Crossing frontiers in tackling pathways of biological invasions

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Abstract

Substantial progress has been made in understanding how pathways underlie and mediate biological invasions. Yet, key features of their role in invasions remain poorly understood, available knowledge is widely scattered, and major frontiers in research and management are insufficiently characterized. We review the state of the art, highlight recent advances, identify pitfalls and constraints, and discuss major challenges in four broad fields of pathway research and management: pathway classification, application of pathway information, management response, and management impact. We present approaches to describe and quantify pathway attributes (e.g. spatio-temporal changes, proxies of introduction effort, environmental and socio-economic contexts) and how they interact with species traits and regional characteristics. We also provide recommendations for a research agenda with particular focus on emerging (or neglected) research questions, and present new analytical tools in the context of pathway research and management.

Keywords: alien species, biological invasions, impact, management, propagule pressure

1. Introduction

Invasions of alien species begin with the human-assisted movement of living individuals or propagules across biogeographic barriers (Blackburn et al. 2011). The accelerating world-wide movement of people and goods is driving the increasing rate at which biological invasions are occurring (e.g. Essl et al. 2011; Seebens et al. 2013). As a result, the contributions of specific pathways – i.e. "*any means that allows the entry or spread of an […] alien species*" into a region (FAO 2007) – to introduction and subsequent invasion, and the changes in the importance of pathways over time, are receiving increasing attention from scientists and policymakers (e.g. EC 2011; CBD 2014). Information on pathways is fundamental to alien species risk assessments, management, monitoring and surveillance (e.g. Clout & Williams 2009; Simberloff & Rejmanek 2011). For example, prevention strategies that consider pathways together with protocols focused on individual taxa are essential for reducing the arrival of new and damaging species in a particular region (e.g. Keller et al. 2009). To aid these efforts, a standardized pathway terminology and classification has been proposed (Hulme et al. 2008), and additional work has contributed to a better understanding of socio-economic and other factors that affect the dissemination of propagules to and within new regions (Wilson et al. 2009).

Despite recent advances in the understanding of pathways, key features of their role in invasions remain poorly understood, available knowledge is widely scattered, and major frontiers in research and management are insufficiently characterized. However, the urgency of implementing improved policies calls for the re-evaluation of strengths and gaps in current approaches. Here, we address four key issues concerning research and management of introduction pathways: pathway classification, application of pathway information, management response, and management impact (Tables 1, 2). For each issue, we outline priorities for research and their implications for policy, and we focus on factors that affect the likelihood of entry and spread of alien species in a region.

2. Pathway classification

2.1 Apply consistent pathway classification, hierarchy and terminology

An invasion pathway includes both the vector(s) that carries an organism and the route along which it travels (Carlton & Ruiz 2005). The multitude of potential pathways clustered within broad transport or commerce categories (Lodge et al. 2006) has galvanized considerable effort to classify and aggregate them. One approach has been to look at the dispersal events themselves, defining events in terms of the consequences for the organisms moved (see Appendix S1). This can provide useful insights, e.g. highlighting differences between historical natural dispersal and human-mediated dispersal (Wilson et al. 2009), but it is often hard to translate such insights into management action. The other main approach is to focus on how pathways can be regulated and managed to enhance prevention of invasions. Most basically, pathways can be distinguished either by whether they are deliberate (intentional) or accidental (unintentional), and/or in terms of the introduction mechanism: 1) importation of a commodity, 2) arrival of a transport vector, or 3) natural spread from a region where the species is itself alien. These mechanisms can be divided into five pathways of introduction (release, escape, contaminant, stowaway, corridor), and an additional category (unaided), to describe the natural spread of a species after its initial introduction into another territory (Hulme et al. 2008).

These six categories defined by Hulme et al. (2008) have been further modified and developed into a hierarchical pathway classification, which was adopted by the Convention on Biological Diversity (CBD 2014) (Appendix S2). This scheme was developed within the framework of the Global Invasive Alien Species Information Partnership (GIASIPartnership, http://giasipartnership.myspecies.info/), tested using major global (Global Invasive Species Database, GISD), regional (Europe: Delivering Alien Invasive Species Inventories for Europe, DAISIE) and national (Great Britain: Great Britain's Non Native Species Information Portal, GBNNSIP) databases. Pathway terminology has historically varied between alien species databases (Appendix S3), restricting comparisons across alien species data repositories (CBD 2014). The new scheme aims to address this. When compared, 99% of GISD data, 79% of DAISIE data and 81% of GBNNSIP data directly matched with the available categories of the pathway scheme. However, the pathway assignments that did not map directly onto the pathway scheme required additional interpretation, and in some cases the pathway terms within DAISIE and GBNNSIP spanned more than one term within the proposed scheme. Mapping pathways revealed that the relevance of pathways is scale-dependent. For instance, while escape is a dominant pathway at all scales, transport-contaminant is more important at smaller (national, European) scales than on the global scale.

