 1) provides an integrative approach for visualising, quantifying and predicting the risks of biological invasion (Keller et al. 2011; Moslonka-Lefebvre et al. 2012; Paini and Yemshanov 2012; Banks et al. 2015; Frost et al. 2019). Despite

being extensively used to study ecological networks to provide a better understanding of ecosystem functioning (Bascompte et al. 2003; Janssen et al. 2006; Blüthgen et al. 2006; Bascompte and Jordano 2007; Fath and Halnes 2007; Stouffer and Bascompte 2011; Poisot et al. 2016) or disease spread in epidemiology (Meyers et al. 2005; Balcan et al. 2009a), its application to understand the spread of exotic species is more recent (Haak et al. 2017; Drake et al. 2017b, a; Perry et al. 2017). In the context of biological invasion, network analysis has been shown to be particularly useful as a predictive tool by assisting biosecurity practitioners in: (1) Assessing the likelihood for exotic species to enter a given area or spread Seebens et al. 2013; Runghen et al. 2021; (2) Identifying and predicting sites which are likely to promote the entry or spread of exotic species to secondary sites Colautti et al. 2006; Floerl et al. 2009; (3) Identifying and evaluating the contribution of different dispersal pathways to the spread of exotic species—i.e. characterise the different routes to identify sites which could act as hotspots to disperse invasive species (Floerl et al. 2009; Gallardo et al. 2012; Seebens et al. 2013; Letschert et al. 2021). Even when not used as a predictive tool, network analysis can potentially help practitioners to hypothesise how an exotic species might be or has been introduced, or describe the spread of an exotic species. However, one should be cautious about such projections as the identified potential hotspots of exotic species can be subject to a high level of uncertainty. In this section, we further

develop how one could use routinely collected data to study human-mediated dispersal of exotic species to: (1) Generate a human-mediated dispersal network, (2) Use network metrics to understand the dispersal of exotic species and (3) Use probabilistic generative network models to both understand and predict human-mediated dispersal of exotic species.

Representing data as human-mediated dispersal networks

Depending on the type and resolution of data available (Box 1, Table 2, Fig. 3), different network representations can be used. Note that beyond the network representation, data resolution will also determine the accuracy of the human-mediated dispersal network. As a direct consequence, such information might limit the practitioner's ability to predict or describe the invasion process. For instance, it is important to include weighted information (as opposed to unweighted information, Box 1) to realistically represent the actual network and extract relevant information from its analysis (Poisot et al. 2015; Kéry and Schmidt 2008). However, uncertainties might arise when gathering information on the species, sites identified to be impacted by the exotic species and dispersal pathways to build the human-mediated dispersal network (Table 3). Hence depending on the aim of the practitioner (Table 1) and data resolution available, network analysis can be exploited to attempt to answer them.

Box 1: Glossary

What are networks?

Nodes: Components of a system. In the context of human-mediated dispersal networks, individuals, exotic species, taxonomic or functional groups, sites or humans can be represented as different sets of nodes.

Links or edges: Representatives of interactions or connections between nodes.

Weighted or unweighted links: Weighted data give quantitative information about the strength of interactions. It can include, for instance, the frequency at which a place is visited, the geographic distance between trade places (Büttner and Krieter 2018) or the propagule pressure (Wonham et al. 2013).In contrast to weighted networks, unweighted data exclusively consider whether an interaction between two nodes is present or absent (Newman and Girvan 2004).

Directed or undirected links: Directed links run in one direction (Newman and Girvan 2004), such as a trade network where merchants sell goods to purchasers, but the reverse interaction is unlikely true. On the other hand, undirected links depict a two-way relationship between nodes (Newman and Girvan 2004) or in some cases the lack of directional data. Such undirected links can be symmetric or asymmetric, depending on whether or not the nodes are equally dependent on each other (Bascompte et al. 2006). In the context of a human-mediated dispersal network, more specifically a unipartite site–site network, accounting for the directionality of links (when available) in the network is important as this would determine whether or not a certain site would receive an exotic species. More importantly, this could help in determining the rate of spread of an exotic species from and to a given site (Banks et al. 2015).

