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EDITOR'S PERSPECTIVE

Trade, transport and trouble: managing invasive species pathways in an era of globalization

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Summary

1. Humans have traded and transported alien species for millennia with two notable step-changes: the end of the Middle Ages and beginning of the Industrial Revolution. However, in recent decades the world has entered a new phase in the magnitude and diversity of biological invasions: the Era of Globalization. This Special Profile reviews the links between the main drivers of globalization and biological invasions and examines state-of-the-art approaches to pathway risk assessment to illustrate new opportunities for managing invasive species.
2. Income growth is a primary driver of globalization and a clear association exists between Gross Domestic Product and the richness of alien floras and faunas for many regions of the world. In many cases, the exposure of these economies to trade is highlighted by the significant role of merchandise imports in biological invasions, especially for island ecosystems.
3. Post-1950, technical and logistic improvements have accelerated the ease with which commodities are transported across the globe and hindered the traceability of goods and the ease of intercepting pests. New sea, land and air links in international trade and human transport have established novel pathways for the spread of alien species. Increasingly, the science advances underpinning invasive species management must move at the speed of commerce.
4. Increasing transport networks and demand for commodities have led to pathway risk assessments becoming the frontline in the prevention of biological invasions. The diverse routes of introduction arising from contaminant, stowaway, corridor and unaided pathways, in both aquatic and terrestrial biomes are complex. Nevertheless, common features enable comparable approaches to risk assessment. By bringing together spatial data on climate suitability, habitat availability and points of entry, as well a demographic models that include species dispersal (both natural and human-mediated) and measures of propagule pressure, it is possible to generate risk maps highlighting potential invasion hotspots that can inform prevention strategies.
5. *Synthesis and applications*. To date, most attempts to model pathways have focused on describing the likelihood of invader establishment. Few have modelled explicit management strategies such as optimal detection and inspection strategies and assessments of the effectiveness of different management measures. A future focus in these areas will ensure research informs response.

Key-words: alien, exotic, globalisation, model, pest, propagule pressure, weed

Introduction

Alien species are, by definition, taxa that are introduced outside of their natural range either intentionally or unintentionally by human agency (IUCN 2000). It should therefore come as no surprise that the global pool of potential alien species, as well as both the geographic and taxonomic pattern of biological invasions, is strongly shaped by trends in human trade and transport (Perrings *et al*. 2005; Meyerson & Mooney 2007). However, humans have transported and traded plant and animal species for millennia. Indeed, a widely held defining moment in biological invasions dates as far back as 1500 AD, a period associated with the end of the Middle Ages, the European rediscovery of the Americas, global exploration, the birth of colonialism and the start of radical changes in patterns of human demography, agriculture, trade and industry (Preston, Pearman & Hall 2004).

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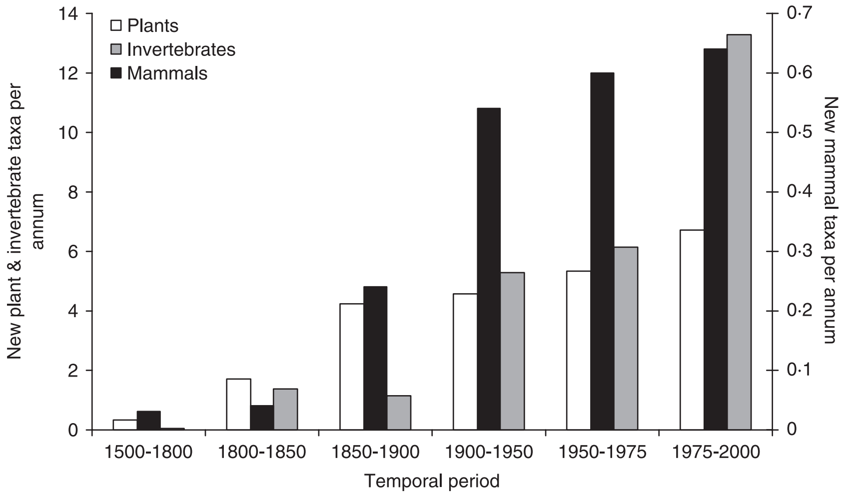

Fig. 1. Annual rates of increase in the establishment of alien mammals (data from Genovesi *et al.* 2009), invertebrates (data from Roques *et al.* 2009) and plants (data from Pyšek *et al.* 2009) in Europe since 1500 AD.

However, data on the introductions of alien species into Europe highlight that not until 1800 AD was a progressive increase in the annual rate of alien mammal, invertebrate and plant introductions observed (Fig. 1). Similar trends are seen for plants in North America (Mack 2003). This 'second phase' of biological invasions coincides with the Industrial Revolution, a period of increased international trade across almost all continents facilitated by the construction of canals, highways and railways as well as the introduction of steamships (Findley & O'Rourke 2007). Furthermore, the spread of European species worldwide was undoubtedly aided by 50 million Europeans who emigrated to distant shores between 1820 and 1930, taking with them, whether intentionally or by accident, numerous species (McNeeley 2006).

Yet, the temporal trends in invasions show little sign of abating since 1800. The highest rates of introductions in Europe occurred in the last 25 years and suggest a recent step-change in biological invasions. Furthermore, biological invasions are widely expected to become a greater problem in the future (Lodge *et al.* 2006; Sutherland *et al.* 2008). It therefore appears that the world has entered a 'third phase' of biological invasions, the Era of Globalization. Although many authors have raised an accusing finger at globalization as the source of current problems with invasive species (Lockwood, Cassey & Blackburn 2005; Perrings *et al.* 2005; Streftaris, Zenetos & Papathanassiou 2005; Lodge *et al.* 2006; McNeeley 2006; Meyerson & Mooney 2007), few have attempted to address the specific drivers of globalization or their management.