The unaided pathway poses particular problems. In particular, dispersal barriers are species-specific as alien species with poor dispersal abilities may not be able to overcome obstacles such as large rivers and mountain ranges, which do not act as barriers for good dispersers. Thus, we propose limiting the application of this pathway to the spread from adjacent regions (countries, or states/provinces of large countries) and in the absence of evidence of human assistance.

Of course, the level of detail required in pathway classification will depend on the management goal. For instance, a pest-risk assessor may need quite detailed knowledge of the pathway attributes of an individual commodity, including the region of origin of the commodity, the potential level of infestation, the volume of potentially infested material imported and the maximum pest limit (the minimum number of individuals that could lead to establishment). The European Emergency Measure to ban the import of maple (*Acer*) plants (commodity) from China (origin) for several years provides an example of this approach (EC 2010). Based on the demonstrated risk associated with *Acer* imported from China (Van der Gaag et al. 2008), exporters were obliged to implement measures to prevent the contamination of transported *Acer* plants by the citrus long-horned beetle (*Anoplophora chinensis*). In contrast, quarantine officers inspecting goods at national borders require sufficient information to prioritize search efforts across commodities.

In summary, a hierarchical system of pathways that integrates higher level categories valuable for regulatory purposes (e.g. Hulme et al. 2008) with more detailed subcategories that may be more applicable to specific management (Lodge et al. 2006) seems to best serve the general purposes of inspection, regulation, decision-making, and responsible behavior (Appendix S2).

2.2 Account for uncertainties in pathway assessment and develop minimum harmonization standards

Assigning the entry or spread of alien species to specific pathways is subject to uncertainty; this is most problematic when introductions are unintentional and pathways may therefore be less well documented (e.g. contaminant, stowaway). For example, alien species in canals that connect previously isolated water catchments may travel outside (hull fouling) or inside (ballast water) ships (stowaway), or even travel on their own (corridor). Similarly, for alien species that are mostly introduced accidentally, such as terrestrial and marine invertebrates or pathogens, the exact pathway responsible for a particular introduction is usually unknown. In most alien species databases, these species are assigned post hoc by the assessor to the most likely introduction pathway(s), often based more on assumptions of the assessor, or from inference on the basis of a species' ecology, than on hard evidence. It would be desirable to make such uncertainties transparent, by providing an estimate of the uncertainty attached to the pathway assignment (e.g. Kenis et al. 2007; Bacon et al. 2012; Liebhold et al. 2012). In addition, vague or overlapping delineations of pathways may increase these uncertainties or introduce errors (USDA 2000). It is vital that pathways are defined so that different assessors apply them consistently. This can be achieved by providing guidelines on the delineation and interpretation of pathways (e.g. as a pathway manual, USDA 2000).

2.3 Quantify spatio-temporal changes of pathways

Spatio-temporal changes in pathways mean that the absolute number of species introduced via them changes over time, as do the proportions introduced among pathways (Hulme et al. 2008; Wilson et al. 2009; Liebhold et al. 2012). These fluctuations in the importance of pathways in space and time result from complex interactions between the environment and socio-economic factors (e.g. economic conditions, technology, consumer behavior, fashion, management interventions), traits of the species, the region of origin and recipient regions (e.g. cultural and socio-political ties between regions, means and routes of transport)

(Appendix S4) (Kraus 2009; Katsanevakis et al. 2013; Hulme 2014; Lenda et al. 2014). They imply that a given pathway may exhibit substantial temporal, geographic and taxonomic variation in importance (Figure 1) and undergo substantial changes in key attributes; it may thus differ in importance for the introduction of species that vary in functional traits or regions of origin.

Understanding the spatio-temporal variation in the importance of different pathways requires detailed information on the early stages of invasions (sensu Blackburn et al. 2011), because studies based on established or invasive species alone can give a biased view of the processes at work (e.g. Cassey et al. 2004). As bird introductions were historically well documented, they provide a useful example of the value of information on introduction pathways. Bird translocations accelerated rapidly after 1860 with the foundation of the first acclimatization societies (Blackburn et al. 2015). The changing drivers of translocation have had knock-on effects on the characteristics of species moved, and hence also on the characteristics of species introduced, the likelihood of establishment (Blackburn et al. 2009), and the global biogeography of birds.

3. Application of pathway information

3.1 Expand the taxonomic, environmental and geographic coverage of pathway assessments

To identify gaps in the taxonomic, geographic and environmental coverage of pathways in alien species data repositories, we compiled a list of 238 alien species databases ranging from subnational (e.g. islands, federal states) to global. In total, 196 of these databases were still available online in August 2014 (Appendix S3). The geographic coverage of the databases was uneven, with 16 databases having a global coverage; among the others, North America (n=78) and Europe (n=75) were most often (entirely or partly) covered, while Australia (n=15), Asia (n=10), South America (n=8), and Africa (n=7) comparatively less so (Figure

2c).

