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Grasping at the routes of biological invasions: a framework for integrating pathways into policy

P. E. Hulme[1,2]*, S. Bacher[3], M. Kenis[4], S. Klotz[5], I. Kühn[5], D. Minchin[6], W. Nentwig[3], S. Olenin[7], V. Panov[8], J. Pergl[9], P. Pyšek[9,10], A. Roques[11], D. Sol[12], W. Solarz[13] and M. Vilà[14]

[1]*NERC Centre for Ecology and Hydrology, Banchory, UK;* [2]*National Centre for Advanced Bio-Protection Technologies, PO Box 84, Lincoln University, Canterbury, New Zealand;* [3]*Community Ecology, University of Bern, Switzerland;* [4]*CABI Europe–Switzerland, Delémont, Switzerland;* [5]*UFZ–Helmholtz Centre for Environmental Research, Department Community Ecology (BZF), Halle, Germany;* [6]*Marine Organism Investigations, Ballina, Killaloe, Ireland;* [7]*Coastal Research and Planning Institute, Klaipeda, Lithuania;* [8]*Faculty of Geography and Geoecology, St Petersburg State University, Russia;* [9]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Prùhonice, Czech Republic;* [10]*Department of Ecology, Faculty of Science, Charles University, Vinièná 7, CZ-128 01 Praha 2, Czech Republic;* [11]*INRA Zoologie Forestière BP 20619 F-45166-Olivet, France;* [12]*CREAF, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Spain;* [13]*Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120 Krakow, Poland; and* [14]*Estación Biológica de Doñana, Avd/Parque de María Luisa s/n Pabellón del Perú, E-41013 Sevilla, Spain*

Summary

1. Pathways describe the processes that result in the introduction of alien species from one location to another. A framework is proposed to facilitate the comparative analysis of invasion pathways by a wide range of taxa in both terrestrial and aquatic ecosystems. Comparisons with a range of data helped identify existing gaps in current knowledge of pathways and highlight the limitations of existing legislation to manage introductions of alien species. The scheme aims for universality but uses the European Union as a case study for the regulatory perspectives.

2. Alien species may arrive and enter a new region through three broad mechanisms: importation of a commodity, arrival of a transport vector, and/or natural spread from a neighbouring region where the species is itself alien. These three mechanisms result in six principal pathways: release, escape, contaminant, stowaway, corridor and unaided.

3. 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. 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.

4. Vertebrate pathways tend to be characterized as deliberate releases, invertebrates as contaminants and plants as escapes. Pathogenic micro-organisms and fungi are generally introduced as contaminants of their hosts. The corridor and unaided pathways are often ignored in pathway assessments but warrant further detailed consideration.

5. *Synthesis and applications.* Intentional releases and escapes should be straightforward to monitor and regulate but, in practice, developing legislation has proved difficult. New introductions continue to occur through contaminant, stowaway, corridor and unaided pathways. These pathways represent special challenges for management and legislation. The present framework should enable these trends to be monitored more clearly and hopefully lead to the development of appropriate regulations or codes of practice to stem the number of future introductions.

Key-words: biocontrol, biosecurity, exotic, pests, propagule pressure, regulation, weeds

*Correspondence author. National Centre for Advanced Bio-Protection Technologies, PO Box 84, Lincoln University, Canterbury, New Zealand. E-mail: hulmep@lincoln.ac.nz

Introduction

There is an increasing awareness that the different mechanisms by which alien species become introduced from one location to another play a pivotal role in the subsequent likelihood of biological invasion (Ruiz & Carlton 2003; Perrings *et al*. 2005; Hulme *et al*. 2007). In the absence of detailed data on rates of individual species introductions, accounting for these 'pathways of introduction' may be essential for disentangling the role of species and ecosystem traits in biological invasions as well as predicting future trends and identifying management options (Colautti, Grigorovich & MacIsaac 2006). As a result, an increasing number of studies attempt to quantify the likelihood of invasion using the frequency, scale and reliability of introduction pathways (Garcia-Berthou *et al*. 2005; Lambdon & Hulme 2006; Kenis *et al*. 2007). While there is certainly a need to increase existing knowledge of pathways, it is also imperative that this information is translated into appropriate management responses (Hulme 2006). To date, the management perspective of pathways is still rudimentary and in response we present a framework that attempts to position the scientific findings within the context of current regulatory instruments. For concise presentation, a European Union (EU) focus is taken on regulatory issues, although many of these legislative instruments apply more widely. The framework highlights the patchy nature of appropriate regulations, identifies important gaps and emphasizes that legislative instruments developed in response to past invasion scenarios may not be effective in addressing future threats.

The divergence between the complexity of biological invasions and the subsequent regulatory framework is illustrated by almost 30 different pathways recorded in the Global Invasive Species Database (Fig. 1a) while the Convention on Biological Diversity (CBD) only distinguishes two. The latter separates 'intentional introductions', which refer to the deliberate movement and/or release by humans of an alien species outside its natural range (past or present), from 'unintentional introductions', which describes all other introductions that are not intentional (Miller, Kettunen & Shine 2006). As there are many ways an alien species can enter into a new region, and globalization will ensure that the diversity of pathways will be dynamic and probably increase over time (Perrings *et al*. 2005), it is unlikely that robust regulations will be implemented for each specific pathway. However, a simple division based on human intention is likely to be too simplistic, as, rather than being dichotomous, there is a continuum in the degree of human intention attributable to most pathways (Fig. 2). Thus there is a critical need for an approach that balances comprehensiveness with utility in terms of both understanding the drivers of invasion and guiding management responses. In this account we propose a simplified pathway framework to facilitate the comparative analysis and regulation of invasions by a wide range of taxa across a diversity of biomes. Such an approach is essential to assess risks to biodiversity posed by global change drivers such as invasions (Settele *et al*. 2005) and communicate them to policymakers where legislation is rarely taxon specific (Shine, Williams & Gundling 2000). We examine the framework with reference to data drawn from global and European data sets in order to illustrate the approach, identify existing gaps in current knowledge of pathways and highlight the limitations of existing legislation for managing introductions of alien species.