In this Special Profile, two of the primary drivers of globalization (Baier & Bergstrand 2001): income growth and transport efficiency, are examined in relation to their influence on biological invasions. These drivers shape the origin, frequency and magnitude of species movements along introduction pathways worldwide. In the absence of watertight trade regulations, punitive tariffs and certainty in risk assessment (Perrings *et al.* 2005), the management of pathways represents the frontline in the prevention of biological invasions. With reference to several case studies drawn from the aquatic and terrestrial biomes, current state-of-the-art approaches to pathway risk assessment are presented and used to illustrate new opportunities for management.

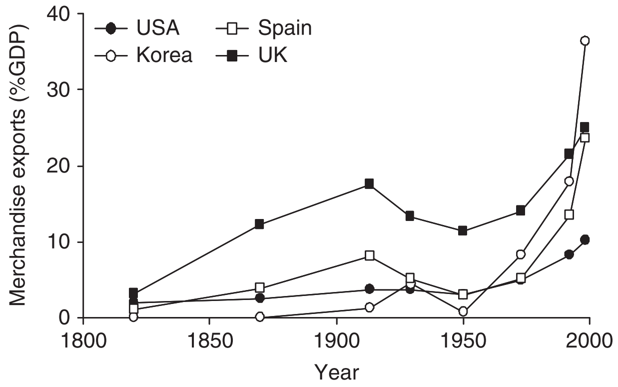

Fig. 2. Merchandise exports as a share of GDP, 1820 to 1998 (per cent) for South Korea, Spain, the UK and USA. Data from Findlay & O'Rourke (2007).

Follow the money

For most of the last 200 years, global trade has gradually increased as economies have grown, but the last 50 years have witnessed an unprecedented acceleration in the importance and value of merchandise trade (Fig. 2). Increased trade in commodities has resulted in a legacy of recent biological invasions. The magnitude of merchandise imports is a significant determinant of the number of species (Westphal *et al.* 2008; Desprez-Loustau 2009; Roques *et al.* 2009) as well as the rate of new species introductions (Levine & D'Antonio 2003) of a wide range of alien taxa. Less precise measures of trade and commerce, such as Gross Domestic Product (GDP, one component of which is net exports) have been found to correlate with the richness of alien spiders (Kobelt & Nentwig 2008), plants, birds, fish and mammals in Europe (Hulme 2007), plants in China (Liu *et al.* 2005) and fish across river basins worldwide (Leprieur *et al.* 2008). However, since GDP is also

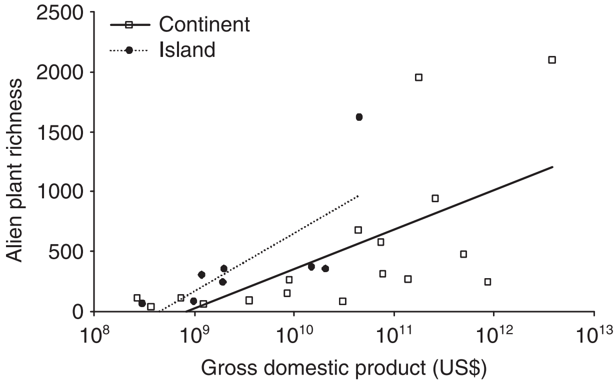

Fig. 3. Relationship between gross domestic product (US$) and alien plant richness for selected island and continental regions of the world. Continents $R^2 = 0{\cdot}42$, $F_{(1,15)} = 10{\cdot}78$, $P < 0{\cdot}01$; Islands $R^2 = 0{\cdot}54$, $F_{(1,6)} = 6{\cdot}98$, $P < 0{\cdot}05$. Data from Dalmazzone (2000).

composed of private capital investments and government expenditure, it also reflects levels of infrastructure (roads, canals, railways etc.) that can also facilitate invasions (see below). Nevertheless, for alien plants, the relationship between richness and GDP is stronger for island states than for continents, reflecting the greater proportion of merchandise imports (38% vs. 26·8%) that contributes to their GDP (Fig. 3). Not surprisingly, island ecosystems are often the most invaded and threatened worldwide (Donlan & Wilcox 2008). Further evidence of the direct role of trade stems from correlations between specific commodity sectors and the subsequent establishment of alien species via horticulture (Lambdon, Lloret & Hulme 2008), the wild-bird trade (Carrete & Tella 2008), grain shipments (Shimono & Konuma 2008) and aquarium fish commerce (Gertzen, Familiar & Leung 2008). The importance of trade in biological invasions has prompted several authors to extrapolate their findings and predict dire future scenarios for rapidly growing national economies such as China (Jenkins & Mooney 2006; Ding *et al.* 2008). But income growth is a global phenomenon, and over the last 25 years, GDP has grown by over 110% in developed countries and by almost 70% in developing nations (UNCTAD 2007). Although the evidence linking economic growth to biological invasions is striking, little scope currently exist to address this since it is but another example of Nature's capital being undervalued by growth economists, demographers and governments, and this will continue to be the case until such time these perceptions are changed (Dasgupta 2007).

Bigger, better, farther, faster

Although the value of merchandise imports may correlate well with measures of biological invasion, it is likely that knowledge of the volume, frequency, origin and destination of imports as well as the mechanism by which goods are transported will help better characterize risks. Data from 2005 (UNCTAD 2007) highlight that global trade is dominated by dry cargo (46%), followed by oil and oil products (31%), coal and mineral ores (18%) and finally grain (4%). While international standards exist regarding the properties of oil, ore and grain supplies, the heterogeneous nature of most other commodities represents the greatest risk of alien species introductions. Alien species can often enter as contaminants of traded goods, for example, phytosanitary pests on agricultural produce or timber (Hulme *et al.* 2008). Understanding the scale, mechanisms and historical trends in the trade in dry cargo is an essential foundation for any tools aimed at managing the risk of invasions.