We found that, across environmental realms, a similar proportion (40-60%) of these databases provided information on introduction pathways for the majority of species included (Figure 2a). However, only 20% (terrestrial) to 36% (marine) of the databases consistently provided the rather basic distinction of intentional vs. unintentional introduction. The number and delineation of pathways varied considerably among databases, with a peak of 6-10 pathway categories for all environments (Figure 2b). In particular, there are only a few large-scale data sets that collated introduction pathways for many species in a standardized way. GISD has a global scope and uses a standardized pathway classification, but it covers a lower number of species (c. 2,500 species) than DAISIE, the European inventory of alien species, which covers more than 12,000 species and where pathways are recorded in a standardized way for c. 6,500 species (DAISIE 2014).

Finally, we note a paucity of detailed information on pathways in alien species databases. Supporting information on definitions for interpreting pathways was missing in 79% (marine) to 92% (terrestrial) of the databases included, and an assessment on temporal trends in pathways was missing in 95% (marine) to 97% (terrestrial) of the databases (Figure 2a). Furthermore, information on species for which multiple pathways are relevant was often poorly captured particularly with respect to the importance of each pathway.

3.2 Analyze and predict trends in pathways

Currently, many pathway studies do little more than describe the diverse routes by which alien species may have been introduced into a region. A major challenge to a predictive approach to invasion pathways is the quantitative assessment of the risk they pose in introducing or spreading harmful alien species (Pyšek et al. 2011). Ideally, several key variables would be needed to provide a more quantitative assessment of pathway risk (Hulme

2009): a) strength of association between species and commodity/vector/corridor at point of export; b) volume of the commodity/vector/corridor imported; c) frequency of importation; d) species survivorship and population growth during transport/storage; e) suitability of environment for species establishment in the importing region (e.g. climate matching); f) appropriateness of the time of year of importation for species establishment; g) ease of species detection within consignments/vectors/corridors; h) effectiveness of management measures e.g. fumigation, inspection regime; i) how widely the commodity/vector is subsequently distributed in the importing region; and j) likelihood of transfer from the commodity/vector/corridor to a suitable habitat. Such parameters are known for very few species, and even then only for quite specific pathways (Hulme 2014). If each species transported along a particular pathway has variable parameter values, scaling up pathways to address invasion patterns at the regional level becomes increasingly difficult. Consequently, much of the prediction of pathway risk relies on proxies for propagule pressure which may include coarse trade data on transport routes, commodity imports (e.g. volume of agricultural products imported), volume of specific commodities (e.g. nursery stock) or other measures of introduction effort (e.g. area planted).

Recent advances in satellite imagery and geographic information systems, together with improved availability of socio-economic data have allowed for the development of global-scale proxies of invasion pathways such as proximity to transport routes, bilateral trade, population density and human influence on ecosystems (Appendix S5). Utilizing such proxies, several studies have contributed to the quantification of pathways. For instance, a recent study demonstrated that the inclusion of proxies of propagule pressure in habitat suitability models increased predictive accuracy by 20% (Gallardo & Aldridge 2013). Using global shipping data, Seebens et al. (2013) analyzed the role of global ship traffic on marine invasions and found that most introduced species originate from sites of intermediate geographic distances to destination ports. Helmus et al. (2014) showed that the distribution of alien lizards (*Anolis* spp.) on Caribbean islands depends on the degree of economic isolation of these islands.

These findings suggest that carefully chosen and validated proxies of invasion pathways may provide a good reference to the likelihood of establishment and should be routinely integrated into predictive frameworks to inform geographically targeted policies for preventing and managing invasions. If this is not done, we might underestimate the species and areas with the highest invasion risk (Gallardo & Aldridge 2013). However, such quantification of the importance of specific pathways requires detailed data, which are not always available, especially for species that are introduced accidentally. Moreover, multiple introduction events, possibly through different pathways and from different locations, may complicate these predictions due to new genetic combinations that may arise from intraspecific hybridization (genetic 'admixture'), as illustrated by invasive populations of the Harlequin ladybird (*Harmonia axyridis*) in Europe (Lombaert et al. 2010).

3.3 Account for the interaction of pathways with impacts of invasions

Pathways of introduction are related to impacts of invasions in two ways. First, the number of individuals of a species transported and successfully introduced through a pathway will directly influence the impact associated with this pathway (Wilson et al. 2009). It is foreseeable that pathways carrying high quantities of alien species are more likely to introduce alien species that become established than pathways that carry low quantities (Lockwood et al. 2009). For example, if most alien plant pests and pathogens presently arrive through the live plant trade, it is because this trade has increased dramatically in recent years and because entire plants are able to carry high numbers of hidden pests and pathogens (Brasier 2008; Liebhold et al. 2012). Second, the impact of a pathway results from the impact of the individual alien species introduced by this pathway. Continuing with the plant pests example, wood and, especially, wooden packaging materials are responsible for the introduction of a few but very damaging wood-boring insects; in North America, these even have a higher impact on woody plants than the more numerous sap feeders and defoliators that are typically introduced by live plants (Aukema et al. 2011).