A simplified framework to integrate introduction pathways

Although CBD defines introductions as movement of an alien species that 'can be either within a country or between countries or areas beyond national jurisdiction' (Miller, Kettunen & Shine 2006), alien status is an attribute associated with a specific political or administrative region and, as a result, national and regional data sets describing pathways often tend to catalogue only the means of initial introduction into a region and rarely distinguish the process of subsequent spread (Fig. 1a). Movement of alien species across biogeographical boundaries, where potential ecological impacts may be great, may not be captured by existing regulations where such boundaries occur within a single political or administrative region. Existing pathway classifications often distinguish between pre- and post-border movement. Such a nomenclature works well within a specific national border and reflects a logical sequence of events. It breaks down in cases such as Europe, where post-border movement in one nation can be sufficiently marked to spill-over into neighbouring territories and results in a pre-border introduction. Although the proposed framework primarily addresses the means by which alien organisms arrive and enter into a new region, it needs to include such spill-over events. This is in part because of the particular political geography of Europe but is relevant wherever contiguous political borders occur.

Knowledge of the means of initial introduction is crucial for developing preventative methods such as screening systems, interception programmes, early warning strategies and import regulations (Hulme 2006). Alien species may, as a direct or indirect result of human activity, arrive and enter into a new region through three broad mechanisms: the importation of a commodity, the arrival of a transport vector, and/or natural spread from a neighbouring region where it is itself alien. The three mechanisms result in six principal pathways, reflecting a gradient of human involvement: release, escape, contaminant, stowaway, corridor and unaided (Fig. 2).

The trade in commodities may either directly or indirectly lead to the introduction of alien species from one region to another. The alien species may itself be the commodity, usually, but not necessarily, a commercially valuable species that is traded. Alien species traded as commodities may become introduced either as an intentional release, for example game animals, biocontrol agents and landscape plants, or as an unintentional escape from captivity, for example from gardens, fur farms, aquaculture and zoos. The term 'escape' covers a variety of circumstances that differ in the degree of human intention and range from unforeseen events, such as a flood that washes alien plants from a pond into a river, to an owner who, in clearing weeds from a pond, throws the waste

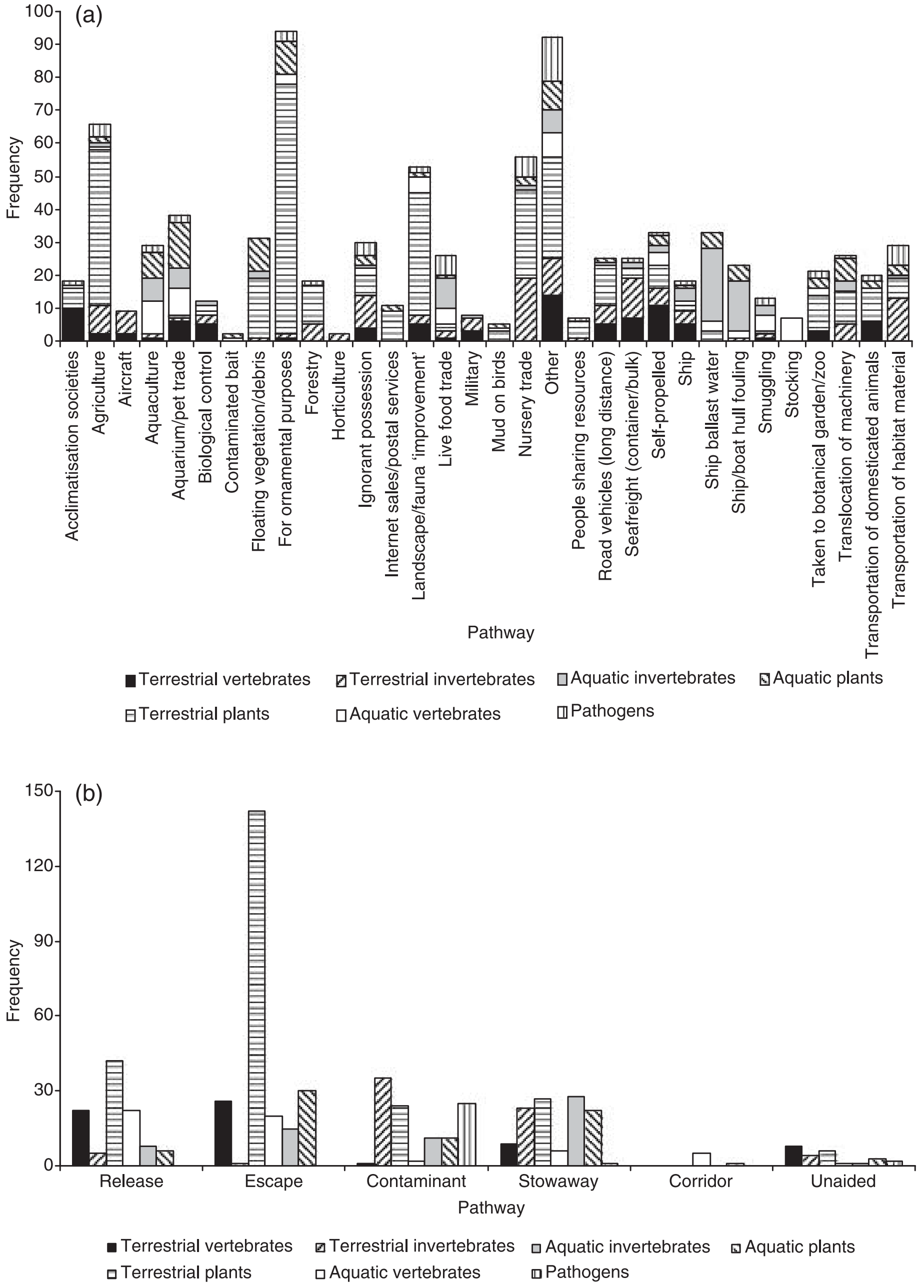

Fig. 1. Frequency of different pathways facilitating the establishment in the wild of more than 400 alien taxa listed in the Global Invasive Species Database (www.issg.org/database, accessed on 10/01/2007) presented by (a) the pathways categories promoted by the Global Invasive Species Information Network and (b) the present framework.

into a neighbouring stream. Aliens may also occur as a contaminant of a commodity. A typical example of a contaminant pathway is weed seed transported with international grain shipments and introduced into the wider environment through agricultural activities (Hulme 2005) but this category also includes the introduction of obligate pathogens and parasites of 'live' goods (including timber). While the commodity is introduced intentionally, the contaminant is introduced unintentionally. Commensal species are also often introduced as contaminants, as illustrated by seaweeds and crustaceans attached to oysters traded for mariculture (Minchin 1997). A key attribute of the contaminant pathway is that both the occurrence and associated species traits can be partially predicted from a knowledge of the commodities themselves. The magnitude and trend in the trade of particular commodities, such as agricultural produce, timber products and aggregates, may provide a proxy for estimating the potential propagule pressure of specific contaminants.