Networks (or graphs): Set of nodes that interact. Networks are commonly used to represent and understand large amounts of interactions in different natural and non-natural systems (Newman 2010).In the context of human-mediated dispersal of exotic species nodes are connected through human actions such as transportation routes of goods (Floerl et al. 2009; Kaluza et al. 2010; Keller et al. 2011; Letschert et al. 2021) or travelling patterns of people (Runghen et al. 2021).

Network topology: The way links are distributed between and across nodes (Bullock et al. 2018). Note that it is also sometimes referred to as "network structure".

Unipartite network: Set of nodes of the same type that are linked (Fig. 3). For example, canals and roads connect sites (nodes of the same type) (Bullock et al. 2018).

Bipartite network: Set of nodes of two types that are linked (Fig. 3), but where only links between the different type are allowed. For example, nodes can represent visitors and sites (nodes of two types) linked by trips (Runghen et al. 2021).

Descriptors of network topology

Note that network topology descriptors are particularly crucial in the context of human-mediated dispersal networks as they determine which site is more likely to receive exotic species, or even rate of spread of exotic species (Banks et al. 2015).

Connectance: It indicates the proportion of realised interactions among all possible nodes (Olesen and Jordano 2002). For example, a visitor–site bipartite network where many visitors visit many sites is more connected than a visitor–site bipartite network where visitors only visit a one or two places. As a result, one could assume that sites which are more connected are more likely to receive exotic species.

Modularity or Compartmentalisation: It evaluates if a network is composed of subsets, modules or compartments of nodes that interact more frequently among themselves than with other nodes of the network (Bascompte et al. 2003; Guimerà et al. 2010; Newman 2010; Stouffer and Bascompte 2011). For instance, in trade networks, local sites may represent compartments of a regional network. That would imply that trade is more common among local sites than between distant sites. As a result, dispersal of exotic species might be more likely to happen between local sites rather than distant ones.

Nestedness: It is the degree up to which the interacting assemblage of a node is a subset of the interacting assemblage of nodes with more interactions (Pires et al. 2014). For instance, in a species–site bipartite network, the extent of nestedness would describe the distribution of species across sites.
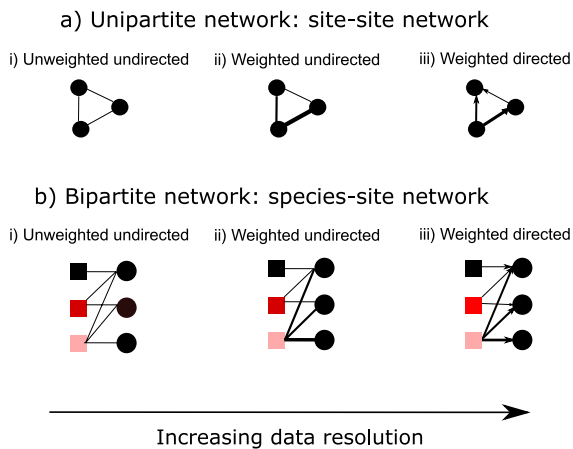
a) Unipartite network: site-site network

i) Unweighted undirected   ii) Weighted undirected   iii) Weighted directed

b) Bipartite network: species-site network

i) Unweighted undirected   ii) Weighted undirected   iii) Weighted directed

Increasing data resolution

Fig. 3 Using a network approach to study human-mediated dispersal of exotic species. Depending on the resolution of the data available (refer to Table 2), different network representations can be used to depict the human-mediated dispersal networks. a) The site–site network is a unipartite network (i.e. a network with one type of node). Here, nodes are sites and links represent types of interactions amongst the different sites (e.g. the frequency/rate of dispersal from one site to another). b) The species–site network is a bipartite network comprising nodes of two types: sites and species, and links occur only *between* the different types of nodes to represent the presence of the exotic species at the given site. Note that the types of interactions, represented as links, can be either: (1) Weighted or unweighted to represent the frequency/rate of path use, and (2) Directed or undirected, depending on the granularity of data available. For example, when presence–absence data of the exotic species at the different sites are available, an undirected unweighted network can be created. However, if the abundances of the species are also available, a weighted undirected network can be constructed. If data is also available on the direction of the movement of the exotic species, a directed network can be used. In the case of a species–site network, this would entail having information on the direction of movement of the host dispersing the exotic species to the various sites. As a result, this would enable one to identify the importance of the given sites in maintaining a source population of exotic species. Note though that the latter is more directly applicable to the case of unipartite site–site networks