Interactions between pathways and the impacts of invasions are correlative rather than causative. Nevertheless, a better understanding of these interactions is essential because it informs management and regulation by providing a focus on the most threatening pathways, and by preventing the emergence of new high-risk pathways. So far, the relationship between pathways and impacts, or traits related to impact, has been poorly studied. Examples mentioned above and others (e.g. García-Berthou et al. 2005; van Wilgen et al. 2010; Evans et al. 2014) concern single taxonomic or functional groups of invaders. Cross-taxon analyses relating pathways and impact *per se* are much more complicated because they require reliable methods of comparing impact-levels across taxa. Such methods have been developed recently (e.g. Nentwig et al. 2010; Blackburn et al. 2014) but await validation at a large scale before they could be used reliably as tools for comparing impacts and pathways among taxa and environments. Furthermore, to develop preventive measures focusing on pathway management, assessments must not only consider broad pathway categories, but also specific vectors (e.g. commodities) and the ways that particular sectors/enterprises mediate dissemination within regions following introduction. In other words, while it is interesting to know that the live plant trade is an increasingly important vector of introduction for plant pests (Brasier 2008; Liebhold et al. 2012), from a management perspective it is more important to know which commodities from which regions provide the highest risks. Pathway/commodity/import risk assessments are increasingly being carried out, but their adoption strongly varies among sectors and, within sectors, among regions. Even in the well-regulated plant-health sector, variations are substantial: some countries implement a commodity risk assessment for all new importations (commodity × origin), while others still base their plant-health regulation on species-based pest risk assessments, applying commodity risk assessments on a casual basis.

3.4 Account for the interaction of environmental, socio-economic and management factors with pathways

Many socio-economic changes affect pathways (Appendix S1). Global trade is steadily increasing, and so is the general likelihood of new introductions worldwide (Figure 3a). However, trade routes are dynamic, and the transport of commodities from different regions of the world can result in very different pathway risks (Bacon et al. 2012). For example, imports of maize from the US resulted in the establishment of the Western Corn Rootworm (*Diabrotica virgifera*) in Europe (Miller et al. 2005), but imports from Argentina are free from this pest because the species is not established there. Changes in attributes of pathways (Appendix S1), trade agreements (or bans), trade regulations (e.g. border inspections), and consumer perceptions also contribute to shifts in the importance of pathways. For instance, most bilateral trade routes connect locations with similar climate, i.e. 50% of the world trade volume was exchanged during 2005 between countries with small differences in annual mean temperature ($\Delta T < 5°C$) and precipitation ($\Delta P < 300$ mm, Figure 3b, d). In the last sixty years, the average difference in annual mean temperatures between the largest trading partners (exchanging 50% of the world trade volume) decreased (Figure 3C), raising the likelihood that alien species find suitable climatic conditions in the recipient country. For mean annual precipitation, the pattern strongly fluctuates without any clear trend (Figure 3e). Changes in attributes of pathways (Appendix S1), trade agreements (or bans), trade regulations (e.g. border inspections), and consumer preferences also contribute to shifts in the importance of pathways.

Environmental changes can affect pathways directly, allowing faster transport of commodities and the connection of previously unconnected locations. A notable example is the melting of Arctic sea ice that has opened a cold-water trade route between Atlantic and Pacific ports, fostering the exchange of cold-adapted marine species between oceans that have been biogeographically separated for the last two million years. The new Arctic trade routes are expected to result in a large wave of new invasions to boreal and polar regions (Miller & Ruiz 2014). Environmental changes can also indirectly affect the relative importance of existing pathways (e.g. by changing land use), which in turn affects sensitivity to new invaders and opens new pathways for exporting pests.

Environmental and socio-economic changes may also act in concert. For example, the Suez Canal is the primary route of introduction of alien species into the Mediterranean. The movement of species through this canal has been facilitated by a combination of factors, primarily by the periodic enlargement of the Canal which, by the mid-20th century, had eliminated the salinity barrier posed by the Bitter Lakes that, for nearly a century, had limited the natural spread of alien species (Katsanevakis et al. 2013; Galil et al. 2014). Likewise, the doubling of the capacity of the Panama Canal (creating a new traffic lane and allowing more and bigger ships to transit), scheduled for completion in 2016, has important implications for the transfer and establishment of alien species (Galil et al. 2014; Muirhead et al. 2015).

4. Management response: pathway specific policy and enforcement

The importance of managing pathways as part of any strategy to reduce the escalation of biological invasions is widely acknowledged (e.g. Pyšek & Richardson 2010). Pathway management has been incorporated into the Aichi targets of the CBD, which have been widely adopted, e.g. by the EU in its ‘EU Biodiversity Strategy 2020’ (EC 2011). Pathway-specific policies most commonly have been implemented by animal and plant health authorities, primarily to reduce the damage caused by pests and diseases to livestock, aquaculture, fisheries, forestry, crops and plants for planting. Most pathway policies in this area relate to pest and disease contaminants of specific imported commodities (CBD 2014), although there has been a recent push to tackle other pathway types, for example the import of timber packaging (FAO 2009) and stowaways in containers (FAO 2010).