The arrival and entry of alien species can be associated directly with human transport via one or more vectors (e.g. ship, train, aircraft and automobile) but be independent of a specific commodity. Such introductions are classed as stowaways, cf. to hide in a vehicle, ship or aeroplane in order to travel without permission (Rundell & Fox 2002). Stowaways

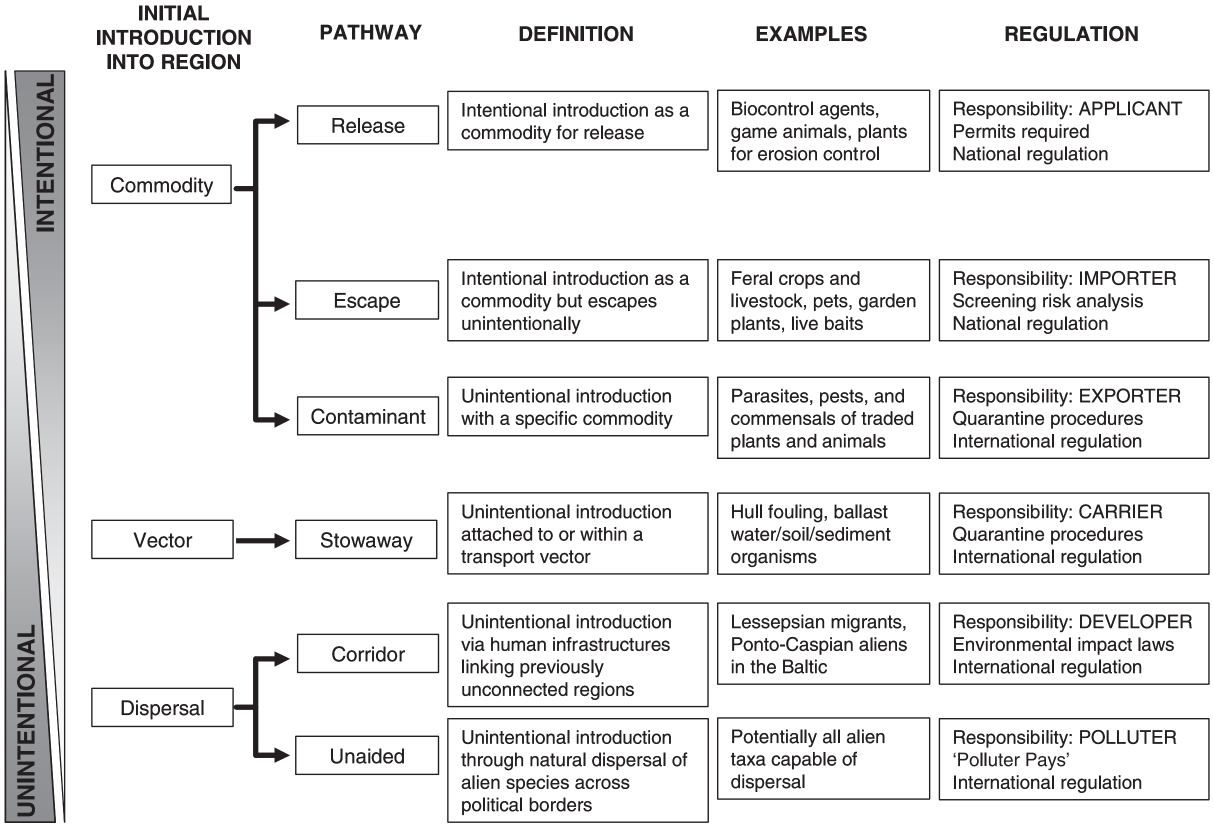

Fig. 2. A simplified framework to categorize pathways of initial introduction of alien species into a new region. Alien species may, as a direct or indirect result of human activity, arrive and enter into a new region through three broad mechanisms: the importation of a commodity, the arrival of a transport vector and/or natural spread from a neighbouring region where the species is itself alien. Five pathways are associated with human activity either as commodities (release and escape), contaminants of commodities, stowaways on modes of transport and opportunists exploiting corridors resulting from transport infrastructures. The sixth category highlights alien species that may arrive unaided in a region as a result of natural spread (rather than human transport) following a primary human-mediated introduction in a neighbouring region. For each pathway a brief description is presented with examples. The different regulatory approaches for each pathway are also illustrated. While a case is often made regarding differences between intentional vs. unintentional introductions, the scheme highlights a gradient of human intention that reflects the difficulty in distinguishing between ignorant and premeditated action.

include organisms that foul the hulls of ships, are transported as seeds or resting stages in soil attached to vehicles and in ballast water, as well as in shipping containers, cargo and airfreight (Mikheyev & Mueller 2006). In contrast to contaminants of commodities, the stowaway pathway is defined more by the tempo and mode of transport, which may provide a proxy for propagule pressure, rather than any specific attributes of a commodity.

The CBD definition of introduction explicitly identifies the role of human agency in the movement of alien species and can be readily identified in the description of release, escape, contaminant and stowaway pathways. However, humans may also facilitate the natural spread of alien species across administrative and biogeographical borders. The corridor pathway refers to the introduction of aliens into a new region following the construction of transport infrastructures in whose absence spread would not have been possible (Hansen & Clevenger 2005; Gollasch, Galil & Cohen 2006; Galil, Nehring & Panov 2007). Although anthropogenic corridors may simply facilitate the spread of a species within a political territory, they may on occasion connect previously isolated biogeographical regions where the likelihood of environmental impacts might be greater. Such trans-biogeographical corridors include canals (connecting river catchments and seas), tunnels (linking mountain valleys) and bridges (between islands and mainlands).