In 2006, more than 90% of global trade was carried by sea with a cargo-carrying fleet of over 50 000 ships transporting more than 1 million deadweight tonnes (IMO 2008). The increase in size, speed and number of the global cargo carrying fleet has led to a fourfold rise in the volume of global imports since the 1970s (Fig. 4; UNCTAD 2007). Unheard of before the 1960s, the container is now the standard unit of cargo, and today's giant containerships typically operate between purpose-built ports that facilitate rapid transfer of containers to subsequent road, rail and canal transport. In 1973, container ships were carrying 4 million TEUs (twenty-foot equivalent units); by 1983, this had risen to 12 million, and by 2007, it is estimated that global loaded container trade reached 141 million

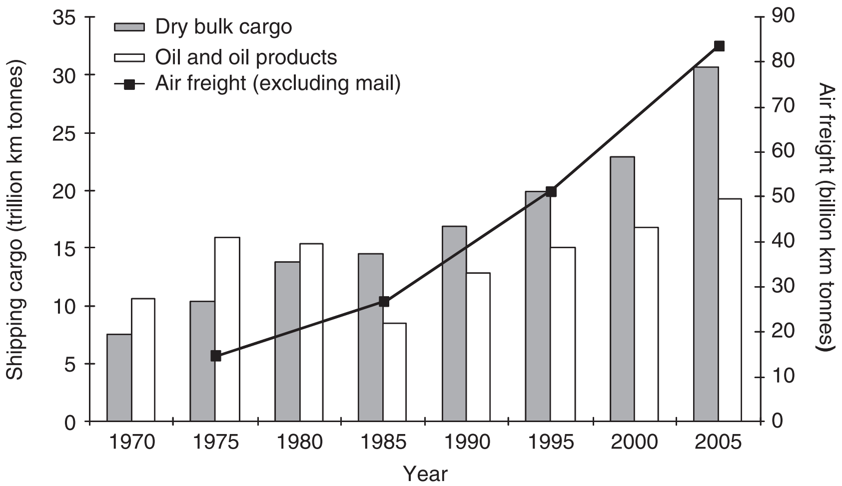

Fig. 4. Trends in global shipping cargo volumes and air freight, 1970–2005. Data from UNCTAD (2007) and DfT (2006) respectively. Note the three orders of magnitude difference in the scales of the left and right hand ordinate axes.

Table 1. Extent of transport infrastructures and ports of entry for global regions. Data from USDOT (2007)

		Length of transport network (km)			No. of ports of entry	
Region	Area (km^2)	Roads	Rail	Inland canals	Seaports	Airports
Asia	48 670 642	7 301 968	410 410	160 259	179	4735
Africa	30 092 557	1 691 297	81 867	55 264	210	4571
Americas						
North	21 321 300	7 334 867	342 648	469 099	52	18 473
Central	758 883	204 122	18 889	6 452	118	1 752
South	17 818 505	2 399 260	87 586	104 793	98	1 797
Europe	5 952 610	5 996 840	285 852	22 520	134	2 427
Oceania	8 509 148	967 624	45 842	21 125	78	1 335

Table 2. Key variables required to asses the risk of unintentional species entry as a result of contaminant, vector or corridor pathways, after EPPO (2007)

Strength of association between species and commodity/vector/corridor at point of export
Volume of the commodity/vector/corridor imported
Frequency of importation
Species survivorship and population growth during transport/storage
Suitability of environment for species establishment in the importing region
Appropriateness of the time of year of importation for species establishment
Ease of species detection within consignments/vectors/corridors
Effectiveness of management measures e.g. fumigation, inspection regime
How widely the commodity/vector is subsequently distributed in the importing region
Likelihood of transfer from the commodity/vector/corridor to a suitable habitat

TEUs (UNCTAD 2007). Containers pose a novel problem in that, in addition to the goods transported, alien flora and fauna can be associated as stowaways inside or on the surface of the container (Hulme *et al*. 2008). As a result, knowledge of the origin and transport history of the container itself (which may differ from the goods it contains) may be required to assess the risks of unwanted introductions.

Aviation has rapidly expanded as the global economy has grown. International air freight has increased eightfold since the 1970s, yet still represents a tiny fraction of global trade (Fig. 3). Although a small player in terms of freight, aviation has superseded shipping as the major form of international passenger transport. In 2006, 4·4 billion people passed through the world's main airports (ACI 2007). Furthermore, airports facilitate greater penetration into global regions than marine ports, worldwide numbers of the former exceeding the latter more than 20-fold (Table 2). There is increasing evidence that aviation is a more significant route of pest entry than might be expected based solely on cargo volumes. Of 725 000 pest interceptions at US ports of entry between 1984 and 2000, 73% occurred at airports rather than seaports (9%), with twice as many pests associated with baggage than cargo (McCullough *et al*. 2006). However, while fewer pest interceptions may be associated with the larger volume of goods transported by sea, shipping poses additional risks indirectly related to the goods transported. Aquatic alien species may stowaway on ships, either by fouling hulls or in ballast water, often to arrive in port environments suitable for establishment (Hulme *et al*. 2008). Estimates suggest movements of ballast water alone account for the transport of 10 000 species everyday (Streftaris, Zenetos & Papathanassiou 2005). Thus, independently of the goods transported, the number of ports, frequency of port visits and the volume of goods (and magnitude of ballast water exchange) will influence risks.

