3 Pathways in Plant Invasions

Ingo Kowarik and Moritz von der Lippe

3.1 Introduction

At least at a global scale, species transfer through human agency is much more frequent, efficient and effective than through natural mechanisms and has no parallel in evolutionary history (Elton 1958; Mack et al. 2000). As propagule pressure is one of the most powerful bottlenecks in invasions (Williamson 1996), human-mediated dispersal is a key process in the range expansion of non-native plant species.

Due to the role of biological invasions as a major threat to biodiversity, recent research has aimed at identifying pathways in invasions which can be regulated to prevent or, at least, curb negative impacts of non-native species (Carlton and Ruiz 2005). Information on the functioning and effectiveness of different pathways is therefore necessary to set priorities in regulation or management (Mack 2003).

In literature on human-mediated plant dispersal, "pathway" is used in two ways: functionally, to describe why and how species are moved by human-mediated agency and geographically, to describe explicit parts of landscapes where dispersal proceeds. Consequently, Carlton and Ruiz (2005) aimed at a more detailed analysis of pathways and proposed to analyse "causes" as the human motivation for introducing species, "vectors" as physical means or agents by which a species is transported, and "routes" and "corridors" as geographic paths over which a species is transferred.

Pathways of plant dispersal vary conspicuously with time (Poschlod and Bonn 1998; Mack and Lonsdale 2001) and at different spatial scales (Pyšek and Hulme 2005; Pauchard and Shea 2006), and so does the underlying human motivation. We illustrate here the relative importance of different pathways in the accidental and deliberate transfer of species in space and time. In order to do so, we describe the usefulness of differentiating first between processes leading to the introduction of a species to a new range and those which subsequently provide secondary releases of the species within its

new range. Then, we argue for a detailed analysis of propagule transport and release as two sub-processes of dispersal. Both may be driven by human agency with or without intention for long periods after initial introduction. We thus emphasise the need to analyse "causes" of plant dispersal far beyond the reasons for introducing a species to a new range.

3.2 Introductions to a New Range: Relative Role of Deliberate Versus Accidental Transfer of Species

Since the first human migrations and the beginning of agriculture and keeping of livestock, humans have purposefully or accidentally transferred plants whenever they have moved themselves, together with animals, seeds and other goods (Hodkinson and Thompson 1997). If this occurs at regional to continental scales, then such transfers result in species introductions, defined as a range expansion of a species through human agency by overcoming major geographical barriers (Richardson et al. 2000).

Both deliberate and accidental plant introductions have long been associated to human migrations. Palaeobotanical studies have revealed a significant influx of new species to Central Europe since the Neolithic period, which evidently increased during the Roman period (Willerding 1986). Most early introductions occurred accidentally, probably as impurities in crop seeds or by attachment to animals. Consistently, accidental introductions dominate pre-1500 introductions to Central Europe, as shown by the Czech flora (Table 3.1).

Table 3.1 Role of deliberately and accidentally introduced species in the non-native Czech flora (modified from Pyšek et al. 2002)

Introduction period	Status	Number of species	Mode of introduction		
			Deliberate	Both	Accidental
Archaeophytes (pre-1500)	Casual	74	30	4	40
	Naturalised	237	17	25	195
	Invasive	21	2	4	15
	Total	332	49	33	250
Neophytes (post-1500)	Casual	817	400	47	370
	Naturalised	160	94	18	48
	Invasive	69	45	4	20
	Total	1,046	539	69	438
Total	Casual	891	430	51	410
	Naturalised	397	111	43	243
	Invasive	90	47	8	35
	Total	1,378	588	102	688

The Romans transferred a broad array of cereals and other useful plants within their empire (Franz 1984). *Castanea sativa* may have started spreading at this time, but its dispersal has been promoted mostly by further cultivation since medieval times (Conedera et al. 2004). Charlemagne's decree *Capitulare de villis*, in 812 AD, enhanced the use of introduced, mainly Mediterranean plants, far beyond the northern limits of their ranges (Franz 1984).

In the post-Columbian period, the number and efficiency of deliberate introductions greatly increased due to the magnitude of intercontinental transfer of organisms (Crosby 1986). The temporal sequence of introductions from different donor areas to Central Europe echoes the history of voyages and discoveries, as illustrated by woody plant introductions to Central Europe (Fig. 3.1a). At a regional scale, the sequence of invasions follows the pattern of infra- and intercontinental introductions (Fig. 3.1b), with an exceedingly variable lag phase which averaged 170 years for trees and 131 for shrubs (Kowarik 1995). As global commerce grows, the frequency of introductions of ornamentals to new areas will continue to increase. A huge potential exists, for example, for importing thousands of previously unavailable Chinese species to the United States (Mack 2001).

Ornamentation is the predominant purpose for introducing plant species, as shown by American plant introductions to Europe (Forman 2003) or the non-native species of the Czech flora which were introduced deliberately: 74 % were ornamentals, 22 % nutritional plants, 14 % medicinal plants, 11 % fodder plants, 6 % were used for landscaping, 5 % as bee plants, and all less than 2 % each as forest crops or oil, dye and fibre plants (Pyšek et al. 2002).

In recent decades, the relative importance of intentional introductions has increased at the infra- and intercontinental scale, as advances in seed cleaning and quarantine measures reduced the efficiency of accidental pathways (Mack and Lonsdale 2001).

3.2.1 Introduction Mode and Invasion Success

Global transfer of goods and people has also fostered the unintentional transport of "hitchhiking" plants. As was illustrated early by the seminal *Flore adventice de Montpellier* (Thellung 1912), accidental introductions may dominate the regional non-native species pool but are clearly less important among the naturalised species (Table 3.2). This also holds at a greater spatial-temporal scale, as for post-1500 introductions to the Czech Republic (Table 3.1) and especially for most recent introductions. Among those now-naturalised species first recorded in Australia between 1971 and 1995, only 2 % are known to be accidental introductions (Mack and Lonsdale 2001).