Alien species may of course arrive in a region without direct or indirect human assistance through natural dispersal. The brown seaweed *Sargassum muticum* (Yendo) Fensholt is believed to have been introduced initially to the coasts of northern France as a contaminant of commercial oysters but has subsequently spread naturally via drifting plants to the English south coast and the Netherlands (Wallentinus 1999). The unaided pathway characterizes the circumstances where natural spread of an established alien species results in the appearance of this species in a new biogeographical or political region from a donor region where it was previously introduced through any of the five pathways described above. There is increasing recognition that species arriving through the unaided pathway must be recognized as aliens (Pyšek *et al*. 2004). Corridors and unaided pathways lead to the appearance of new alien species in a region in the absence of direct human transport but, whereas species arriving through the former may be native or alien in the donor area, the unaided pathway only involves the movement of aliens from the donor region.

These pathway categories are not mutually exclusive for alien species, and an organism may be introduced through more than one pathway. For example, the toxic dinoflagellate *Alexandrium catenatum* Halim, originating from Japan, may have arrived in France by aeroplane as a contaminant of imported oysters or as a stowaway in ship ballast and subsequently discharged into French coastal waters (Lilly *et al*. 2002).

Comparing introduction pathways across taxa and ecosystems

The new framework reduces the variety of invasion pathways down to a manageable yet comprehensive six-way classification. Any loss of specific detail relating to individual pathways is countered by the ease with which the simplified framework facilitates comparisons across taxa and biomes (compare trends in Fig. 1). Corridors appear to be associated with aquatic rather than terrestrial environments, highlighting the importance of canal networks in the movement of alien species. However, once the corridor pathway is excluded, there are similarities in aquatic and terrestrial environments for vertebrate pathways, with releases and/or escapes being the main mechanism ($\chi^2 = 5{\cdot}32$, d.f. 4, NS). This similarity is not found in comparisons of terrestrial vs. aquatic plants ($\chi^2 = 21{\cdot}20$, d.f. 4, $P < 0{\cdot}01$) or invertebrates ($\chi^2 = 27{\cdot}60$, d.f. 4, $P < 0{\cdot}01$), which differ significantly. Unlike terrestrial plants, which are often deliberately released for landscaping, pasture improvement and land reclamation, aquatic plants are less frequently released deliberately but more often escape or are stowaways attached to river/canal traffic. Escapes represent a significantly greater source of introductions for aquatic rather than terrestrial invertebrates, as these are often important elements of mariculture or used as bait in angling. Across both aquatic and terrestrial ecosystems, considerable variation is found for the different taxa ($\chi^2 = 154{\cdot}3$, d.f. 8, $P < 0{\cdot}001$). Vertebrate pathways tend to be characterized by deliberate releases, invertebrates by contaminants and plants by escapes (Fig. 2b). It is not surprising to note that pathogenic micro-organisms, fungi and parasites are generally introduced as contaminants of their hosts. Corridors and unaided pathways encompass a minority of species introductions compared with the other four pathways. However, both pathways, often largely ignored in assessments, warrant further detailed consideration. Most species are associated with only a single pathway (62·5%) and only a minority (5·6%) are found associated with three or more pathways.

Introduction pathways in Europe

While the trends represented in the Global Invasive Species Database illustrate the utility of the framework, data are heterogeneous in terms of global coverage, taxonomic composition and emphasis on invasive alien rather than alien species. Comparison of the general patterns in the pathway categories for terrestrial and aquatic alien taxa drawn from a range of European regions may be more appropriate for identifying trends and gaps (Table 1).

A significant proportion of non-native plants and animals established in Europe have resulted from intentional releases. Alien vertebrates have often been released into the wild as game animals or in attempts to improve local fauna (Table 2). Associated with intentional establishment of game are alien plants introduced for cover and aquatic invertebrates as bait. Pathogens, invertebrates and vertebrates have all been successfully established as biocontrol agents in Europe (Crivelli 1995; Kenis *et al*. 2007). Intentional releases often result in widespread establishment of aliens as a result of care during transport, supplementary feeding, repeated introductions and/or the release of a high number of individuals.

The escape of alien plants and animals from managed environments is frequent and includes feral crops, livestock and farmed fishes, liberation of animals from fur farms, escapes of ornamental species and disposal of unwanted pets. Although relatively rare on an individual basis, the frequency of escapes is often high because of the large number and widespread distribution of individuals that together present many opportunities for escape. The significance of escapes for the spread of alien plants (aquatic and terrestrial), reptiles, amphibians and mammals (proportionally more so than birds or aquatic animals) illustrates the need for regulation of this pathway (Table 1). Few invasions of terrestrial invertebrates originate from escapes, but populations of the Asian harlequin ladybird *Harmonia axyridis* (Pallas) in Europe probably come from specimens that escaped from greenhouses where this predator was used as a biological control agent (Majerus, Strawson & Roy 2006).

The introduction of aliens as contaminants may often be predicted from their association with specific commodities. Pests, pathogens and parasites are often introduced with their hosts. In Europe, the majority of introductions of alien insects are associated with the international plant trade (Kenis *et al*. 2007). In particular, aphids and scale insects are often carried inconspicuously with their host plant. Not surprisingly, contaminants feature strongly in the introduction of insects and this would be expected for most parasites and pathogens as well (Table 1). In Europe, seed contaminants of grain supplies and feed-stuffs account for around one-quarter of all known introductions (Hulme 2005). The transport of soil and aggregates provides another route of entry for a variety of micro-organisms, plants and animals, often as resting stages such as seeds, spores and eggs.