There are relatively few comprehensive pathway-focused policies at the international and regional level to reduce impacts on the wider environment and biodiversity (Hulme et al. 2008). Even at the national level, only a handful of countries have implemented introduction pathway policies comprehensively, with most others either having no or piecemeal policies (e.g. EC 2013). While animal and plant health policies are focused largely on contaminants, the range of pathways that introduce species harmful to biodiversity is broader, with escapes being the most common (CBD 2014). The policies that do exist are usually related to the release and escape pathways: in the EU, for example, most Member States have some provisions prohibiting the deliberate release of non-native species, i.e. 12 have import restrictions covering between 1 and 136 species, and 13 have restrictions on holding and keeping alien species (EC 2013).

Where international and regional pathway policies have been introduced for alien species outside of plant and animal health regimes, they are commonly based on voluntary codes and agreements (e.g. Simons & DePoorter 2009; CBD 2014), the effectiveness of which may not be particularly high (Hulme 2011). An important exception, once it comes into power, will be the International Convention for the Control and Management of Ships' Ballast Water and Sediments, which seeks to reduce the impacts of marine invasive alien stowaways by regulating the treatment of ballast water. However, despite work beginning in 1992, the convention was adopted only in 2004, and remains yet unratified (IMO 2014). These delays reflect the difficulty and complexity of implementing international, legally binding pathway policies. Nonetheless, the ballast water convention is one of the most substantial measures introduced to regulate an introduction pathway on environmental grounds.

The European Commission has adopted a new regulation to address the gaps in alien species regulation for the EU (EC 2014). It includes extensive provisions to prevent the keeping, sale and transport of specific species, suggesting a focus on the regulation of intentional release and escape pathways. Provision for unintentional pathways is less prescriptive, with general requirements to prioritize pathways and develop pathway action plans, with particular reference to voluntary actions and codes of good practice. Clearly, the near-abolition of border inspections between EU-countries will be a major challenge for regulating these pathways. Nevertheless, the regulation will represent a significant improvement in the coordination, implementation and consistency of pathway management across the EU. It is designed to complement plant and animal health regulations, including the aquaculture regulation (EC 2007), and it is important that it will be integrated with existing pathway management mechanisms in these areas where appropriate.

5. Management impact: are policy and management responses addressing pathways effective in reducing alien species accumulation?

Policies for pathway management aim to reduce rates of establishment of alien species (and ultimately impacts). Although it has been shown that strengthening alien species policies does provide net socio-economic benefits (Keller et al. 2007), it has proven difficult to demonstrate a direct link between a specific management implementation and subsequent changes in establishment rates (e.g. Fowler et al. 2007; Bacon et al. 2012; Liebhold et al. 2012). The reasons for this include the lack of baseline data on species introductions prior to the implementation of the measures and the gradual application of measures, in particular in the case of international treaties, which make before-after comparisons difficult. An example of gradual application is the national regulations on aquaculture that were enforced, based on agreed Codes of Conduct (e.g. ICES 2005), prior to acceptance of the EU Regulation concerning the use of alien and locally absent species in aquaculture (EC 2007). The apparent lack of evidence for the effectiveness of pathway management could also be attributed to the seemingly weak signal of impact of the new measures or regulations against the rapid increase in trade and transport volume, which is a major reason for the increasing number of alien species establishing.

Aquaculture has been a marine pathway for which important management measures have been taken (EC 2007). While the trend of new introductions by all other main marine pathways has been increasing, the incidence of new aquaculture-related introductions in Europe has clearly declined, suggesting the effectiveness of management measures (Katsanevakis et al. 2013). A few studies have also addressed the effect of regulation-driven changes in establishments through terrestrial pathways, including the reduced establishment rates for forest pests after the Plant Protection Acts were enacted in the USA and Canada in the 20th century (Roques 2010), and the adoption of ISPM 15 on the treatment of wooden packaging material (Haack et al. 2014). However, border inspection and interception data, upon which some of these studies are based, are only available for the few countries that keep detailed interception records, and these rarely cover the period prior to the policy change. Indeed, most inspection methods and interception data do not allow for thorough analysis (e.g. Bacon et al. 2012; Liebhold et al. 2012). Key reasons for the non-suitability of interception data are the unequal sample sizes, non-random sampling and the failure to record the inspections where no incursions were detected. Improved inspection data collection is therefore vital, and one example of appropriate inspection methodology and data collection is the Agricultural Quarantine Inspection Monitoring program (AQIM) in the USA (Liebhold et al. 2012). In this program, which only applies to selected pathways and commodities, samples are taken at random from all consignments during the sampling period, and sampling is based on hypergeometric statistics. Compliant (uncontaminated) consignments are also recorded.

Adoption of similar inspection and recording protocols by other countries, in particular several years prior to legislative changes, would facilitate analysis of the policy's impact.