Both accidental and deliberate introductions contribute to the group of non-native species with detrimental effects. At a landscape scale, the importance of the introduction mode varies strongly. About one-half of the 50
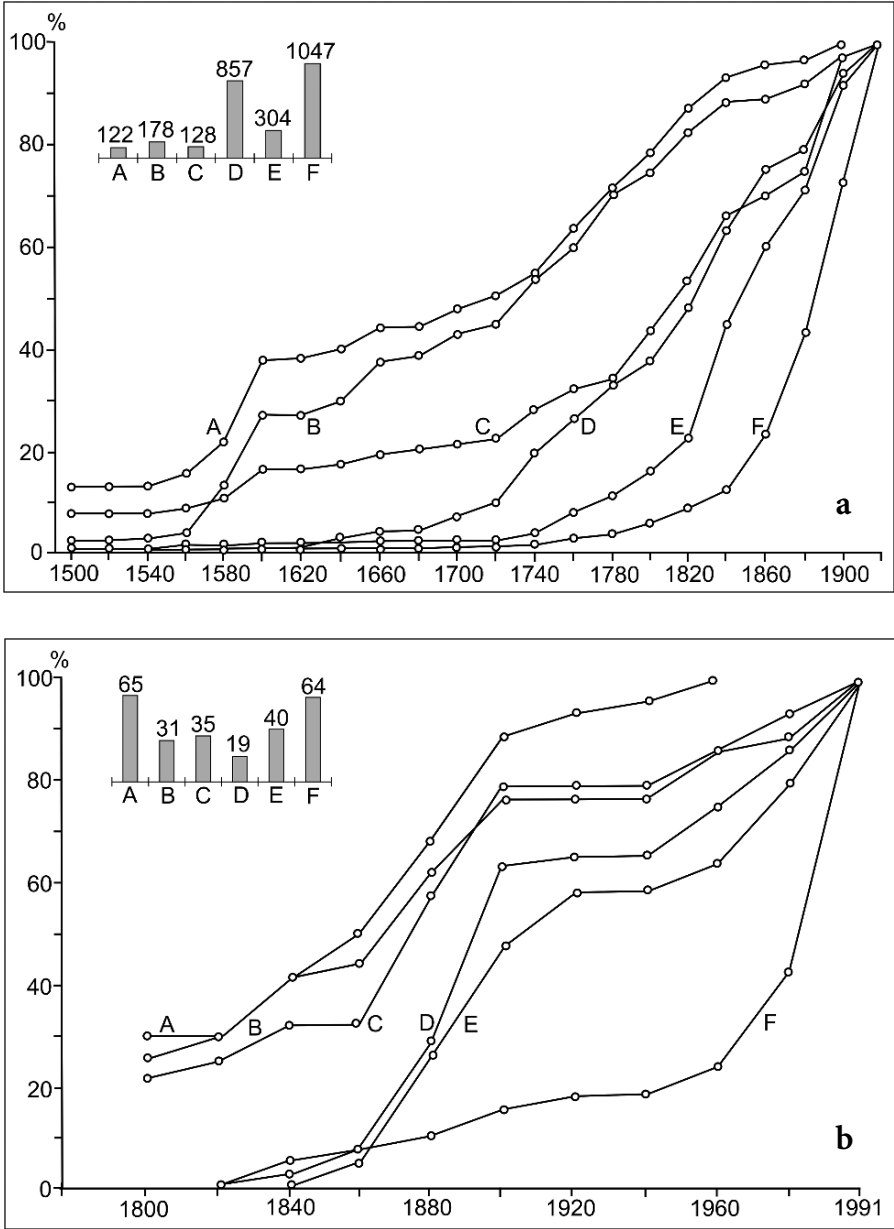
Fig. 3.1a, b Temporal sequence of **a** woody plant introductions from different donor areas to Central Europe and of **b** successive invasions by species from the same donor areas in Brandenburg, Germany, reflecting the history of infra- and intercontinental introductions at a regional scale. The *inserted columns* in **a** show absolute numbers of introductions from *A* parts of Europe excluding the Mediterranean, *B* the Mediterranean, *C* western Asia, *D* North America, *E* Central Asia and *F* East Asia. The *cumulative curves* illustrate the relative importance of introductions from different donor areas for

Table 3.2 Invasion success of accidentally versus deliberately introduced alien plant species to the region of Montpellier (southern France), expressed by the rate of naturalisation of alien species (data from Thellung 1912)

Pathway of introduction	Total of alien species	Subset of casual species		Subset of naturalised species	
	Number	Number	%	Number	%
Total species number	800	693	86.6	107	13.4
a) Deliberate introductions	148	87	58.8	61	41.2
b) Accidental introductions with	621	575	92.6	46	7.4
Wool	526	507	96.4	19	3.6
Seed and feed grains	40	31	77.5	9	22.5
Grain crops	18	18	100.0	0	0
Ballast materials	19	10	52.6	9	47.4
Transportation vehicles	18	9	50.0	9	50.0
c) Resulting from hybridisation	31	31	100.0	0	0

species which are classified as noxious in Germany were introduced accidentally, but all of these are virtually confined to arable fields. Almost all non-agricultural conflicts due to invasive plant species result from deliberate introductions (Kowarik 2003). Except for agricultural weeds, the majority of invasive species have evidently been introduced on purpose, and most of these as ornamentals (Reichard and White 2001; Kowarik 2005). In dealing with conservation issues, deliberate introduction is thus the most efficient driver in plant invasions for most terrestrial ecosystems. In marine ecosystems, however, accidentally introduced plants prevail, due mainly to aquaculture and ballast water which serve as effective pathways for species transfer (Chap. 4).