While air- and seaports are major entry points for international trade and travellers, the commodities arriving at these destinations are subsequently moved, often across international boundaries, by road, rail, canals and even pipelines. Roads, railways and canals represent potential corridors along which alien species may spread as a direct result of the transit of goods and vehicles, as well as indirectly through the local modification of the neighbouring environment by these infrastructures that can facilitate species establishment (Hulme *et al*. 2008). The volume of freight transported by road has consistently grown since the 1960s in both the UK (330%, DfT 2006) and the USA (454%, USDOT 2007). Europe has the highest road and rail density of any continent, while North America leads the way with canals (Table 1). Road density is a significant correlate of spatial patterns in the invasions of plants in China (Weber & Li 2008), insects in Europe (Roques *et al*. 2009) and cane toads *Bufo marinus* in Australia (Urban *et al*. 2008).

In an ideal world, knowledge of the goods traded, their origin and destination as well as the suitability for the receiving environment should enable reasonable estimates of the risks of alien species introduction (e.g. Tatem *et al*. 2006). Indeed, these features of trade are now beginning to be integrated with aspects of species biology in attempts to quantify the risk posed by different introduction pathways and thus prevent the entry of pest species (Table 2). However, a detailed assessment of such pathway analysis for timber pests entering Belgium, revealed that due to the temporal variation in trade from year to year as well as the political and economic aggregation of data, trade information is often of limited use for real-time risk assessment (Piel *et al*. 2008). The efficacy of preventative measures is further reduced by gaps in legislative and regulatory instruments that address unintentional introductions of alien species (Hulme *et al.* 2008). There is therefore a need for pathway risk management to support risk assessment. Recent work has attempted to simplify the characterization of introduction pathways into six broad types (Hulme *et al.* 2008). Alien species transported as commodities may be introduced as a deliberate release or as an escape from captivity. Many species are not intentionally transported but arrive as a contaminant of a commodity, for example, pathogens and pests. Stowaways are directly associated with human transport but arrive independently of a specific commodity, for example, organisms transported in ballast water, cargo and airfreight. The corridor pathway highlights the role transport infrastructures play in the introduction of alien species, while the unaided pathway describes situations where natural spread results in alien species arriving into a new region from a donor region where it is also alien. Of all the pathways, deliberate releases, such as biological control agents (e.g. Phillips *et al.* 2008), or escapes such as feral crops (e.g. Pivard *et al.* 2008) are, in theory, easier to regulate and prevent (Hulme *et al.* 2008). In this Special Profile, several case studies of risk assessment and management are presented for four unintentional introduction pathways: contaminant, stowaway, corridor and unaided. Overall, these case studies highlight the need to understand the spatial processes underlying each pathway and the power of simulation models to improve risk assessment as well as management.

Contaminants: managing the goods to address the bad and the ugly

Pathway risk analysis is often applied to assess the likelihood that a species associated with a particular commodity will become established in the importing region (e.g. phytosanitary pests). Under these circumstances, knowledge of the spatial and temporal trends in the transport of the commodity may provide useful proxies for the likelihood of pest establishment. Raw logs are one of the most important international forestry commodities and a major source of alien species, especially insects and pathogens (Piel *et al.* 2008). Untreated timber is often stored for long periods either at the point of import or following transport to sawmills, prior to processing. The length of storage provides ample opportunity for pest populations to increase and disperse, while movement of timber to processing sawmills exposes a range of habitats to potential colonization. Using this simple pathway framework, Skarpaas & Økland (2009) developed a three-component model that described local pest population dynamics at the storage site (a function of demographic parameters and timber import volumes), likelihood of escape, and the probability of colonizing suitable habitat (a function of distance and dispersal ability). They parameterized their model using data for the European spruce bark beetle *Ips typographus* (as a representative of a range of bark beetle pests) and assessed the utility of different measures in reducing the likelihood of pest spread. These measures included: (i) import less timber so as to reduce the number of pests introduced; (ii) process timber sooner to leave less time for pests to develop; (iii) import timber later, leading to less time for the storage population to exploit timber; (iv) irrigate timber to reduce pest survival in stored timber; (v) debark timber at source resulting in fewer pest individuals per import volume; (vi) store timber in an enclosed building so that fewer pest individuals escape; and (vii) store timber far from forests, reducing the likelihood of pests colonizing suitable habitat. The simulations were particularly sensitive to assumptions regarding pest dispersal and the effectiveness of wood treatment. However, one counter-intuitive conclusion is that, of all the management measures examined, managing the volume and timing of timber import had the least effect on pest dynamics. The success of control treatments depended on their efficacy and evidence presented indicates that neither irrigation nor debarking is entirely successful at removing the risk. On the other hand, storage within a warehouse reduces introduction risks considerably. However, increasing the distance between the storage and forest habitat had the most consistent impact on reducing risks. The implications of this work in terms of determining the likelihood of invasion is that rather than focusing on the volume of imports, knowledge of the distribution of storage sites and sawmills and their proximity to suitable forest habitat may provide a first approximation of risk. Such spatial data are often available and, if integrated with climate suitability and dispersal data, could be used to generate maps of risk hotspots associated with particular storage or processing sites.

Stowaways: vectors as victims, harbours as hosts

It is likely that ever since humans first set sail on the open sea, marine organisms have hitched a ride attached to hulls. Fouling is the process through which sessile plants and invertebrates attach themselves to submerged objects, such as boat hulls, with a resultant reduction in the fuel efficiency and speed of affected ships, which increases their operating costs. As a response, the hulls are treated with biocidal antifoulant paints that require regular re-application to maintain their effectiveness (Costa, Aldridge & Moggridge 2008). Floerl *et al.* (2009) use the varying effectiveness of antifoulant paints to classify yachts as susceptible, infected or resistant to colonization by hull-fouling organisms. They then applied an epidemiological model to simulate the spread of a hypothetical marine invader by hull fouling on recreational yachts (vectors). The model was integrated into an actual transportation network in New Zealand characterized by transport nodes (ports, harbours and marinas) that differed in traffic volume (frequency of vector movements) and connectivity (movement of vectors to other locations) to other transport nodes. Stochastic simulations were used to assess the importance of the initial node of establishment by the invader on the spatial pattern and rate of spread. Busy transport nodes (hubs) were associated with a high density of susceptible vectors, a large area of available habitat and a high likelihood of receiving infected vectors from other locations. Nodes with a high degree of vector traffic and connectivity to other nodes were also likely to give rise to a larger number of new satellite populations faster than incursions in less well-connected nodes.