The interior and exterior of aircraft, ships, trains and other vehicles provide countless opportunities for the arrival and entry of stowaways. The most evident group of stowaways includes aquatic species that foul the hulls of boats and ships (Table 1). A detailed survey of alien species introduced by shipping into the North Sea region revealed that stowaways (mainly crustaceans and bivalves) were found in 96% of hull samples but in only 38% and 57% of ballast water and

Table 1. General trends in the introduction pathways of a range of terrestrial and aquatic alien taxa in different regions of Europe. Values are the numbers of species introduced and species may be represented in more than one category; ? indicates that this pathway could not be distinguished

	Pathway category							
Taxon/region	Release	Escape	Contaminant	Stowaway	Corridor	Unaided	Unknown	Source
Vascular plants								
Czech Republic	103	671	267	24	0	?	15	Pyšek, Sádlo & Mandák (2002)
Germany	424	479	511	361	0	?	40	Kühn & Klotz (2002, 2003)
Scotland	7	186	39	35	0	0	4	Welch *et al*. (2001)
Mediterranean islands	130	660	80	110	0	0	26	Hulme *et al*. (2007)
Insects								
Austria and Switzerland	12	1	199	110	0	14	18	Essl & Rabitsch (2002); Kenis (2005)
France	66	1	334	181	0	4	11	A. Roques, unpubl. data
Reptiles and amphibians								
Europe	39	9	6	6	0	3	59	Gasc *et al*. (1997); Lever (2003)
Birds								
Europe	61	43	0	2	0	8	15	Lever (2006); Long (1981)
Mammals								
Europe	71	20	1	6	0	1	2	Long (2003)
Fish								
Spain and Portugal	22	4	1	0	0	0	0	Garcia-Berthou *et al*. (2005)
Ireland	8	2	0	0	0	1	0	D. Minchin, unpubl. data
Baltic States	32	0	0	1	0	0	0	Olenin (2005); Olenin, Leppäkoski & Daunys (2007)
European Russia	34	3	1	1	12	5	1	Panov, unpublished
Aquatic invertebrates								
Ireland	10	6	16	17	0	1	4	D. Minchin, unpubl. data
Baltic States	10	3	1	15	3	12	2	Olenin (2005); Olenin, Leppäkoski & Daunys (2007)
European Russia	18	0	4	46	26	8	6	Panov, unpublished
Aquatic plants								
Ireland	6	14	2	4	0	4	8	D. Minchin, unpubl. data
Baltic States	3	3	0	0	0	0	1	Olenin (2005); Olenin, Leppäkoski & Daunys (2007)
European Russia	1	0	0	5	2	3	0	Panov, unpublished

Table 2. Primary sources for the releases and escapes of alien reptiles and amphibians, birds and mammals in Europe. Values are the numbers of species introduced and species may be represented in more than one category

	Reptiles and amphibians	Birds	Mammals
Releases			
Agriculture	1	0	12
Biological control	2	1	3
For food/game	8	61	31
Fauna 'improvement'	28	44	47
Research	2	0	0
Escapes			
For food	10	7	4
As pet	9	75	12
From zoos	1	48	20
From fur farms	0	0	27

sediment, respectively (Gollasch 2002). Many alien species for which the exact introduction pathway is unknown are likely to be stowaways. The horse-chestnut leafminer *Cameraria ohridella* Deschka and Dimic has spread widely in Europe and, while movement of ornamental planting material could exacerbate spread, most dispersal is undoubtedly through transport on cars, lorries and railway wagons (Gilbert *et al*. 2005). Many alien insects are detritivores or predators and often found in any kind of container (Kenis *et al*. 2007). In general, stowaways appear less associated with a specific commodity but more with particular vectors, and increased trade and travel will increase the importance of this pathway.

Although major infrastructural developments will increase the likelihood of introductions resulting from commodities, contaminants and stowaways as a result of increased transport traffic, the infrastructures may also provide invasion corridors. The construction of canals has enabled the transfer of species from one region to another and they have their greatest impact when they connect two or more biogeographical areas that were previously isolated from each other (Gollasch, Galil & Cohen 2006; Galil, Nehring & Panov 2007). The progressive interconnection of canals and rivers has facilitated the invasion of native species from the Caspian and Black Seas into the Baltic and North Seas (Table 1; Galil, Nehring & Panov 2007). It can be difficult to distinguish the corridor pathways of species that have moved through the infrastructure as contaminants in ballast water or as stowaways on hulls of ships. Identification of free-living species within the canal network would give an indication of potential natural spread along the infrastructure. The corridor pathway tends to be less important in the introduction of terrestrial biota and is probably underestimated but it is likely to occur through tunnels, bridges and even the heavily modified roadsides, which act as hospitable corridors connecting different regions (Table 1; Hansen & Clevenger 2005).

Once introduced, alien species may spread across the region through natural, rather than human-assisted, dispersal. Relatively high average estimates of the rate of spread of introduced species have been made for both terrestrial (89 km $year^{-1}$) and marine (50 km $year^{-1}$) environments (Grosholz 1996; Pyšek & Hulme 2005). Over time it is quite likely that species successfully introduced to a single location will spread to other regions, where they may be recorded for the first time as alien. European examples include the macro-alga *Sargassum* drifting from France to the UK, the Harlequin ladybird spreading from Belgium to the rest of Europe, red swamp crayfish *Procambarus clarkii* Girard moving from Spain to Portugal, the ruddy duck *Oxyura jamaicensis* Gmelin reaching Spain following its establishment in the wild in the UK and the raccoon dog *Nyctereutes procyonoides* Temminck colonizing Europe from neighbouring regions of the former USSR. Given the impressive rates of spread of alien species the likelihood is that the unaided pathway is significantly underestimated in most analyses (Table 1).

Trends in the global and European data appear superficially similar, with the primary pathway in both data sets being the same for terrestrial and aquatic plants (escape), terrestrial invertebrates (contaminant) and aquatic invertebrates (stowaways). Vertebrates tend to be proportionally more represented by releases in Europe but by escapes in the global data set. More detailed comparison (excluding the few data on corridors) reveals that, while trends in either data set do not differ significantly for terrestrial invertebrates or aquatic plants ($\chi^2 = 8{\cdot}32$ and $\chi^2 = 12{\cdot}24$, respectively, both d.f. 8, NS), the European data set is less well represented by the unaided pathway for terrestrial plants and vertebrates ($\chi^2 = 122{\cdot}56$ and $\chi^2 = 22{\cdot}57$, respectively, both d.f. 8, $P < 0{\cdot}01$) and escapes for fish ($\chi^2 = 37{\cdot}05$, d.f. 8, $P < 0{\cdot}01$). The only data for which an analysis of corridors was appropriate were for aquatic invertebrates, where European data had a higher representation of the corridor pathway and fewer escapes ($\chi^2 = 36{\cdot}21$, d.f. 10, $P < 0{\cdot}01$). Differences were also seen within the nations of Europe (Table 1), showing that pathways can often be idiosyncratic and reflect historical, geographical and economic attributes of a region as much as the characteristics of the alien species themselves.