Centrality: node-level descriptor. Relative importance of a node with respect to the other nodes in the network. The importance is measured according to the number of interactions of the focal node and the number of interactions of the nodes that interact with the focal node (Opsahl et al. 2010). For instance, sites that have many and strong connections to other sites are important to maintain the global network structure and then have a high centrality value. In the context of a

human-mediated dispersal network, this would imply that the site would be an important source of exotic species.

If the practitioners only had data on the dispersal paths and the sites where the exotic species was identified, they could represent the potential human-mediated pathways as links between nodes through which exotic species disperse (Banks et al. 2015). As such, the human-mediated dispersal network is represented as a unipartite network (Box 1). Nodes would represent the sites and the links would represent the dispersal paths connecting the sites (Fig. 3). Additionally, practitioners can attribute weights to the links in the network representation of the dispersal pathways to better understand the contribution of each pathway to dispersing the exotic species if information of the intensity of the different paths were also available.

Similarly, if data were to be available on either the exotic species or the vector, and the sites at which the exotic species were or could be dispersed, a bipartite network could be generated. The vector–site network (or species–site network) would thus have vectors (or species) represented as a set of nodes and sites represented as another set of nodes. Links in such networks would represent the paths through which the exotic species would be dispersed either directly (Runghen et al. 2021) or indirectly (Drake et al. 2017a; Bullock et al. 2018). Note that direct dispersal of exotic species includes the introduction and/or spread of exotic species either intentionally or unintentionally by a dispersal vector via trade and transportation networks (Hulme 2011b; Banks et al. 2015; Runghen et al. 2021). Indirect dispersal of exotic species, on the other hand, might arise as a consequence of anthropogenic disruption of the environment or the unintended management such as through habitat improvements (Drake et al. 2017a; Bullock et al. 2018) which facilitate the dispersal of exotic species. The latter is often referred as human-altered dispersal (Bullock et al. 2018). To depict the indirect dispersal of exotic species, spatial networks are often used (Banks et al. 2015). For instance, Bullock et al. (2018) represented a metacommunity where habitat patches represented a set of nodes and links represented the different

Table 3 Uncertainties associated with available information when building a human-mediated dispersal network

Network accuracy	Pre-border level	Post-border level
High	The identity of the potential exotic species is known, practitioners have information about the potential dispersal routes through which the exotic species might be spread, hence they can identify potential entry sites	Both the sites occupied by the exotic species and the dispersal paths are known
Sufficient	The identity of the exotic species is known, hence using the biological attributes of the exotic species practitioners can infer potential dispersal paths through which the exotic species is more likely to be spread	Species identity and occupied sites are known, the potential dispersal paths are unknown, hence we can identify dispersal routes basing on the biological attributes of the species
Limited	The exact identity of the potential exotic species is unknown, but using ongoing socio-economic activities in a given area practitioners can identify some potential dispersal paths	Both the occupied sites and the dispersal paths are unknown or partially known based on the biological attributes of the exotic species

infrastructures through which the exotic species would be dispersed.

Using network metrics to describe and understand interactions in human-mediated dispersal networks