Finally, to understand how many prohibited items enter a country, ‘blitzes’ haven proven effective. These are brief 100% inspections of selected pathways, introduction hubs or high-risk commodities. This approach has already been successfully used several times. For instance, 100% of the baggage of 153 incoming flights to Los Angeles from high-risk countries involving 16,997 passengers has been inspected within one week in May 1990 (US Congress 1993). In this case, it could be demonstrated that substantial illegal imports of fruits, vegetables and animal products occurred. Blitzes can also be used to evaluate the effectiveness of new regulations.

6. The way forward: emerging research questions and new approaches

6.1 New data sources

A new generation of alien species databases that integrate data from different domains is currently being developed for several major taxonomic groups (e.g. birds, vascular plants). These databases are rich sources for pathway-related studies. They offer information on alien species introduction (e.g. years of first records, pathways), distribution (e.g. invasion status, abundance, regions of origin), and ecology (e.g. traits) together with environmental (e.g. climate) and socio-economic data (e.g. proxies for human disturbance and propagule pressure, Appendix S1) of the regions considered.

For vascular plants, the recently developed GloNAF database (GloNAF core team, unpublished), which currently covers >10,000 alien species in >500 regions of the world, has been combined with data on the global bilateral trade network to analyze the global flow of alien species, changes over time, and likely future trajectories (Seebens et al., in review).

For birds, Dyer & Blackburn (unpublished) have compiled a spatially and temporally explicit database on the distributions of 973 alien bird species (incl. >400 species that have established apparently viable populations) called GAVIA (Global AVian Invasions Atlas). GAVIA more than doubles the number of known introduced bird species, relative to the previous best information, and increases the number of established species known by a similar proportion. Analyses of these new data will allow on-going spatio-temporal changes in pathways to be explored further, which will in turn direct future research and policy priorities. For example, evidence of a shift in the geographical focus of the bird trade from Eurocentric acclimatization and trade to East Asian pet markets suggests it is important to study the drivers of Eastern markets (e.g. Su et al. 2014).

Biological invasions are not a new phenomenon, and there are many historical examples that are well documented in the literature, often in great detail. Text-mining of this corpus has the potential to rediscover and quantify historic vectors, pathways and trends. Historical information was, for instance, used to determine the alien status and the causes and pathways of introductions of fish and crayfish species that had been thought to be native before (Clavero & Villero 2014). Studies of modern invasions often miss the whole time course, and it is only possible to understand the process by looking back in time. Text-mining has only just become possible since the establishment of large digital repositories of literature, such as BHL (www.biodiversitylibrary.org), and interest in this approach is now increasing rapidly (e.g. Vellend et al. 2013).

6.2 New techniques and analyses

Spatio-temporal changes in pathways and other covariates of invasions

To the best of our knowledge, little work has been done on the relationship between invasion pathways and other important covariates of invasions, and on how these interactions change over time and in different regions. For instance, it is likely that the traits of species introduced have changed over time and across pathways (Blackburn et al. 2009). Thus, ornamental plants differ in their suite of traits from plants introduced for other reasons, but fashions in ornamentals (e.g. specific characteristics desired in gardens) change over time. Large datasets on species traits (e.g. TRY-database for vascular plants, Kattge et al. 2011) are increasingly becoming available and are fundamental for understanding such changes and their consequences in terms of introduction risk. Due to expected differences in life-history traits across pathways, and different timing of the importance of pathways, species are likely to differ in the area they occupy in their new range.

Network analysis of pathways

Pathways rarely involve the simple movement of propagules from point A to point B. More commonly, they are a complex web composed of a variety of actors performing as hubs and nodes in the network (Seebens et al. 2013). Knowledge of these networks is essential to discover the choke points where control can be targeted cost effectively (Kölzsch & Blasius 2011).

The use of network modeling is established in the field of epidemiology (Harwood et al. 2009). Diffusion models of the migration of plants and animals have been widely used to investigate the movements of alien species within the landscape, yet such models ignore long-distance dispersal often associated with the introduction of alien species. Thus, these models are not always appropriate when considering movements through a trade network (Hastings et al. 2005). The connectivity between nodes is as much related to their transport links and cultural ties as they are to their physical proximity (Helmus et al. 2014).

Identifying future changes of pathways: horizon scanning

Horizon scanning is the systematic examination of potential threats and opportunities within a given context (Sutherland et al. 2011), to prioritize the threat posed by potential new alien species in a region. This is an essential tool for anticipating which alien species are likely to cause future problems so that preventative action can be taken. Horizon scanning has historically focused on species, but attention could be given to pathways, or species-pathways interactions. The methods employed for horizon scanning have generally combined extensive literature reviews, to ascertain species of concern, and some form of risk assessment. Roy et al. (2014) deployed a method for horizon scanning to create an ordered list of alien species that are likely to arrive, establish and have an impact on biodiversity within Britain over the next ten years. The species which was ranked on first place by the authors – the Killer shrimp (*Dikerogammarus villosus*) – was found within the first year after the horizon scanning effort had been completed. Information on origins and pathways of arrival for the species was collated within this horizon-scanning approach and could be used for underpinning and prioritizing management for pathways of arrival. Indeed, Roy et al. (2014) predict that the stowaway pathway (in land, air or sea transport vehicles) is likely to be the most common mechanism of introduction but recognizes that multiple pathways of introduction are anticipated for many species.