Knowledge of vector traffic, transport hubs and environmental suitability can be refined to generate risk maps for specific marine invaders. Herborg, O'Hara & Therriault (2009) provide an example of this approach for the invasive colonial tunicate *Didemnum vexillum*, a potential colonist of the Pacific coast of Canada. The tunicate has poor natural dispersal ability and thus spread is likely to be related to the movement of marine vessels and aquaculture. By identifying the most likely vectors and estimating vector traffic derived from geo-referenced monitoring data, a map of hotspots for each vector could be generated. This hotspot map was then superimposed on spatial data relating to environmental suitability derived from a Generic Algorithm for Rule-set Prediction (GARP) model based on known occurrences of the tunicate along the west coast of North America. The subsequent risk map highlighted areas most at risk from *D. vexillum* and indicated the types of vectors most likely to introduce the tunicate into these risk areas.

These two studies address slightly different aspects of managing stowaway organisms where knowledge of the vector dynamics is essential. Building on the best elements of both studies, an integrated approach should: (i) identify the importance of different vectors; (ii) quantify the spatial dynamics of vectors; (iii) estimate the environmental suitability of the region to specific aliens; and (iv) calculate the connectivity of different nodes in the transport network. Together, such an approach can generate risk maps that help identify nodes where initial introduction to the network is likely to occur as well their role in the subsequent spread (in the absence of management) to other nodes. As a result, managers can target surveys at likely ports of entry but also focus eradication campaigns at the major dispersal hubs. It is quite possible that different nodes in the network play different roles dependent on the origin, volume and type of vectors they receive.

Corridors: on the road and off the rails

Linear features in a landscape, such as rivers, canals, roads and railways are often viewed as habitat corridors that help direct the movement of organisms through less hospitable habitat, facilitating exchange between populations and thus population persistence (Van der Windt & Swart 2008). Although often seen as playing a role in the conservation of native species, such corridors may also facilitate the spread of alien invasive organisms (Hulme 2006). This is particularly true of anthropogenic corridors due to high levels of human activity, proximity of disturbed habitats and the availability of vectors (cars, trains, boats) that assist in the dispersal of individual organisms. However, the occurrence of alien species in highly disturbed, anthropogenic habitats is perhaps less of a concern than where the corridor pathway facilitates the spread of aliens into conservation or economically important habitats. Thus, an analysis of the corridor pathway needs to account for the features that facilitate the occurrence of aliens along the corridor as well as the likelihood of their subsequently colonizing other habitats. Cameron & Bayne (2009) examine both perspectives in relation to earthworm invasion in northern Canada. Using a hierarchical sampling strategy, the correlates of earthworm occurrence along roads in a boreal forest landscape as well as the degree of local spread from roadsides could be established. At the landscape scale, easting and northing (likely proxies for climate), distance to agriculture, shrubs and trees, and road age were significant variables underlying earthworm occurrence. At the local scale, earthworm abundance was related to road age, distance from the roadside, and tree cover. Overall, earthworms were more likely to occur, be more abundant and have spread farther from older roads but only where there was reduced forest cover. From a management perspective, since road age is an important determinant of colonization, it appears that earthworms are not introduced with the construction of the infrastructure but arrive subsequently most probably via cocoons on vehicles. Earthworms are unlikely to be picked up from the corridor by passing traffic, thus the primary source is likely to be areas of agricultural land from which human-mediated dispersal is still occurring. Rates of spread from roadsides were estimated to be >10 m year^{-1}, and at older sites, earthworms were found more than 100 m away. The rate of natural dispersal along the corridor is much lower than that attributable to vehicular transport. Nevertheless, future trends in the length and density of road construction combined with patterns of vehicular and natural dispersal predict almost half of all suitable forest could be colonized by earthworms in the next 50 years. The spatial patterns in earthworm invasions parallel those found for the invasive common reed *Phragmites australis* in Canada (Jodoin *et al*. 2008), again emphasizing the importance of road age.

Can corridor pathways be managed to limit rates of invasion? This requires the disentangling of the effects of natural and human-mediated spread. Where rates of human-mediated spread are high and the vectors known, a strategy similar to the management of stowaways may be appropriate. For canal corridors, ensuring high maintenance standards for anti-hull-fouling measures as well as bilge and ballast water discharges would be valuable. Such measures are less straightforward to adopt for road and rail vehicles. For natural spread along corridors, the environment may be managed to limit spread. This is probably easier in terrestrial than aquatic ecosystems. For earthworms, this might involve planting of black spruce *Picea mariana* or tamarack *Larix laricina* stands that are inhospitable to earthworms (Cameron & Bayne 2009). Shrub and tree planting along roadsides has also been suggested as a means of limiting the spread of common reed in Canada (Jodoin *et al*. 2008) and cane toads in Australia (Brown *et al*. 2006).