3.2.2 Coinciding Pathways of Deliberate and Accidental Introductions

The example of the seed trade illustrates how deliberate and accidental pathways may coincide, thereby increasing vector efficiency. Deliberate transfer of seeds has led to an efficient infra- and intercontinental exchange of arable

---

20-year time spans over a period of 400 years (data from Kowarik 1992). The *inserted columns* in **b** show absolute numbers of spontaneously occurring non-native woody species in the region of Brandenburg from the same donor areas (*A–F*) as shown in **a**. The *cumulative curves* illustrate the relative importance of spontaneously emerging species from different donor areas for 20-year time spans over a period of 200 years, calculated from data in regional floras (100 %=210 species; species occurring in more than one donor area were calculated repeatedly; data from Kowarik 1992)

crops, grasses and legumes. Crops have always been potential weeds, and vice versa (Gressel 2005). De-domestication by endo- or exoferality evidently functions as a prerequisite of potential invasions by many crop species (Gressel 2005). Among the deliberately sown species, mainly perennials have started to spread, such as African grass species which were previously used to establish pastures in tropical America (Williams and Baruch 2000).

Since early times, the deliberate transfer of crop seeds has provided a powerful pathway for accidental introductions through seed impurities. The Roman period, for example, provided a significant influx of Mediterranean species to the flora of arable fields in occupied territories north of the Alps (Willerding 1986). In the 19th century, transport routes of crop seeds could be precisely reconstituted based on the native area of associated species (Thellung 1915). The commercialisation of the seed trade undoubtedly enhanced the spread of associated weeds (Mack 1991). Prior to the establishment of efficient seed-cleaning procedures during the last century, 6 billion seeds per year are believed to have been sown accidentally with clover and grass seeds in Great Britain (Salisbury 1953). On arable fields, the recent sharp decline of many species dispersed with crop seeds indirectly highlights the key role of seed transfer in accidental introductions (Kornas 1988).

Interestingly, crop seeds were often deliberately contaminated with seeds of other species to boost sales profits falsely by increasing harvest mass or declaring a higher-rated origin for the goods, e.g. by adding the North American *Ambrosia artemisiifolia* to seeds of other provenances (Nobbe 1876). Today, *Ambrosia*, which had been also introduced as a true American seed import, is a noxious species in Europe due to its allergenic effects (Chauvel et al. 2006).

The distribution of garden plants or forest crops also integrates deliberate and accidental pathways of species transfer, as weeds often co-occur with crops in the soil (Prach et al. 1995; Hodkinson and Thompson 1997). The highly invasive *Chondrilla juncea* was initially introduced to Australia attached to imported vine-stocks (Mack and Lonsdale 2001).

3.2.3 Invasions at the Infra-Specific Level Through Deliberate Introductions

Reintroductions of native species frequently occur in grasses and leguminoses as well as in woody species because their seeds can often be produced at a lower cost abroad. As introduced provenances of native species, especially cultivars, differ genetically from regional populations, their transfer probably provides highly effective, albeit clandestine pathways for invasions at the infra-specific level. In Spain, introduced provenances of *Dactylis glomerata* spread from sown to natural grassland and affected endemic taxa of the same species by competition and hybridisation (Lumaret 1990). Many tree nurs-

eries prefer to use introduced seeds to produce native species. Seeds of the hazelnut (*Corylus avellana*), for example, are mainly imported from Italy and Turkey to Germany (Spethmann 1995). Such introductions are believed to affect regional genetic diversity, and they are economically relevant due to possible decreases in frost tolerance, resistance against pathogens, and rates of establishment and growth (Jones et al. 2001).

3.3 Deliberate Secondary Releases Within the New Range

Human-mediated introductions to a new area are a prerequisite for but no guarantee of the subsequent establishment and spread of species at regional and landscape scales. Inter- or infra-continental transport routes between donor and recipient areas mostly have botanical gardens, tree nurseries or seed companies as introduction foci. From here, invasions rarely occur directly, in contrast to that of *Matricaria discoidea* which spread from the botanical garden in Berlin (Sukopp 1972).

Evidently, most invasions by deliberately introduced species spread from invasion foci which were set by secondary releases during decades and centuries subsequent to the initial introduction of a species to a new range (Kowarik 2003). Horticulture and seed companies function mainly as interfaces between continental and regional scales by determining species availability on the market. By this, they indirectly enhance the further regional functions of plantations as invasion foci.

Socioeconomic factors, such as varying market routes or prices through time, influence customers' choice of a species for long periods after an initial introduction to a region. For example, in a sample of 534 ornamentals, species which had escaped cultivation had been for sale more frequently both in the 19th century and today than was the case for non-escaping species (Dehnen-Schmutz et al. 2006). The economically motivated use of plant species may change conspicuously over time, as the fate of the North American black cherry (*Prunus serotina*) in Europe for the last 350 years exemplifies. A switch from a rare ornamental to a forest crop in the 19th century, and broad usage for other reasons during the following century resulted in manifold invasions and finally in control (Starfinger et al. 2003). Similarly, the increasing popularity of *Rhododendron ponticum* in the British Isles facilitated its subsequent spreading (Dehnen-Schmutz and Williamson 2006).

Forestry is a good example of the changing importance of pathways to invasion in time and space. At the end of the 18th century, hundreds of species were introduced to Europe, tree nurseries and experimental forest plantations being the main targets of intercontinental transport routes. About 500 non-native species were listed in 1787 for a single plantation near Berlin (Kowarik 1992). Of these, only those which were planted afterwards in large quantities

at the landscape scale (*Robinia pseudoacacia*, *Quercus rubra*, *Pinus strobus*, *Pseudotsuga menziesii*; Kowarik 2003) became important invaders. Through forestry, in recent decades at least 100 million ha of plantations with non-native species (84 % conifers) have been established in the southern hemisphere (Zobel et al. 1987). Although relatively few in terms of species numbers, invasions by conifers have led to far-reaching ecological and economic consequences (Richardson and Rejmánek 2004).