Applying the framework: policy implications of pathways

The CBD has identified major gaps in the binding international regulatory framework related to pathways. They include hull fouling; civil air transport; aquaculture/mariculture; military activities; emergency relief aid; international development assistance; scientific research; tourism; pets, aquarium and garden pond species; live bait and live food; plant seeds; biocontrol agents; *ex-situ* animal breeding programmes; incentive schemes linked to re-afforestation; and interbasin water transfer and canals (Miller, Kettunen & Shine 2006). Developing legislation for each and every one of these unique pathways, identifying the different sectors involved and reaching binding agreements will be a massive challenge. By categorizing pathways into only six broad classes, the framework may assist the development of overarching legislation targeting the shared attributes of most pathways based on the degree of intention, means of transport and subsequent introduction (Fig. 2 and Table 3). Development of legislation and codes of practice will have to address different sectors in each pathway, for example hunting federations for releases, pet and ornamental plant trade for escapes, importers for commodities, transport organizations for stowaways, civil engineers for corridors.

In principle, intentional releases of alien species should be the most straightforward pathway to address through legislation. The Bern Convention on Conservation of European Wildlife and Natural Habitats, enshrined in the EU Birds and Habitat Directives, requires each contracting party to 'strictly control the introduction of non-native species' and recommends that the introduction of non-native species into the environment should be prohibited. Exceptions may be authorized on the condition that the potential consequences of such introductions are assessed beforehand. The Food and Agriculture Organization (FAO) Code of Conduct for the Import and Release of Exotic Biological Control Agents highlights elements to be considered when assessing the risks of deliberate releases. Although the European and Mediterranean Plant Protection Organization (EPPO) provides guidance for best practice (including a positive list of biocontrol agents without known negative side-effects), member countries do not always follow these recommendations. The Forest Reproductive Material Directive allows the prohibition and restriction of marketing of reproductive material from 46 tree species and includes several alien trees known to naturalize in parts of Europe. Member states select those trees they wish to regulate, but evidence of continued marketing of alien species in countries where they are known to naturalize highlights that risk assessments focus more on adverse affects on forestry than the natural environment.

The EU Zoo Animals Directive relating to the keeping of wild animals in zoos places a responsibility for 'preventing the escape of animals in order to avoid possible ecological threats to indigenous species and preventing intrusion of outside pests and vermin' (Miller, Kettunen & Shine 2006). Unfortunately, many alien species are not kept in zoos. Thus, escapes are difficult to regulate unless the responsible parties can be held successfully to account for deliberate or negligent escapes: the location of premises where collections of non-native species are held should be known, the conditions under which they are kept (i.e. the security of their quarters) should be

Table 3. Examples of legislation, regulations and codes of conduct that are relevant to the management of invasion pathways in Europe (further details of these instruments can be found in Shine, Williams & Gundling 2000; Fasham & Trumper 2001; Miller, Kettunen & Shine 2006)

Instrument	Description	Pathways					
		Release	Escape	Contaminant	Stowaway	Corridor	Unaided
Bonn Convention Migratory Species	Migratory species of wild animals	√					
Bern Convention European Wildlife	Conservation of European wildlife	√					
UN Convention Law of the Sea	Introductions to marine environment	√	√	√	√		
ICES Code of Practice	Transfer of marine organisms	√	√				
FAO Code of Conduct Fisheries	Aquaculture introductions	√	√	√			
FAO Code of Conduct Biocontrol	Safe import and release of agents	√	√				
EU Wildlife Trade Regulations	Trade in four specific alien species		√				
Birds and Habitat Directives	Deliberate introductions into wild	√					
Forest Reproductive Material Directive	Use of alien tree material	√	√				
Plant Health Directive	Pest and pathogens injurious to plant health (quarantine pests)			√			
Zoo Animals Directive	Containment of wild animals (and diseases) in zoos		√	√			
Animal Disease Directives	Economically important alien diseases of animals			√			
Cereal Seed Directive	Quality and purity of cereal seed including contaminant weed seed			√			
IPPC Phytosanitary Measures	Quarantine pests, environmental weeds and wood packaging		√	√			
African-Eurasian Migratory Waterbird Agreement	Status of alien waterbirds in collections		√				√
International Civil Aviation Organization Resolution	Alien stowaways in aircraft				√		
Ballast Water Management Convention	Ballast water and sediment			√			

IPPC, International Plant Protection Convention.

specified and enforced, and escaped organisms should be traceable back to their owners. These conditions are not met under any European legislation (Fasham & Trumper 2001). For example, the International Council for the Exploration of the Sea (ICES) has developed a code of practice for movement and translocations of fisheries products and for the introduction of species for culture purposes in order to limit the risk of escapes, yet it has not always been closely followed (Reise, Gollasch & Wolff 1999). Under the Wildlife Trade Regulations, four alien vertebrate species are banned from import and movement within the Europe (Miller, Kettunen & Shine 2006). As all four are already established in many parts of Europe, it is questionable how effective these regulations will be in limiting their spread or how such regulations can help prevent the introduction of other alien species. These legislative limits highlight that escapes will continue to be a major pathway for alien species introductions. This probably also explains why escapes represent a main pathway for plants because, even where adult specimens are confined to gardens, it is usually impractical to prevent seed dispersal, while for many animals attempts can be made to impound them securely in a specific location.

The Plant Health Directive contains measures to be taken in order to prevent the introduction and spread of serious pests and diseases of plants and plant produce. Several animal health directives exist that target pathogens and pests of food-producing animals, including aquaculture species. These 'health' directives identify the pests and pathogens banned from entry into the EU as well as the animal and plant commodities requiring sanitary certificates. These directives only briefly address the risks to the wider natural environment (particularly where pathogens may be spread to native species) and do not include pests and pathogens that do not threaten commercially valuable species. However, the International Plant Protection Convention (IPPC) has recently initiated measures that address invasive alien plants of natural areas (Miller, Kettunen & Shine 2006). The 'Cereal Seed' Directive has established seed certification schemes to ensure imported seed meets prescribed standards of freedom from 'weed' seeds, but these instruments can never be 100% effective. Certification guarantees at most 99·9% seed purity and thus, even today, cereal seed samples can be contaminated by alien species (Hulme 2005). Given the large numbers of seed sown each year this is significant in terms of overall propagule pressure.