Unaided pathways: identifying and establishing internal borders

Once introduced into a region through trade and transport, an invasive species may spread via natural means to other regions where it is regarded as alien. Since many alien species spread via both human-mediated (e.g. contaminants, stowaways, corridors) and natural dispersal, the importance of the unaided pathway is often underestimated (Hulme *et al.* 2008). As a result, it is probably the least-well managed pathway. Forrest, Garner & Taylor (2009) develop the idea of internal borders that can be identified from knowledge of the natural environmental barriers to dispersal and establishment of alien species and thus enable gaps in the barriers to be prioritized for management. In the marine environment, barriers can result from oceanographic features such as zones of upwelling, or current systems that lead to restricted exchange between water masses or seaward advection. In freshwater environments, limnological conditions such as high or low water conductivity, stream slope and catchment boundaries can limit the spread of aquatic alien species (Spens, Englund & Lundqvist 2007). Barriers are easier to visualize in terrestrial environments and include such features as mountain ranges. Since biogeographic boundaries can be associated with these dispersal barriers, it may be possible to infer the existence and location of these barriers according to biogeographic zones in native species assemblages. In these circumstances, 'Least-cost modelling' could be employed to assign dispersal costs to distinct landscape features and the least-costly dispersal paths across the landscape, and thus likely routes of invasion, calculated using a geographical information system (Epps *et al.* 2007). Even in the absence of adequate data on dispersal, dispersal costs can often be assigned solely from expert opinion. Once such a cost-surface is generated it may be possible to assess how existing dispersal barriers may be breached by human activities through canals, tunnels or even undersea cables that provide a hard substrate for colonization on an otherwise soft sediment seabed. Gaps in these natural barriers can then become the focus for management action, such as the establishment of exclusion zones or targeted surveillance (Bogich, Liebhold & Shea 2008).

Managing invasion pathways: the route ahead

This Special Profile has highlighted a number of different approaches to assess risks arising from contaminant, stowaway, corridor and unaided pathways. These examples explore the influence of many of the key variables underpinning pathway risk assessment (Table 2). A common feature of these approaches is the understanding of invasions as spatial processes and the integration of different variables to generate 'risk maps' highlighting hotspots of invasion likelihood (Buckley 2008). However, in addition to bringing together spatial data regarding climatic suitability, habitat availability and points of entry, risk maps should also include species dispersal parameters (both natural and human-mediated) and measures of propagule pressure.

Network models of vector movement between nodes are increasingly being used to assess the spatial dynamics of marine stowaways (Herborg *et al.* 2009; Floerl *et al.* 2009; Forrest *et al.* 2009) and species spread along freshwater corridors (Muirhead & Macisaac 2005). There is considerable potential to expand these approaches to other vectors (e.g. trains, motor vehicles, aircraft etc.) and corridors (e.g. railways, roads). Accurate assessment of dispersal kernels not only helps determine the likelihood a species will spread to suitable habitats (Dauer, Mortensen & Vangessel 2007; Skarpaas & Økland 2009) but also indicates the suitability of different management approaches such as the effectiveness of exclusion zones and natural as well as human-made barriers to spread.

An often untested assumption of pathway models is that the more individuals are introduced to a region, the more likely it is for establishment to occur. Propagule pressure has rapidly become a catch-all term in invasion biology to cover the number, frequency and spatial extent of introductions (Lockwood *et al.* 2005). Skarpaas & Økland (2009) explicitly model an Allee effect for the bark beetles that suggests invasion is highly dependent on the number of individuals introduced. In contrast, Sagata & Lester (2009) experimentally assess the relationship between the number of Argentine ants *Linepithema humile* introduced to a site and subsequent establishment. They conclude that propagule pressure has low predictive power especially in taxa that exhibit behavioural plasticity. Another experimental approach, this time examining the establishment success of an aquatic invader *Hydrilla verticillata*, highlighted that propagule pressure was only important in the absence of competition from native species (Chadwell & Engelhardt 2008). Thus, caution is required when assuming that propagule pressure is important and studies should attempt to distinguish which component of propagule pressure might drive invasion dynamics.

To date, most attempts to model pathways have focused on describing the likelihood of invader establishment and rather few have attempted to model explicit management strategies. This is symptomatic of other aspects of invasion ecology (Hulme 2003, 2006), but research needs to inform managers. Key areas in pathway management include optimal detection and inspection strategies (e.g. Surkov *et al.* 2008) and assessments of how effective different management measures (e.g. fumigation of commodities, open sea ballast-water exchange, anti-foulant biocides, pest exclusion zones and dispersal barriers) are at preventing invasion and/or how they might be improved. This will ensure research informs action rather than only identifying the scale of the problem.

References

ACI (2007) *Annual Report 2006*. Airports Council International, Geneva, Switzerland.

Baier, S.L. & Bergstrand, J.H. (2001) The growth of world trade: tariffs, transport costs, and income similarity. *Journal of International Economics*, **53**, 1–27.

Bogich, T.L., Liebhold, A.M. & Shea, K. (2008) To sample or eradicate? A cost minimization model for monitoring and managing an invasive species. *Journal of Applied Ecology*, **45**, 1134–1142.

Brown, G.P., Phillips, B.L., Webb, J.K. & Shine, R. (2006) Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation*, **133**, 88–94.

Buckley, Y.M. (2008) The role of research for integrated management of invasive species, invaded landscapes and communities. *Journal of Applied Ecology*, **45**, 397–402.

Cameron, E.K. & Bayne, E.M. (2009) Road age and its importance in earthworm invasion of northern boreal forests. *Journal of Applied Ecology*, **46**, 28–36.

Carrete, M. & Tella, J.L. (2008) Wild-bird trade and exotic invasions: a new link of conservation concern? *Frontiers in Ecology and the Environment*, **6**, 207–211.