3.3.1 Cultivation as a Driver in Plant Invasions

Cultivation provides a powerful pathway for subsequent plant invasions at regional and landscape scales by enhancing the establishment of founder populations (Mack 2000) and, even beyond the threshold of naturalisation, species range expansion by bridging adequate but spatially isolated sites (Kowarik 2003).

The maintenance of cultivated individuals by humans may function in protecting non-native plant populations from detrimental environmental effects which may otherwise prevent establishment and further spread (Mack 2000). The vector strength of cultivation is illustrated by the fact that 25 % of 328 cultivated non-native woody species emerged spontaneously in Hamburg's residential areas, as reported by Kowarik (2005). Cultivating species in large quantities provides a high propagule pressure, known to be a decisive driver in plant invasions (Williamson 1996). Several studies demonstrate a close correlation between the quantity of cultivation and subsequent invasion events, for example, for *Eucalyptus* species introduced to South Africa (Rejmánek et al. 2005).

Through regional transfer, deliberate secondary releases may create myriads of potential invasion foci and thereby bridge, often repeatedly, spatial or environmental barriers. Except for agricultural weeds, all problematic invaders in Germany have been frequently dispersed on purpose by a broad array of pathways of secondary releases, which often provide a shift from urban to semi-natural and natural habitats (Kowarik 2003). Deliberate releases also facilitate invasions by amplifying propagule exposure to natural, or other human-mediated, dispersal vectors at the landscape scale. Vertebrates, for example, disperse 50 % of naturalised plant species in Australia (Rejmánek et al. 2005).

In northern Germany, the vector strength of secondary releases was assessed at the landscape scale by analysing the origin of problematic plant populations. The invasion foci of 63–76 % of more than 100 populations could be directly traced back to deliberate releases. Virtually all populations of *Prunus serotina* descended from local forestry plantations. In *Fallopia* species, plantings (20 %), and deposition of garden waste (29 %) and soil (20 %) led to the establishment of over two-thirds of all problematic popula-

tions. In *Heracleum mantegazzianum*, plantings (9 %), sowings by beekeepers (20 %), and deposition of propagules with garden waste (18 %) or soil (4 %) provided key pathways for spreading (Schepker 1998; Kowarik 2003).

Dumping waste into rivers may effectively induce further spread of aquarium plants. Anthropogenically increased water temperature may even enhance tropical species in temperate regions (Hussner and Lösch 2005). For both water and terrestrial plants, deliberate releases to "enrich" nature have been quite effective. Invasion of *Elodea canadensis* started soon after 1859 when the species was released into some lakes near Berlin and, for the small region of Frankonia, 75 species are known to have been planted even at natural sites by amateur botanists (Kowarik 2003).

3.3.2 From Clumped to Linear Patterns

As Pauchard and Shea (2006) state, propagule movement tends, at a regional scale, to follow landscape corridors such as rivers or roads. Secondary releases may overlay the resulting linear patterns, as they lead mostly to clumped releases of species. These result initially in clumped populations adjacent to the site of release, which may persist for decades and centuries as indicators of earlier horticulture (Kowarik 2005). Since the end of the 16th century, *Tulipa sylvestris* has been used as an ornamental north of the Alps. In northwest Germany, about 50 % of all populations and 72 % of populations with more than 10,000 individuals are confined to historical gardens and similar sites of early horticulture. When exposed to rivers, a shift to linear dispersal occurred only rarely (Kowarik and Wohlgemuth 2006). Such shifts to long-distance dispersal frequently occur in many successful invaders and may efficiently overlay former release patterns, for example, in *Heracleum mantegazzianum*, *Impatiens glandulifera* and *Fallopia* species in Europe (Pyšek and Prach 1993). In the United States, more than 370,000 ha of *Tamarix* stands result from plantations along rivers and subsequent dispersal by moving water (Pauchard and Shea 2006).

3.4 Accidental Transfer of Non-Target Species

Among the huge diversity of human-mediated modes of accidental transport of species (Thellung 1912; Ridley 1930; Bonn and Poschlod 1998), two principal ways can be distinguished: (1) the transport by direct association of propagules to a conveyer, such as the attachment of seeds to cars by mud, and (2) the transport of propagules associated with goods which are moved by one or more conveyers. Deliberate and accidental transfer of species may coincide, as illustrated by the pathway of crop seed transfer described above.

Where and how quickly vehicles and ships – or people and animals, as living conveyers, move depend on the method and route of transport. Transport efficiency expressed in terms of number, velocity and spatial reach of moved propagules (Carlton and Ruiz 2005) is not necessarily equivalent to vector efficiency. Transport vectors differ noticeably in the way propagules are released during or after transport. We thus emphasise the role of release processes, which can clearly determine the efficiency of a dispersal pathway and resulting invasion patterns.

3.4.1 Transfer by Goods: Spatial-Temporal Separation of Propagule Transport and Release

In deliberate transfers of target species, the processes of transporting and releasing propagules are usually separated in time and space. Release through cultivation regularly occurs after transport and leads initially to clumped patterns of resulting offspring. As an exception to this general rule, transport losses of target species may provide continuous propagule release during transport, resulting in linear patterns of emerging populations. This is most evident in seed crops which are accidentally dispersed by spilling from loading areas of trains or trucks and subsequently emerge along transport corridors (Suominen 1979). Oilseed rape (*Brassica napus*), for example, can establish large populations alongside roads which may persist over long periods and are associated with major transport routes to oilseed processing plants (Crawley and Brown 2004).