The deliberate importation of soil is regulated by import licenses under the Plant Health Directive. In the EU, soil from other member states may be imported without the need for documentation, soil from other parts of continental Europe may be imported if accompanied by a phytosanitary certificate, while the import of soil from all other countries is prohibited unless for scientific research (under conditions of strict containment and destruction). However, the regulations do not apply to soil attached to plants introduced for horticulture, the most probable source for the introduction of the New Zealand flatworm *Arthurdendyus triangulatus* Dendy into the UK.

In contrast to the wide range of legislation targeting alien introductions through trade in commodities, the regulatory background to prevent introductions through stowaways, corridors and unaided pathways is negligible (Table 3). The International Convention for the Control and Management of Ships' Ballast Water and Sediments proposes ballast water exchange by ships in the open sea to flush out alien species, but ships are not always able to exchange ballast water safely under all sea-state conditions (International Maritime Organisation 1997). Adopted in 2004, this convention requires ratification by 30 states but only six states had signed up by 2006 (Miller, Kettunen & Shine 2006). The International Civil Aviation Organization Resolution on Preventing the Introduction of Invasive Alien Species supports actions to reduce the threat from alien species introductions, primarily stowaways, arriving on aircraft (Miller, Kettunen & Shine 2006). Unfortunately, the resolution is non-binding. No similar resolution exists in relation to marine transport assisting the movement of alien species on hulls or in the ships themselves. The Environmental Impact Assessment Directive and the Strategic Impact Assessment Directive address the impact on the natural environment of major infrastructural developments. Although potentially applicable to the assessment of risks posed by infrastructural developments that link previously unconnected catchments, seas and biogeographical zones, these directives have not been applied to alien species issues (Miller, Kettunen & Shine 2006).

Managing natural dispersal through legislation is a challenge and the only regulations that address the potential long-distance spread of alien species are for waterbirds (Table 3) and action is currently being undertaken against the ruddy duck (Smith, Henderson & Robertson 2005). Unfortunately, even where the evidence of extensive spread is overwhelming, management actions may face stiff resistance, for example the failure to cull the grey squirrel *Sciurus carolinensis* Gmelin in Italy (Bertolino & Genovesi 2003). It would be interesting to see whether the Environmental Liability Directive could be used to apply the 'polluter-pays' principle to penalize the negligent introduction of harmful aliens into the natural environment. Under this directive there needs to be one or more identifiable polluters, the damage must be concrete and quantifiable and a causal link should be established between the damage and the identified polluter (Miller, Kettunen & Shine 2006). Whether member states could be held responsible for the negligent spread of invasive aliens into a neighbouring country will have to be seen.

Appraising the framework

The framework presents a significantly reduced set of pathways that facilitates comparisons across taxa, is applicable to terrestrial and aquatic biomes and ties in closely with legislative perspectives. One of the strengths of this approach is that it takes its definitions from real data collated for many higher taxa across a large geographical area. In Europe, commodities, whether arising from deliberate releases or escapes, account for a significant proportion of alien species in terrestrial, freshwater and marine environments. The majority of alien plants established in Europe have arisen from garden or aquarium/pond escapes, while the freshwater alien fauna is largely a result of aquaculture escapes and deliberate release by anglers. In the marine environment, stowaways, contaminants and introductions via corridors account for a high proportion of aliens, whereas contaminants clearly dominate in insects. In theory, intentional releases and escapes should be the most straightforward to monitor and regulate, but in practice developing legislation appropriate for the economic sectors responsible for such introductions has proved difficult. Although voluntary codes of practice have been promoted within the horticulture and pet trade, adoption of the polluter-pays principle, where the costs of recapture, eradication and control are allocated to the agent responsible for an unlawful introduction or escape, appears distant.

Identifying the responsible party involved in the introduction of alien species will facilitate management and regulation (Fig. 2). Deliberate releases should be undertaken under licence, through the issuing of permits and only following detailed risk assessment. The applicant should explicitly show that the benefits of the release outweigh the costs in a risk analysis framework (e.g. host-range testing for biological control, the likelihood of spread and effect on native plant communities for erosion control plants). The probability that an organism in captivity will escape is often high yet, as in the case of pets and garden plants, most owners have limited understanding of biosecurity issues. Under these circumstances, importers offering these species for sale should be responsible for screening species for potential risk, excluding high-risk species from the market, establishing codes of conduct among suppliers and informing buyers of the potential environmental risks. The risk assessment should be similar to those designed for deliberate releases with an additional understanding of the circumstances under which escapes might occur. There should also be an expectation that traded goods are free from contaminants and an exporter should ensure appropriate phyto- and zoosanitary principles are applied on all commodities exported, in terms of risks to both agriculture as well as the natural environment. A clear strategy for preventing and dealing with contaminants when found should be developed. There would be considerable benefits in standardizing the approaches in the legislation addressing releases, escapes and contaminants as these pose similar levels of risk of invasion, albeit for different taxa. Stowaways are introduced with vectors, either on the vectors themselves or on containers transported by the carrier. It should be the carrier's responsibility to ensure ballast water does not contaminate local waters with stowaways, the surfaces of the transport are not encrusted with alien organisms and that cargo and freight have not been colonized by alien species. Most transport infrastructures have the potential to facilitate the introduction of alien species from one region to another but preventing such introductions by establishing barriers is rarely completely effective. Thus responsibilities of the developer should relate to monitoring and responding to evidence of species incursions and/or spread. Unfortunately,