Chadwell, T.B. & Engelhardt, K.A.M. (2008) Effects of pre-existing submersed vegetation and propagule pressure on the invasion success of *Hydrilla verticillata*. *Journal of Applied Ecology*, **45**, 515–523.
Costa, R., Aldridge, D.C. & Moggridge, G.D. (2008) Seasonal variation of zebra mussel susceptibility to molluscicidal agents. *Journal of Applied Ecology*, **45**, 1712–1721.
Dalmazzone, S. (2000) Economic factors affecting vulnerability to biological invasions. *The Economics of Biological Invasions* (eds C. Perrings, M. Williamson & S. Dalmazzone) pp. 17–30. Edward Elgar, Cheltenham, UK.
Dasgupta, P. (2007) Nature and the economy. *Journal of Applied Ecology*, **44**, 475–487.
Dauer, J.T, Motensen, D.A. & Vangessel, M.J. (2007) Temporal and spatial dynamics of long-distance *Conyza canadensis* seed dispersal. *Journal of Applied Ecology*, **44**, 105–114.
Desprez-Loustau, M-L. (2009) The alien fungi of Europe. *Handbook of Alien Species in Europe* (ed. DAISIE), pp. 15–28. Springer, Berlin.
DfT (2006) *Transport Statistics Great Britain, 2006 Edition*. Department for Transport, TSO Publications, Norwich, UK.
Ding, J.Q., Mack, R.N., Lu, P., Ren, M.X. & Huang, H.W. (2008) China's booming economy is sparking and accelerating biological invasions. *Bioscience*, **58**, 317–324.
Donlan, C.J. & Wilcox, C. (2008) Diversity, invasive species and extinctions in insular ecosystems. *Journal of Applied Ecology*, **45**, 1114–1123.
EPPO (2007): *Guidelines on Pest Risk Analysis: Decision-support Scheme for Quarantine Pests PM5/3(3)*. European & Mediterranean Plant Protection Organization, Paris, France. http://archives.eppo.org/EPPOStandards/PM5_PRA/PRA_scheme_2007.doc
Epps, C.W., Wehausen, J.D., Bleich, V.C., Torres, S.G. & Brashares, J.S. (2007) Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology*, **44**, 714–724.
Findlay, R. & O'Rourke, K.H. (2007) *Power and Plenty: Trade, War, and the World Economy in the Second Millennium*. Princeton University Press, Princeton, NJ, USA.
Floerl, O., Inglis, G.J., Dey, K. & Smith, A. (2009) The importance of transport hubs in stepping-stone invasions. *Journal of Applied Ecology*, **46**, 37–45.
Forrest, B.M., Gardner, J.P.A. & Taylor, M.D. (2009) Internal borders for managing invasive marine species. *Journal of Applied Ecology*, **46**, 46–54.
Genovesi, P., Bacher, S., Kobelt, M., Pascal, M. & Scalera R (2009) Alien mammals of Europe. *Handbook of Alien Species in Europe* (ed. DAISIE), pp. 119–128. Springer, Berlin.
Gertzen, E., Familiar, O. & Leung, B. (2008) Quantifying invasion pathways: fish introductions from the aquarium trade. *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1265–1273.
Herborg, L-M., O'Hara, P. & Therriault, T.W. (2009) Forecasting the potential distribution of the invasive tunicate *Didemnum vexillum*. *Journal of Applied Ecology*, **46**, 64–72.
Hulme, P.E. (2003) Biological invasions: winning the science battles but losing the conservation war? *Oryx*, **37**, 178–193.
Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology*, **43**, 835–847.
Hulme, P.E. (2007) Biological invasions in Europe: drivers, pressures, states, impacts and responses. *Biodiversity Under Threat* (eds R. Hester & R.M. Harrison), pp. 56–80, Issues in Environmental Science and Technology, 2007, 25, Royal Society of Chemistry, Cambridge
Hulme, P.E., Bacher, S., Kenis, M., Klotz, S., Kuhn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pyšek, P., Roques, A., Sol, D., Solarz, W. & Vila, M. (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology*, **45**, 403–414.
IMO (2008) *International Shipping and World Trade: Facts and Figures*. International Maritime Organization, Maritime Knowledge Centre, London.
IUCN (2000) *Guidelines for the Prevention of Biodiversity Loss Caused by Alien Invasive Species*. International Union for the Conservation of Nature, Gland, Switzerland.
Jenkins, P.T. & Mooney, H.A. (2006) The United States, China, and invasive species: present status and future prospects. *Biological Invasions*, **8**, 1589–1593.
Jodoin, Y., Lavoie, C., Villeneuve, P., Theriault, M., Beaulieu, J. & Belzile, F. (2008) Highways as corridors and habitats for the invasive common reed in Quebec, Canada. *Journal of Applied Ecology*, **45**, 459–466.
Kobelt, M. & Nentwig, W. (2008) Alien spider introductions to Europe supported by global trade. *Diversity and Distributions*, **14**, 273–280.
Lambdon, P.W., Lloret, F. & Hulme, P.E. (2008) How do introduction characteristics influence the invasion success of Mediterranean alien plants? *Perspectives in Plant Ecology Evolution and Systematics*, **10**, 143–159.
Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T. & Brosse, S. (2008) Fish invasions in the world's river systems: when natural processes are blurred by human activities. *Plos Biology*, **6**, 404–410.
Levine, J.M. & D'Antonio, C.M. (2003) Forecasting biological invasions with increasing international trade. *Conservation Biology*, **17**, 322–326.
Liu, J., Liang, S.C., Liu, F.H., Wang, R.Q. & Dong, M. (2005) Invasive alien plant species in China: regional distribution patterns. *Diversity and Distributions*, **11**, 341–347.
Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K.R., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T. & McMichael, A. (2006) Biological invasions: Recommendations for US policy and management. *Ecological Applications*, **16**, 2035–2054.