Accidental transfer of species associated with goods leads preferentially to discontinuous patterns of release and clumped populations of the emerging offspring. This may occur both during and after transport. Harbours and train stations are hotspots of non-native diversity which have long been recognised (Thellung 1915; Brandes 1993); this is mostly due to the release of propagules during the switch from one conveyer to another. Associated cleaning procedures often enhance clumped propagule release. *Citrus* fruits, for example, were once often protected by hay on their way from southern to northern European regions. At the end of the train journeys, the packing material was usually discarded at the stations. Jauch (1938) reports 814 species which were moved this way, most of them originating from southern Europe. The release of solid ballast material in the vicinity of ports is another example of a highly efficient transport vector associated with clumped patterns of propagule release at the endpoint of transport routes (Thellung 1915; Ridley 1930). Analogous patterns occur when using water as weighting material, but marine release sites facilitate subsequent long-distance dispersal more effectively than do terrestrial ones (Chap. 4).

As another pathway for accidental introductions, wool imports show a clear separation between propagule transport and release, and also illustrate

how changes in technology may affect vector efficiency through curbing propagule release. More than 1,600 species, mostly from the southern hemisphere, have arrived in Europe associated with wool (Probst 1949). Only a few (e.g. *Xanthium spinosum*, *Senecio inaequidens*; Thellung 1915; Ernst 1998) crossed the threshold of naturalisation (Table 3.2). The confinement of most wool adventives to the vicinity of wool industry sites reflects how propagules were released after transport. Formerly, waste from wool processing contained high amounts of viable seeds and was dispersed, often as organic manure, adjacent to the factories (Salisbury 1964). Today, wool transports still provide a worldwide transfer of propagules, but the number of wool adventives in the field has decreased conspicuously due to changes in the way waste from wool processing is treated and released (Bonn and Poschlod 1998).

3.4.2 Direct Association with Vehicles: Coincidence of Transport and Release

Traffic routes were associated with plant invasions even before modern road construction started. The early colonisation of North America by European settlers induced multiple range expansions of non-native species, often following trails and primitive roads (Crosby 1986). The inventions of railways and cars in the 19th century substantially increased the role of traffic as a dispersal vector. Apart from an association with transported goods, propagules can be transported directly through adhesive dispersal on the surface of vehicles.

In contrast to most vectors which promote the intercontinental introduction of species to a new range, and also in contrast to transfers by means of transported goods, the direct attachment of propagules to vehicles provides a vector where the processes of reception, transport and release of propagules largely overlap in time and space. Road vehicles, for example, continuously disperse seeds during their journey and this may coincide with the attachment of further diaspores to the vehicle from the roadside flora. Along the route of transport, propagules released by one car can be attached to a following one. Vectors which provide such interlinked chains of reception, transport and release of diaspores lead to linear distribution patterns along transport networks. These retrace the transport route, which acts concurrently as corridor of seed release. This continuous release of seeds during transport also enhances the probability of exposing propagules to other, both natural and human-mediated dispersal vectors.

3.4.2.1 Adhesion to Vehicles

The adhesive association of propagules to the surface of vehicles can occur accidentally along the whole route of a vehicle's journey. The attachment of propagules to cars has been confirmed through analyses of seed samples from the surface of cars (Hodkinson and Thompson 1997). The attachment of propagules to cars as transport vectors is mediated by mud (Clifford 1959; Hodkinson and Thompson 1997). The efficiency of propagule reception by vehicles depends on exposure to potential seed sources. Thus, cars which were driven in rural surroundings and on unpaved roads had much higher seed contents than cars from urban areas and paved roads (Hodkinson and Thompson 1997). Although not tested experimentally, it can be assumed that the attachment potential of propagules to trains is lower than that for cars, as direct contact to seed sources is limited in the former case.

Various parts of vehicles, such as the tires, wheel arches, tire wells, hood and trunk grooves and window washer grooves, can support the accumulation of mud and seeds on the surface of vehicles (Hodkinson and Thompson 1997). Occasional events of long-distance dispersal may also be facilitated by unintended internal transport, e.g. in engine blocks, passenger spaces or trunks. Corresponding to the varying duration of seed adhesion on different parts of vehicles, the transport distances cover a broad spatial scale associated with short- to longer-distance dispersal. As an example, initial roadside populations of coastal species in the United Kingdom were found at great distances from coastal seed sources, probably due to long-distance dispersal by vehicles (Scott and Davison 1985). At the local scale, dispersal from these initial populations was enhanced in the direction of traffic flow, demonstrating also short-distance effects of vehicles on seed dispersal.

3.4.2.2 Transport Routes: from Patterns to Processes

The relevance of traffic as a pathway in plant invasions is usually determined from observed distribution patterns of non-native species along traffic routes. As these depend both on dispersal processes and on characteristic site conditions of roadside and railway corridors, the vector, i.e. the underlying processes causing these distributional patterns, can be retraced only indirectly. This necessitates a differentiation of site- and vector-dependent mechanisms, both of which may enhance plant migration along transportation systems: (1) seed dispersal by vehicles (Hodkinson and Thompson 1997) and (2) high disturbance and altered site conditions which provide safe sites for the establishment of numerous non-native species and form suitable migration corridors (Hansen and Clevenger 2005). Both processes are mutually dependent, as site conditions along transport routes can favour the establishment of

populations of non-native species which are dispersed by vehicles and which, in turn, can act as seed sources for subsequent adhesion to vehicles.