Alongside systematic methods for gathering and reviewing information (e.g. literature reviews and risk assessments), consensus methods provide robust and repeatable means of collaborative decision-making leading to prioritization (Sutherland et al. 2011). The breadth of expertise required to implement horizon scanning should not be underestimated. Identifying emerging pathways requires multidisciplinary collaboration combining expertise on socio-economic perspectives alongside consideration of detailed invasion biology.

Geographic profiling

Geographic profiling is a statistical tool originating from criminology (Le Comber & Stevenson 2012; Stevenson et al. 2012). Using spatial (or preferably even spatio-temporal) data on invasions, it is possible to locate the source of a disease outbreak or an alien species of unknown origin. To do so, this method uses two complementary concepts: a distance-decay function (invasions are less likely further away from a source) and a buffer-zone function. The buffer zone originally described the area surrounding the anchor point (e.g. residence) of a criminal, because it was believed that criminals would perform fewer crimes on their "own doorsteps" due to an increased risk of being recognized. In the biological context the buffer zone may represent an area less suitable for growth and reproduction of off-spring in the immediate vicinity of a parent individual (e.g. due to competition or allelopathy), although all of these elements can be switched on or off in the models. Once the source of an invasion is located, this can facilitate (i) identifying the pathway that led to it and (ii) better-targeted management actions.

7. Conclusions

The future of a progressive pathway classification to inform alien species prevention will need to move away from qualitative classification towards quantitative approaches (Leung et al. 2012). Ideally, such a characterization of pathways should (a) identify causal chains between a putative pathway and levels of invasion in the region of interest; (b) assess the diversity, abundance and survivorship of already introduced and potential new alien species along the pathway; (c) describe spatial (in terms of suitability of different origins), taxonomic and temporal (rate and magnitude of potential introductions) variation in pathway risk; (d) describe the past and likely future magnitude of impact caused by the invasions enabled by the specific pathways; and (e) present means to assess and regulate the problems posed by the pathway.

The pivotal need for cross-sectoral and international cooperation in conjunction with the large and increasing number of alien species data repositories (Figure 2) has raised the need for defining and implementing minimum pathway standards (Ojaveer et al. 2014). Currently, data incompatibility is a frequent limitation to interoperability between databases, effectively blocking automated aggregation of data and limiting federation of services. This lack of harmony arises both intentionally, due to the specific research requirements, and unintentionally, either due to a lack of communication of standards or competition between standards. It would be desirable, for example, if the recently developed and tested GIASIPartnership-pathway scheme would become a pathway standard, as also recommended by the CBD.

Within any framework, classifying invasion pathways is a multi-layered task. An overly simplified standardization forces complex data into broad categories, thus many important details can be lost. In contrast, complicated standards loose the advantages of cross-compatibility. A solution, rapidly gaining favor in many disciplines, is the development of hierarchical domain ontologies. Such ontologies provide a means to create a structured controlled vocabulary for a domain. This is an area for future research on invasion pathways.

In this article, we have focused on factors affecting the likelihood of entry of alien species in a region. However, effective management also demands a wider consideration of pathways, including the elucidation of the many socio-economic and other factors that create, define, and mediate the dimensions of particular pathways (Hulme 2015). Further consideration of such wider contexts of pathways is important for improving the effectiveness of management.

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Table 1. A simplified illustration of the consecutive stages that connect research on pathways with options for management. Shown are the priority research questions and recommendations that are addressed in the main text.

	Purpose	Research Priorities	Recommendation(s)
PATHWAY CLASSIFICATION	Providing principles and definitions	Apply consistent pathways classification, hierarchy and terminology	Use six categories (release, escape, contaminant, stowaway, corridor, unaided) at a broad level, and refine these using a hierarchical classification
		Account for uncertainties in pathway assessment	Develop a pathway manual for interpreting pathways and communicating uncertainty (c.f. USDA 2000)
		Quantify spatio-temporal changes of pathways	Integrate historic and current proxies for quantifying introduction effort and spatio-temporal changes in pathway analyses (cf. Appendix S4, S5)
		Develop minimum harmonization standards	Develop and test a common standard on pathways between existing alien species databases to ensure interoperability (e.g. GIASIPartnership-pathway scheme) and structured ontologies
PATHWAY INFORMATION APPLICATION	Linking pathways with real-world data on invasion pathways	Expand the taxonomic, environmental and geographic coverage of pathway assessments	Identify gaps in coverage of alien species databases (cf. Figure 3) and direct resources to close them
		Account for the interaction of species traits and ecology with pathway features	Develop next generation alien species databases that integrate data from different domains (i.e. species, source region and native region attributes)
		Account for the interaction of environmental, socio-economic and management factors with pathways	Move towards a quantitative classification of pathways, and analyze the interaction of species, pathway and region attributes

Table 2. A simplified illustration of key aspects of pathway management. Shown are the priority management questions and recommendations that are addressed in the main text.