Mack, R.N. (2003) Plant naturalizations and invasions in the eastern United States: 1634–1860. *Annals of the Missouri Botanical Garden*, **90**, 77–90.
McCullough, D.G., Work, T.T., Cavey, J.F., Liebhold, A.M. & Marshall, D. (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. *Biological Invasions*, **8**, 611–630.
McNeely, J.A. (2006) As the world gets smaller, the chances of invasion grow. *Euphytica*, **148**, 5–15.
Meyerson, L.A. & Mooney, H.A. (2007) Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment*, **5**, 199–208.
Muirhead, J.R. & Macisaac, H.J. (2005) Development of inland lakes as hubs in an invasion network. *Journal of Applied Ecology*, **42**, 80–90.
Perrings, C., Dehnen-Schmutz, K., Touza, J. & Williamson, M. (2005) How to manage biological invasions under globalization. *Trends in Ecology & Evolution*, **20**, 212–215.
Phillips, C.B., Baird, D.B., Iline, II, McNeill, M.R., Proffitt, J.R., Goldson, S.L. & Kean, J.M. (2008) East meets west: adaptive evolution of an insect introduced for biological control. *Journal of Applied Ecology*, **45**, 948–956.
Piel, F., Gilbert, M., De Canniere, C. & Gregoire, J.C. (2008) Coniferous round wood imports from Russia and Baltic countries to Belgium. A pathway analysis for assessing risks of exotic pest insect introductions. *Diversity and Distributions*, **14**, 318–328.
Pivard, S., Adamczyk, K., Lecomte, J., Lavigne, C., Bouvier, A., Deville, A., Gouyon, P.H. & Huet, S. (2008) Where do the feral oilseed rape populations come from? A large-scale study of their possible origin in a farmland area. *Journal of Applied Ecology*, **45**, 476–485.
Preston, C.D., Pearman, D.A. & Hall, A.R. (2004) Archaeophytes in Britain. *Botanical Journal of the Linnean Society*, **145**, 257–294.
Pyšek, P., Lambdon, P.W., Arianoutsou, M., Kühn, I., Pino, J. & Winter, M. (2009) Alien vascular plants of Europe. *Handbook of Alien Species in Europe* (ed. DAISIE), pp. 43–61. Springer, Berlin.
Roques, A., Rabitsch, W., Rasplus, J-Y., Lopez-Vamonde, C., Nentwig, W. & Kenis, M. (2009) Alien terrestrial invertebrates of Europe. *Handbook of Alien Species in Europe* (ed. DAISIE), pp. 63–79. Springer, Berlin.
Sagata, K. & Lester, P.J. (2009) Behavioural plasticity associated with propagule size, resources, and the invasion success of the Argentine ant *Linepithema humile*. *Journal of Applied Ecology*, **46**, 19–27.
Shimono, Y. & Konuma, A. (2008) Effects of human-mediated processes on weed species composition in internationally traded grain commodities. *Weed Research*, **48**, 10–18.
Skarpaas, O. & Økland, B. (2009) Timber import and the risk of forest pest introductions. *Journal of Applied Ecology*, **46**, 55–63.
Spens, J., Englund, G. & Lundqvist, H. (2007) Network connectivity and dispersal barriers: using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (*Esox lucius*) among lakes. *Journal of Applied Ecology*, **44**, 1127–1137.
Streftaris, N., Zenetos, A. & Papathanassiou, E. (2005) Globalisation in marine ecosystems: The story of non-indigenous marine species across European seas. *Annual Review of Oceanography and Marine Biology*, **43**, 419–453.
Surkov, I.V., Lansink, A., van Kooten, O. & van der Werf, W. (2008) A model of optimal import phytosanitary inspection under capacity constraint. *Agricultural Economics*, **38**, 363–373.
Sutherland, W.J., Bailey, M.J., Bainbridge, I.P., Brereton, T., Dick, J.T.A., Drewitt, J., Dulvy, N.K., Dusic, N.R., Freckleton, R.P., Gaston, K.J., Gilder, P.M., Green, R.E., Heathwaite, A.L., Johnson, S.M., Macdonald, D.W., Mitchell, R., Osborn, D., Owen, R.P., Pretty, J., Prior, S.V., Prosser, H., Pullin, A.S., Rose, P., Stott, A., Tew, T., Thomas, C.D., Thompson, D.B.A., Vickery, J.A., Walker, M., Walmsley, C., Warrington, S., Watkinson, A.R., Williams, R.J., Woodroffe, R. & Woodroof, H.J. (2008) Future novel threats and opportunities facing UK biodiversity identified by horizon scanning. *Journal of Applied Ecology*, **45**, 821–833.

Tatem, A.J., Hay, S.I. & Rogers, D.J. (2006) Global traffic and disease vector dispersal. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 6242–6247.
UNCTAD (2007) *Review of Maritime Transport*. United Nations Conference on Trade and Development, Geneva, Switzerland.
Urban, M.C., Phillips, B.L., Skelly, D.K. & Shine, R. (2008) A toad more traveled: the heterogeneous invasion dynamics of cane toads in Australia. *American Naturalist*, **171**, E134–E148.
USDOT (2007) *North American Transportation Highlights*. United States Department of Transportation – Bureau of Transportation Statistics, Washington, D.C.
Van der Windt, H.J. & Swart, J.A.A. (2008) Ecological corridors, connecting science and politics: the case of the Green River in the Netherlands. *Journal of Applied Ecology*, **45**, 124–132.
Weber, E. & Li, B. (2008) Plant invasions in China: What is to be expected in the wake of economic development? *Bioscience*, **58**, 437–444.
Westphal, M.I., Browne, M., MacKinnon, K. & Noble, I. (2008) The link between international trade and the global distribution of invasive alien species. *Biological Invasions*, **10**, 391–398.

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