It is thus difficult to assess the vector strength of adhesive dispersal by vehicles as such because plant migration patterns along transportation corridors usually reflect the confounding effects of site characteristics and the agency of traffic as well as of other dispersal vectors. Nonetheless, several studies provide evidence that dispersal by vehicles does indeed enhance the range expansion of non-native plant species. First, time series of roadside invasions reveal a linear and sequential range expansion along roadsides (Kopecky 1988; Ernst 1998), indicating that spreading is due to dispersal *within* the corridor, rather than to adjacent seed sources. Second, along transport systems, isolated founder populations of invasive species can be found (Scott and Davison 1985; Ernst 1998) which are likely to result from long-distance dispersal by vehicles. Furthermore, non-native species may contribute a large share of the seeds found in mud samples from vehicles, for example, about 70 % in the sludge of a car wash in Canberra, Australia (Wace 1977).

At the local scale, road verges are among the habitat types with the highest proportion of non-native species and usually comprise more non-native species than does the adjacent landscape (Gelbard and Belnap 2003; Hansen and Clevenger 2005). Roadside populations of non-native plant species can act as focal points for invasion into the adjacent landscape. In grassland habitats, an increase in non-native species richness can be observed up to 100 m from the edge of transportation corridors (Tyser and Worley 1992; Gelbard and Belnap 2003). Roads also enhance plant transfers into protected areas (Tyser and Worley 1992).

Similarly to road traffic, linear distribution of non-native species has been observed along rail tracks (Hansen and Clevenger 2005). Long-distance dispersal along the railway system has been acknowledged as a major driver in the rapid spread of *Senecio inaequidens* (Ernst 1998). In addition to continuous dispersal during train travel, discontinuous release of propagules occurs at stations. However, similarly to road vehicles, it is difficult to unequivocally identify the functioning of railroad tracks as migration or dispersal corridors.

Effects of transport corridors on plant invasions at larger scales are indicated by a positive correlation between the density of the transportation system and the density and richness of non-native plants of an area (Vilà and Pujadas 2001). At the regional scale, migration along transport corridors can cause altitudinal shifts in species distribution (Kopecky 1988).

3.4.3 Role of Living Conveyers

Since the earliest migrations, people and their domesticated animals (Chap. 2) are known to have transferred plant species accidentally at local to continental scales. Propagules may be externally moved through attachment to footwear, clothing, fur or hoofs, and internally through the digestive tract.

Studies on dispersal by livestock illustrate a huge potential for long-distance dispersal. A flock of 400 sheep can move about 8 million diaspores during a single vegetation period, with a retention period of up to 100 days in the fleece of a sheep (Poschlod and Bonn 1998). Wandering herds can cover distances of hundreds of kilometres and lead to a continuous release of propagules during transport. This provided, for example, an efficient spread of *Xanthium spinosum*, which was eventually called shepherd's plague (Thellung 1915). Although transhumance is today less widespread in Europe, long-distance dispersal through domesticated animals still occurs as livestock are moved by trains or other vehicles at least at regional to infra-continental scales, often integrating straw and fodder as additional vectors for plant dispersal. In North America, invasions by *Bromus tectorum* were facilitated in this way (Mack 1981). During the period of colonisation in the southern hemisphere, livestock most likely led to an efficient intercontinental transfer of plant species through the establishment of pasture regimes in the southern hemisphere or even by releasing domesticated animals as a living larder for early voyagers on isolated oceanic islands (Crosby 1986).

High numbers of propagules associated with the dung of cattle, sheep and horses indicate pathways of dispersal via endozoochory (Poschlod and Bonn 1998). Viable seeds of numerous exotic species have been found in horse dung along recreational riding trails (Campbell and Gibson 2001). Although in this case only one species moved into the adjacent forest, the large number of exotic species in horse dung reflects a potential of horseback activities for inducing invasions. Within German biosphere reserves, sheep transfer the invasive *Lupinus polyphyllus* by endozoochory (Otte et al. 2002). Sheep also provide a potential pathway for crop dispersal, as they have been shown to be capable of excreting viable canola seeds for up to 5 days after consumption (Stanton et al. 2003). This could lead to seed transfer from grazed stubble paddocks to habitats outside of cultivated fields, facilitating the establishment of feral crop populations.

Human population size is a good predictor for non-native plant species richness (McKinney 2002), but the understanding of underlying processes is still limited. Despite the enormous increase in human mobility in the last decades, only a few studies have directly analysed the role of humans in moving species by attachment to footwear or clothing (Clifford 1956; Falinski 1972). The anecdotal spread of *Plantago major* in North America as "Englishmen's foot" (Crosby 1986) clearly indicates the measurable strength of this vector. Association with footwear of travelling botanists, tourists and sports-

men may provide an infra- and intercontinental transfer of species, as shown by Clifford (1956) and Powell (1968). Sportsmen have also introduced seeds of invasive species to Hawai'i on their shoes (Higashino et al. 1983). Still little is known about the role of humans in dispersing propagules after consumption. The frequent germination of tomatoes on river banks in Germany suggests an efficient seed transfer from the human digestive tract via sewage to rivers as natural corridors of transport (Schmitz 2004).

3.5 Conclusions

Humans promote plant dispersal at local, regional and continental scales. In processes leading to the introduction of a species to a new range, human agency is a prerequisite for subsequent invasions. Even at more local to regional scales, however, human-mediated dispersal can be crucial for invasion success but seems to be still underestimated. Both accidental and deliberate vectors of plant invasions are engaged in the further spread of non-native species following their initial introduction and sometimes, as in horticulture, the vector of initial introduction can be the same as the one which fosters range expansion in the new area. As a consequence, prevention and management of invasions should address processes which lead to the initial introduction of a species to a new range as well as those enhancing subsequent invasion success within the new range through secondary releases or accidental transfer of propagules.