	Purpose	**Management Priorities**	**Recommendation(s)**
MANAGEMENT RESPONSE	Reducing the invasion risks of pathways	Consider pathways in alien species risk assessments	Develop prevention strategies that consider pathways (e.g. pathway/commodity/import risk assessments) and – where appropriate – protocols focused on individual alien species
		Consider the wider context when regulating pathways	Take into account the socio-economic factors that create, define, and mediate the introduction and dispersal of alien species
		Identify gaps in pathway management	Use new data (e.g. inspection data, next generation databases) and techniques (e.g. network analyses, horizon scanning, geographic profiling) to identify current and emerging major pathways and source regions
		Evaluate the effectiveness of different policy instruments (voluntary vs. binding ones)	Improve inspection and interception data collection methodology (cf. AQIM-standard), expand it to priority pathways and commodities not yet covered, and make these data available for analyses
MANAGEMENT IMPACT	Measuring the effectiveness of management and policy	Design and apply pathway indicators	Develop and apply pathway indicators based on standardized data
		Provide data for assessing the effectiveness of alien species pathway policy	Ensure that standardized data are collected and reported when introducing new pathway regulations (e.g. legislations, codes of conduct)
		Monitor alien species policy and	Provide assessments of pathway policies that allow to

		management impact on pathways	disentangle the impact of their implementation

Figure legends

Figure 1. Geographic, taxonomic, and temporal variation in the importance of the main pathways of introduction for alien marine species (a), freshwater species (b), or terrestrial arthropods (c). The size of the pie charts indicates the approximate numbers of alien species per recipient country of first introduction. Species of European origin have been counted in the country of first introduction in their alien range. Species with unknown pathways were not included in the pie charts but were included in the bar charts (European total). Outermost regions were excluded. For clarity, data are not shown for countries with very low numbers of first introductions. A few species that were linked to more than one pathway were given a value of $1/k$ for each of the k associated pathways, so that the overall contribution of each species to the pie charts was always 1. Temporal trends of new introductions (right panels) are given as black lines (right axes). The pathway 'Suez Canal' (a) refers to Red Sea species that moved unaided into the Mediterranean via the Suez Canal. Data on pathways and countries of first introduction were retrieved from the European Alien Species Information Network – EASIN; Katsanevakis et al. (2012).

Figure 2. Pathways as implemented in major alien species databases (see Appendix S3 for databases included). (a) The numbers of databases for different environments (terrestrial, marine and freshwater; total n = 182) and the proportions that contain species information on introduction pathways, provide guidance on pathway classification by a manual, and provide information on spatio-temporal changes of pathways. (b) The number of pathway categories in databases (n = 51) concerning different environments. (c) The geographic coverage (continents) of the databases and pathway assessments (n = 196).

Figure 3. The role of bilateral trade in explaining biological invasions. (a) Temporal trends (1950-2009) of total import volume of continents which can be used as a proxy for propagule pressure of alien species. (b, d) The environment-trade niche (i.e. the histogram of trade

volumes exchanged between countries as a function of temperature and precipitation differences, respectively) shows that most goods are exchanged between countries of similar annual mean temperature and precipitation. In fact, 50% of the world trade volume (marked by gray area) was exchanged during 2005 between countries with low differences in temperature ($\Delta T < 5°C$) and precipitation ($\Delta P < 300$ mm). To analyze temporal changes of environment-trade niche widths, a normal distribution was fitted to the histogram of import volumes between countries at least 1000 km apart from each other (red line) and the standard deviation (σ) was extracted. (c, e) The temporal trends of σ during 1948–2009 show distinct and non-linear changes of the niche widths. This indicates that the environmental similarity between countries of highest exchanged trade volumes changed continuously during the last decades. There is a temporal trend towards higher temperature similarity between countries. The 95%-confidence intervals (shaded areas) were calculated by repeating the calculation of σ 1000 times with a subset of 10% of all country-country pairs. Data from Seebens et al. (in review).

Supporting Material

Appendix S1. Changes in major pathway attributes over time, i.e. from a pre-globalized world (before mid-20th century) to a globalized world (after mid-20th century).

Appendix S2. Categorization of pathways for the introduction of alien species developed through the Global Invasive Alien Species Information Partnership (GIASIPartnership).

Appendix S3: Overview on the 196 alien species databases (global to subnational ones) used for analyzing taxonomic, geographic and environmental coverage of pathway assessments. Given are database name, geographic scale (subnational, national, continental, global), environment covered (terrestrial, aquatic, marine), pathway assessments (yes/no), numbers of pathway categories used, availability of a pathway interpretation manual, assessment of temporal changes in pathways (yes/no), and key references.

Appendix S4: Suggested relationships between attributes of species, and source- and recipient-regions with different pathways (based on Hulme et al. 2008).

Appendix S5. Proxies for quantifying introduction effort of alien species by different socio-economic activities.