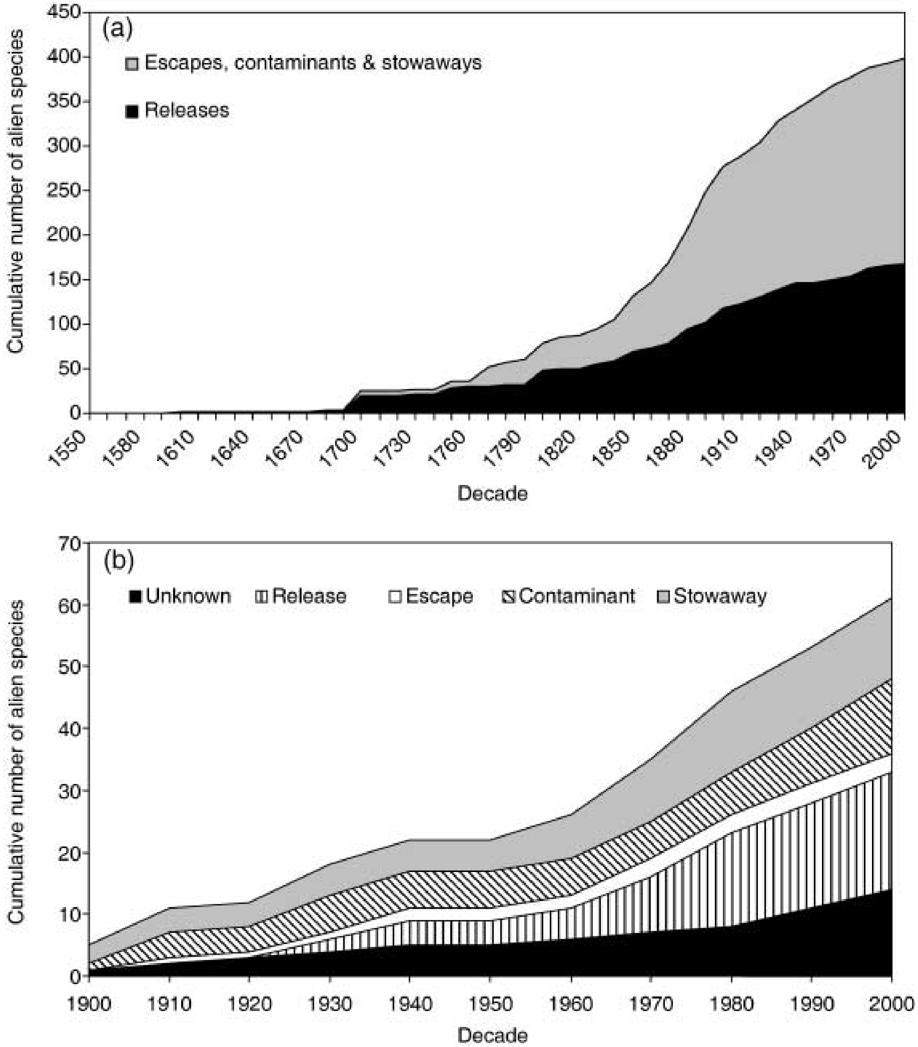

Fig. 3. Temporal trends in the mode of introduction of (a) terrestrial plants and (b) marine species in Nordic countries (data from the North European and Baltic Network on Invasive Alien Species http://www.nobanis.org/, accessed on 10/01/2007).

current environmental impact assessment does not adequately address invasive species (Hulme 2006). Probably the greatest regulatory challenge will be in cases where natural spread occurs but, as such spread is likely to be the result of one or more introduction pathways into the donor region, responsibilities may be identified through knowledge of the initial source (Fig. 2). Existing legislation is often based on the practicality of implementation rather than relative risk. The strong taxonomic links with particular pathways should be a warning against attempts to simply translate risk assessment procedures from one taxonomic group to another, such as in the case of the IPPC, which is attempting to incorporate weed risk assessment procedures within a phytosanitary framework designed for invertebrate pest and diseases. This situation will be made more difficult within large free-trade regions such as Europe that cover a breadth of biogeographical zones, where decisions have to be made regarding species that pose a risk in one territory in relation to their use in territories where they pose no risk, for example planting alien subtropical plants in northern Europe that might be a threat to the cloud forests of the Canary Islands.

However, the current picture is a product of several hundred years of introductions and the evidence to date suggests that the balance of pathways is changing as fewer species are deliberately released and more are introduced through less intentional means (Figs 3 and 4). Such a trend suggests that, while attempts have been made to reduce intentional releases and to some extent escapes, numbers of new introductions continue to occur via contaminant, stowaway, corridor and unaided pathways. These pathways represent special challenges for management and legislation. It is perhaps of greater concern that these pathways are those most frequently associated with invertebrate pests and microbial pathogens. The present framework should enable these trends to be monitored more clearly and hopefully spur the development of appropriate regulations and codes of practice to stem the number of future introductions.

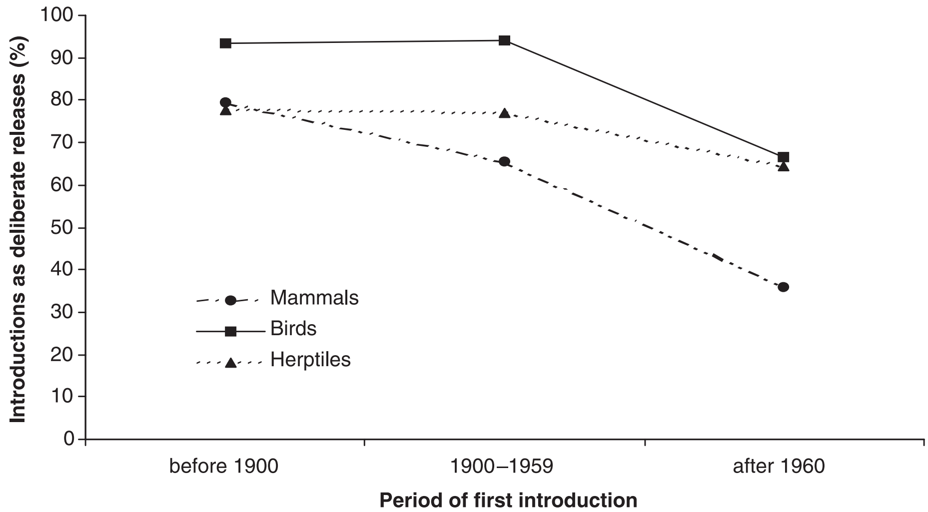

Fig. 4. The proportion of all introduced species arising from deliberate releases of mammals, birds, reptiles and amphibians in Europe over the past *c.* 100 years (for source see Table 1).

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