Interactions in human-mediated dispersal networks are not random. Several regularities which can either promote or hamper the dispersal of exotic species have been found (Chivers and Leung 2012; Kaiser-Bunbury and Blüthgen 2015). Assessing the degree of these regularities, that is to measure the descriptors of the *network topology* (Box 1), allows us to quantify how the different nodes interact among themselves and to predict the likely spread of exotic species (Banks et al. 2015). Due to the wide range of network metrics, choosing metrics which are more likely to be of particular importance in the context of human-mediated dispersal networks can be overwhelming and challenging. That said, as topological network measures are interpretable, one can select measures which can enable us to understand how and why certain sites or groups of sites are more likely to be connected with one another, and thus potentially at risk of invasion. For instance, if we identify potential areas at risk of biological invasion caused by trade, we can represent the trade data as a dispersal vector–site bipartite network (Box 1). By doing so, this would enable one to assess the likelihood for each site to act as a source of exotic species (Dormann et al. 2009). Simultaneously, it would also allow one to get a better understanding of the extent to which the dispersal vector might be contributing to the dispersal of exotic species into the visiting site. As we expect neighbouring sites to be visited by similar dispersal vectors, the similarity in vectors that visit a given set of sites is expected to decay with distance. Therefore, by measuring the *connectance* (Olesen and Jordano 2002), *nestedness* (Pires et al. 2014) and *compartmentalisation* or *modularity* (Bascompte et al. 2003; Guimerà et al. 2010; Newman 2010; Stouffer and Bascompte 2011) of a dispersal vector–site network, we can quantify the likelihood of a site to be invaded and hence measure the rate of spread of an exotic species (Hui et al. 2016) (see Banks et al. (2015) and Frost et al. (2019) for further details on the
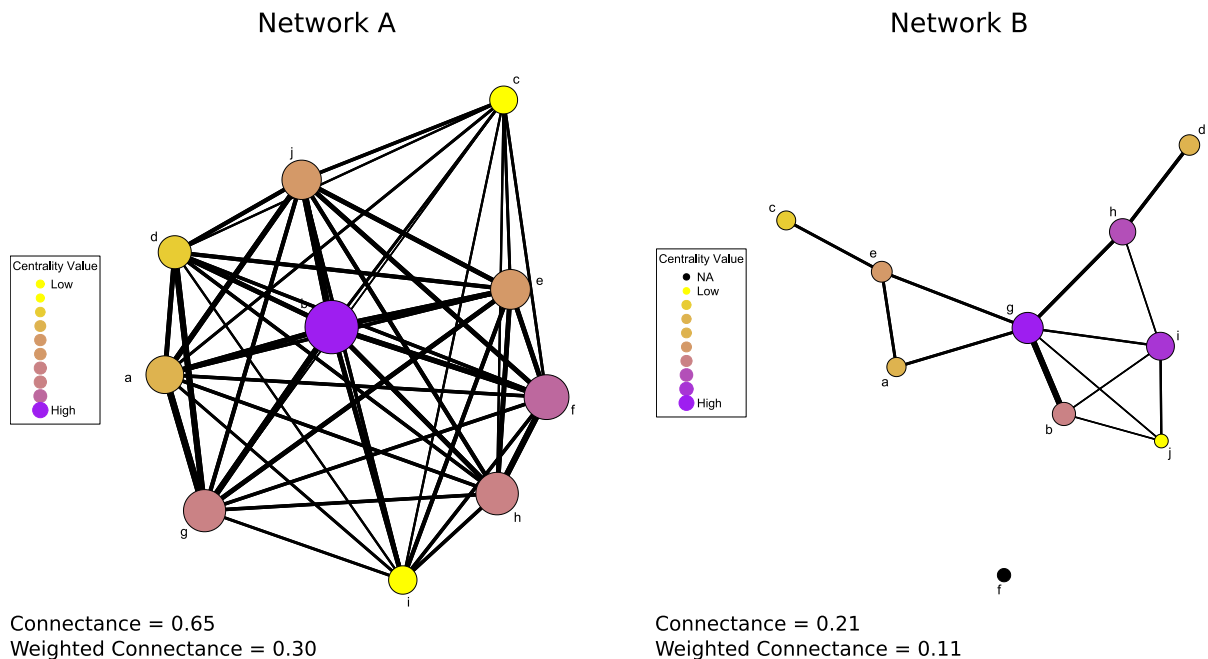
Fig. 4 Using network metrics to describe human-mediated dispersal of exotic species using weighted networks. Nodes represent sites and links represent connecting paths between the sites through which exotic species are dispersed. Network A represents a human-mediated dispersal network with nodes having predominantly a high closeness centrality value (represented in purple). Network B represents a network with nodes having a low closeness centrality value (represented in yellow) or being disconnected from other nodes, then no centrality can be measured (represented in black). As such, sites in Network A are closer and more highly connected to one another (Connectance = 0.65) compared to sites in Network B (Con-

nectance = 0.21). From a biological invasion perspective, one can expect that overall Network A is more likely to be at risk of rapid spread of invasion between sites compared to the more poorly connected Network B. When looking at each individual network, we can see that site b in Network A and site g in Network B both have a high closeness centrality values in their respective human-mediated dispersal networks. Hence, these sites are expected to act as hubs—i.e. sources and sinks of exotic species. As a consequence, sites connected to highly connected sites are also suspected to be at risk of biological invasion. Note that the strength of flow between sites is proportional to the width of the links

interpretation and/or implication of different network metrics in the context of biological invasion).

In addition to the measures of whole network topology, node-level measures provide information on the role of each node depending on their links to other nodes. The centrality value (Fig. 4) of a node indicates whether it has a central role. A high centrality value indicates that a node is connected to many others and that the node might act as a potential hub for the dispersal of exotic species (Banks et al. 2015). On the contrary, if the node has a low centrality value, it will be connected to a few other nodes and be of minimal role in the dispersal of exotic species (Fig. 4) (Opsahl et al. 2010). For example, Floerl et al. (2009) characterised ship movements from survey data and simulated the

trajectory of invasion from sites ranging from busy to less busy. In their network approach, Floerl et al. (2009) categorised sites (primary hubs or bridgehead sites) as nodes linked by sailing craft, which are recognised as one of the dispersal pathways of marine fouling communities. Their simulations showed that busy marinas were more likely to be affected by exotic species. However, both less frequented and busy marinas also acted as bridgehead sites, further contributing to the spread of exotic species. Another study based on the links between marine sites through water-borne traffic found that marine protected areas were at risk of marine invasion as recreational vessels were connecting them to already supporting invasive marine species (Iacarella et al. 2020). The authors characterised the ship movement data and used the Wetted Surface

Areas—i.e. the part of the vessel submerged in water—as a proxy to parametrise the dispersal risk (Iacarella et al. 2020). From a management perspective, insights resulting from this research could enable practitioners to identify and monitor potential sites at risk of human-mediated dispersal of exotic species and to design and implement cost-effective management plans.

Null models can also help us to distinguish whether the observed topology and node properties occur at random or not (Bascompte et al. 2003; Fortuna and Bascompte 2006; Delmas et al. 2019; Bramon Mora et al. 2019). Null models provide a robust approach to statistically compare measures of the observed network against measures estimated from randomised networks (Fortuna et al. 2010). For example, if a network is more modular than randomly expected, one can infer that the spread of an exotic species will be limited because compartmentalisation will minimise its spread (Lurgi et al. 2014). To summarise, the description of human-mediated dispersal networks can enable biosecurity practitioners to preemptively identify how *nodes* or *dispersal pathways* can impact the dispersal of exotic species in different ecological communities (Fig. 3).

Using probabilistic network models to make inferences about human-mediated dispersal networks

Besides network measures and null models, probabilistic generative network models can also be used to describe how nodes or groups of nodes interact with one another in networks. Probabilistic network models include models from the families of Stochastic Block Models (Wang and Wong 1987; Airoldi et al. 2008), Latent Position Models (Holland et al. 1983; Hoff et al. 2002; Athreya et al. 2017), and other process-based models such as Susceptible-Infected-Recovered models commonly used in epidemiology, and niche models used in community ecology (Williams and Martinez 2000; Bansal et al. 2007; Balcan et al. 2009a, b). More generally, probabilistic generative network models allow their users to make inferences and generate hypothesis. For example, in the context of managing biological invasion, such models would allow practitioners to understand how much a suspected dispersal vector could be contributing to the observed abundance of exotic species at a particular site. As such, probabilistic generative network models could be both used to preemptively identify potential hotspots of exotic species and understand how existing sites/dispersal vectors could further contribute to the spread of exotic species at other sites. To understand the generative process behind observed data, various assumptions on how the data were generated would be used. In the context of the human-mediated dispersal of exotic species, that would equate to reconstructing the human-mediated dispersal network based on some assumptions describing the potential mechanisms generating the observed data.

Such an application of network analysis was recently adopted in Runghen et al. (2021). In this study, a Mixed Membership Stochastic Block Model (MMSBM, from the family of Stochastic Block Models) was used to understand visitors' travelling patterns within New Zealand. From a data perspective, no specific information was known about focal exotic species, however visitors were previously identified as potential vectors dispersing exotic species within New Zealand (McNeill et al. 2011). The authors represented the visitation data as a bipartite network: a visitor–site network, where visitors represented one set of nodes and sites represented the other set of nodes. Links in the visitor–site network represented the trips of a given visitor to a given site. The authors used the MMSBM to characterise the travelling patterns of the visitors. The main objective was to get a general understanding of how people tended to travel. So, if visitors were to disperse exotic species, we could identify potential areas at risk of visitor-mediated dispersal. Overall, the authors showed that based on the different visitor–site interactions observed, the MMSBM identified groups of visitors and sites—indicating that people do have characteristic behaviours when they travel in New Zealand. From a human-mediated dispersal point of view, this implied that certain visitor groups would be more likely to contribute to the dispersal of exotic species than others within the country. As a result, Runghen et al. (2021) showed that by using only data on the visitation data—i.e.

the travelling visitors who acted as the unintended vector dispersing exotic species, potential areas at risk of biological invasion were identified. In this particular case, the authors showed that practitioners could use such network models as a tool to characterise the behaviour of vectors to both understand, and, finally, predict the dispersal vectors' contribution in dispersing exotic species. Practitioners could further use this understanding to preemptively identify potential ecological and economic areas which are at risk of human-mediated dispersal.

As highlighted in Fig. 2, the level of uncertainty in the data collected can be particularly high. That said, in most cases, some assumptions either on the potential vector dispersing the exotic species, the target exotic species or even the sites which might be more at risk are known. Hence, by exploiting these assumptions, probabilistic generative network models can further help practitioners as highlighted in above example. For example at the pre-border level, using probabilistic network models can be particularly important, especially in cases 1 and 2 (Fig. 2)—i.e. where the target exotic species are not yet identified or when there is limited information regarding the dispersal routes of exotic species and their potential vectors. At the post-border level, these models could be used to further identify potential sites which are likely to be impacted by biological invasion based on the current behaviour of the dispersal vector. More importantly, such models can help practitioners to get a better understanding of the different dispersal mechanisms of exotic species, or even identify the relative contribution of different potential dispersal pathways.

Future directions

From a management perspective, accurately assessing whether an exotic species has arrived or entered at a site requires having fine-grained data about the exotic species, the sites occupied by them, and finally the different dispersal routes through which the exotic species are spread (McGeoch et al. 2016). However, in most cases knowing whether an exotic species has entered a site or not is challenging to assess. Even if the species has been identified, estimates of the areas where the species is present are not necessarily available to the

biosecurity managers. Here, we highlight how network analyses were used and could be used to give an insight of the potential spread of exotic species in various systems where the ideal data sets are not available.

For instance, Runghen et al. (2021) exploited presence-absence data, which are amongst the most common data readily available to assess the unintended spread of exotic species in protected areas solely based on their travelling patterns at a regional scale. Floerl et al. (2009) and Iacarella et al. (2020) both exploit ship movement data as proxies indicating the risk associated to different dispersal pathways to assess the likelihood of vessels contributing to the dispersal of exotic species associated with marine fouling communities. These studies highlight that despite only low resolution data, they provided insights of potential primary and/or secondary sources of exotic species.

Alternatively, results from network analysis could be combined with other models to get a better overview of human-mediated dispersal of exotic species. For example, Letschert et al. (2021) used network analysis to characterise the movement of ships together with a numeric model inspired by Seebens et al. (2013) to quantify the species' dispersal capacities. The network analysis undertaken by Letschert et al. (2021) also provided the opportunity to develop different preventive and precautionary measures for exotic marine species under different scenarios. Similarly, such models could be extended to other taxa, or in completely different systems to reduce the risk of spread of exotic species even if conditions such as environmental, climatic or even changes in the vector's behaviour would occur. Likewise, just because a vector *could* spread an exotic species, it does not imply that the species will be able to successfully establish. The establishment will depend on the biotic and abiotic conditions at the point at which the propagule is deposited. Consequently, combining results from network analysis and other habitat suitability models would be valuable to determine the potential risk of spread of species, especially in the current context of climate change.

Moving forward, it is vital to collect fine scale data to refine the predictive power of existing tools—e.g. at the level of terrestrial protected areas in the case of visitation data in Runghen et al. (2021) and individual characteristics of vessels in the context of movement of ballast water to make more accurate predictions in the case of Iacarella et al. (2020). The

access to temporal and spatially replicated field data is key to help practitioners to prioritise the management of exotic species Dauer et al. (2007). Therefore, best practices should include monitoring sites along the different trade and/or transportation networks and points of entry which are potentially identified as hotspots of exotic species. For instance, if additional information were to be available, such as the abundance of species at different monitoring sites, the frequency/rate along a particular dispersal pathway, the direction taken by dispersal vectors, traits of exotic species and characteristics of recipient sites, different variants of the probabilistic network models (such as the family Stochastic Block Models and Latent Position Models previously mentioned) could be used (Sweet 2015; Newman and Clauset 2016; Roy et al. 2019; Mele et al. 2019; Peixoto 2018). By using such models, better understanding of the dispersal or spread of exotic species could be achieved. Hence, it could help to validate predictions and hypotheses proposed prior to an exotic species arriving at a site.

In addition to fine scale data, it is crucial to account for the dynamics of networks which can further make assessing and predicting human-mediated dispersal of exotic species to be even more challenging. For example, the construction of roads and tracks to increase accessibility to remote places within a country or the increasing popularity of particular destinations due to social media can influence preferences and the travel pathways taken by humans (Doscher et al. 2011; Moore et al. 2012; Miller et al. 2019). Such dynamics lead to continuous changes in the network topology, and therefore a modification of dispersal pathways for exotic species across the network. Moreover, processes happening within a system at a given level can also affect the different sets of interactions in different networks. For example, a change in national or local government policy might impact the transportation of goods within a country, resulting in a change in dispersal rates of an exotic species. Such complex data could be analysed using a multilayer network approach. By representing the data as a multilayer network, it allows us to consider several networks of the same type as layers and to study them as connected by interlinks (Hutchinson et al. 2019). This approach can also be relevant when analysing temporal data, for instance, to study the network structure after the arrival of an exotic species across time periods, since two layers will be linked by their common species.

Concluding remarks

Accounting for intricate interactions between and amongst species, sites and dispersal pathways when prioritising the management of invasive species can be challenging. Traditionally, risk assessments focused on the identification and likely impacts of potential invasive species and the subsequent monitoring of these species or their vectors. Propagule pressure is often neglected during the early detection phase. With the increase of transportation and trade networks, there is also an increase in both short and long distance dispersal and complexity of networks which causes an increase in the introduction rate of exotics. Unlike natural dispersal, human-mediated movement is mostly governed by socioeconomic activities (Banks et al. 2015). Hence, risk assessments of invasive exotic species spread must also account for the different transportation networks when estimating the likelihood of successful invasion. Though different models are currently available to predict biological invasion for management purposes, they do not always account for long distance dispersal induced by human-mediated dispersal (Hastings et al. 2005; Chivers and Leung 2012). In this regard, network analysis represents a promising tool as it provides an integrative approach for visualising, quantifying and predicting the risks of biological invasions (Keller et al. 2011; Moslonka-Lefebvre et al. 2012; Paini and Yemshanov 2012; Floerl et al. 2009; Banks et al. 2015; Frost et al. 2019). The use of network tools to study biological invasion is recent (Keller et al. 2011; Frost et al. 2019; Hui and Richardson 2019), especially in the context of managing biological invasion (Floerl et al. 2009; Letschert et al. 2021). From a management point of view, practitioners have developed various risk-assessment tools to prevent, control and eradicate biological invasion. To ensure that management plans are working smoothly, monitoring is constantly carried out to assess the effectiveness of their protocols. Here, we detail how network analysis can be used both as a risk assessment and monitoring tool throughout the different phases of invasion. Due to high flexibility in dealing with different types of data and its proxies, we hope that more practitioners will adopt network analysis for management purposes.

Declarations

Conflict of interest The authors have not disclosed any conflict of interests.

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