Distinguishing between the processes of propagule transport and release is useful for a better understanding of vector efficiency and of the spatial patterns of invasions resulting from the release of propagules to the environment. As an additional point, we stress here the role of human intervention as a key driver in both processes (Table 3.3). Often, transport and release of propagules occur both intentionally and accidentally. Additionally, deliberately transported target species may also be released accidentally and, vice versa, unintentionally moved non-target species may be released purposefully into the environment. The classification of vectors according to the underlying human motivation could be a viable approach for the development of policy and management strategies dealing with biological invasions, as it helps to group those vectors which can be governed by similar control measures.

Despite the long history in studying pathways in plant dispersal, our knowledge of the functioning and efficiency of vectors is still limited. In this regard, it is useful to further analyse the strength of different vectors in terms of efficiency of both propagule transport and release and the transition to subsequent stages of invasion success. As has been broadly acknowledged, the focal challenge in assessing the present and future role of vectors is their changing nature over time and space.

Table 3.3 Presence or absence of human motivation as underlying driver in the transport and release of propagules. Both processes can be linked to deliberate or accidental human agency

	Deliberate release of propagules	Accidental release of propagules
Deliberately moved target species	Introduction and subsequent propagation or cultivation of ornamentals	Transport losses in crop seeds by spilling from vehicles or trains
	Deposition of ornamentals as garden waste	
	Planting of introduced species to enrich nature	
Accidentally moved non-target species	Release of propagules with solid or liquid ballast materials	Transport losses of weed seeds associated with crop seeds
	Deposition of propagule-containing waste from wool factories as manure	Deposition of propagules attached to vehicles, animals or to human footwear
	Discharge of propagules which were associated with goods by cleaning procedures (e.g. trains)	
Resulting spatial patterns	Mostly clumped invasion foci by discontinuous release of propagules	Mostly linear invasion foci by continuous release of propagules

References

Bonn S, Poschlod P (1998) Ausbreitungsbiologie der Pflanzen Mitteleuropas: Grundlagen und kulturhistorische Aspekte. Quelle und Meyer, Wiesbaden

Brandes D (1993) Eisenbahnanlagen als Untersuchungsgegenstand der Geobotanik. Tuexenia 13:415–444

Campbell JE, Gibson DJ (2001) The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. Plant Ecol 157:23–35

Carlton JT, Ruiz GM (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species. Island Press, Washington, DC, pp 36–58

Chauvel B, Dessaint F, Cardinal-Legrand C, Bretagnolle F (2006) The historical spread of *Ambrosia artemisiifolia* L. in France from herbarium records. J Biogeogr 33:665–673

Clifford HT (1956) Seed dispersal on footwear. Proc Bot Soc Br Isles 2:129–131

Clifford HT (1959) Seed dispersal by motor vehicles. J Ecol 47:311–315

Conedera M, Krebs P, Tinner W, Pradella M, Torriani D (2004) The cultivation of *Castanea sativa* (Mill.) in Europe, from its origin to its diffusion on a continental scale. Veg Hist Archaeobot 13:161–179

Crawley MJ, Brown SL (2004) Spatially structured population dynamics in feral oilseed rape. Proc R Soc Lond B Biol Sci 271:1909–1916

Crosby AW (1986) Ecological imperialism: the biological expansion of Europe, 900–1900. Cambridge University Press, Cambridge

Dehnen-Schmutz K, Williamson M (2006) *Rhododendron ponticum* in Britain and Ireland: social, economic and ecological factors in its successful invasion. Environ Hist (in press)

Dehnen-Schmutz K, Touza J, Perrings C, Williamson M (2006) The horticultural trade and ornamental plant invasions in Britain. Conserv Biol (in press)

Elton CS (1958) The ecology of invasions by plants and animals. Methuen, London

Ernst WHO (1998) Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in The Netherlands: from wool alien to railway and road alien. Acta Bot Neerl 47:131–151

Falinski JB (1972) Anthropochory in xerothermic grasslands in the light of experimental data. Acta Soc Bot Polon 41:357–368

Forman J (2003) The introduction of American plant species into Europe: issues and consequences. In: Child LE, Brock JH, Brundu G, Prach K, Pyšek K, Wade PM, Williamson M (eds) Plant invasions: ecological threats and management solutions. Backhuys, Leiden, pp 17–39

Franz G (1984) Geschichte des deutschen Gartenbaues. Ulmer, Stuttgart

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv Biol 17:420–432

Gressel J (ed) (2005) Crop ferality and volunteerism. CRC Press, Boca Raton

Hansen MJ, Clevenger AP (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biol Conserv 125:249–259

Higashino PK, Guyer W, Stone CP (1983) The Kilauea wilderness marathon and crater rim runs: sole searching experiences. Newslett Hawaiian Bot Soc 22:25–28

Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. J Appl Ecol 34:1484–1496

Hussner A, Lösch R (2005) Alien aquatic plants in a thermally abnormal river and their assembly to neophyte-dominated macrophyte stands (River Erft, North Rhine-Westphalia). Limnologica 35:18–30

Jauch F (1938) Fremdpflanzen auf den Karlsruher Güterbahnhöfen. Beitr Naturkde Forsch Südwestdeutschland 3:76–147

Jones AT, Hayes MJ, Hamilton NRS (2001) The effect of provenance on the performance of *Crataegus monogyna* in hedges. J Appl Ecol 38:952–962

Kopecky K (1988) Einfluß der Straßen auf die Synanthropisierung der Flora und Vegetation nach Beobachtungen in der Tschechoslowakei. Folia Geobot Phytotax 23:145–171

Kornas J (1988) Speirochore Ackerwildkräuter: von ökologischer Spezialisierung zum Aussterben. Flora 180:83–91

Kowarik I (1992) Einführung und Ausbreitung nichteinheimischer Gehölzarten in Berlin und Brandenburg. Verh Bot Ver Berlin Brandenburg Beiheft 3:1–188

Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species. In: Pyšek P, Prach K, Rejmánek M, Wade M (eds) Plant invasions – general aspects and special problems. SPB Academic, Amsterdam, pp 15–38

Kowarik I (2003) Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. Biol Invasions 5:293–312

Kowarik I (2005) Urban ornamentals escaped from cultivation. In: Gressel J (ed) Crop ferality and volunteerism. CRC Press, Boca Raton, pp 97–121

Kowarik I, Wohlgemuth JO (2006) *Tulipa sylvestris* in northwestern Germany: a non-indigenous species as indicator of former horticulture. Polish Bot Stud 22 (in press)

Lumaret R (1990) Invasion of natural pastures by a cultivated grass (*Dactylis glomerata* L.) in Galicia, Spain: process and consequence on plant-cattle interactions. In: di Castri F, Hansen AJ, Debussche M (eds) Biological invasions in Europe and the Mediterranean Basin. Kluwer, Dordrecht, pp 392–397

Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7:145–165

Mack RN (1991) The commercial seed trade: an early disperser of weeds in the United States. Econ Bot 45:257–273

Mack RN (2000) Cultivation fosters plant naturalization by reducing environmental stochasticity. Biol Invasions 2:111–122

Mack RN (2001) Motivations and consequences of the human dispersal of plants. In: McNeely JA (ed) The great reshuffling: human dimensions in invasive alien species. IUCN, Gland, pp 23–34

Mack RN (2003) Global plant dispersal, naturalization, and Invasion: pathways, modes, and circumstances. In: Ruiz GM, Carlton JT (eds) Invasive species: vectors and management strategies. Island Press, Washington, DC, pp 3–30

Mack RN, Lonsdale WM (2001) Humans as global plant dispersers: getting more than we bargained for. Bioscience 51:95–102

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

McKinney ML (2002) Do human activities raise species richness? Contrasting patterns in United States plants and fishes. Global Ecol Biogeogr 11:343–348

Nobbe F (1876) Handbuch der Samenkunde. Physiologisch statistische Untersuchungen über den Gebrauchswert der land- und forstwirtschaftlichen sowie gärtnerischen Saatwaren. Wiegand, Hempel & Parey, Berlin

Otte A, Obert S, Volz H, Weigand E (2002) Effekte von Beweidung auf *Lupinus polyphyllus* Lindl. in Bergwiesen des Biosphärenreservates Rhön. Neobiota 1:101–133

Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biol Invasions 8:399–413

Poschlod P, Bonn S (1998) Changing dispersal processes in the central European landscape since the last Ice Age: an explanation for the actual decrease of plant species richness in different habitats? Acta Bot Neerl 47:27–44

Powell RH (1968) Harmful plant species entering New Zealand 1963–1967. N Z J Bot 6:395–401

Prach K, Hadinec J, Michalek J, Pyšek P (1995) Forest planting as a way of species dispersal. Forest Ecol Manage 76:191–195

Probst R (1949) Wolladventivflora Mitteleuropas. Voigt-Schild, Solothurn

Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: linking pattern to process. Ecoscience 12:302–315

Pyšek P, Prach K (1993) Plant invasions and the role of riparian habitats – a comparison of 4 species alien to Central Europe. J Biogeogr 20:413–420

Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. Preslia 74:97–186

Reichard SH, White P (2001) Horticulture as a pathway of invasive plant introductions in the United States. Bioscience 51:103–113

Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E (2005) Ecology of invasive plants: state of the art. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species – a new synthesis. Scope 63. Island Press, Washington, DC, pp 104–161

Richardson DM, Rejmánek M (2004) Conifers as invasive aliens: a global survey and predictive framework. Diversity Distrib 10:321–331

Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Natural-
    ization and invasion of alien plants: concepts and definitions. Diversity Distrib
    6:93–107
Ridley HN (1930) The dispersal of plants throughout the world. Reeve, Ashford, Kent
Salisbury E (1953) A changing flora as shown in the study of weeds of arable land and
    waste places. In: Lousley JE (ed) The changing flora of Britain. Botanical Society of
    the British Isles, Oxford, pp 130–139
Salisbury E (1964) Weeds and aliens. Collins, London
Schepker H (1998) Wahrnehmung, Ausbreitung und Bewertung von Neophyten. Eine
    Analyse der problematischen nichteinheimischen Pflanzenarten in Niedersachsen.
    Ibidem, Stuttgart
Schmitz U (2004) Frost resistance of tomato seeds and the degree of naturalisation of
    Lycopersicon esculentum Mill. in Central Europe. Flora 199:476–480
Scott NE, Davison AW (1985) The distribution and ecology of coastal species on road-
    sides. Vegetatio 62:433–440
Spethmann W (1995) In-situ/ex-situ-Erhaltung von heimischen Straucharten. In: Klein-
    schmit J, Begemann F, Hammer K (eds) Erhaltung pflanzengenetischer Ressourcen in
    der Land- und Forstwirtschaft. ZADI, Bonn, pp 68–87
Stanton R, Pratley J, Hudson D (2003) Sheep are potential vectors for the spread of canola
    (*Brassica napus*) seed. Austral J Exp Agric 43:535–538
Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to
    pest to accepted addition to the flora? The perception of an alien plant species
    through the centuries. Biol Invasions 5:323–335
Sukopp H (1972) Wandel von Flora und Vegetation in Mitteleuropa unter dem Einfluß
    des Menschen. Ber Landwirtsch 50:112–139
Suominen J (1979) The grain immigrant flora of Finland. Acta Bot Fenn 111:1–108
Thellung A (1912) La flore adventice de Montpellier. Mém Soc Sci Nat Cherbourg
    38:622–647
Thellung A (1915) Pflanzenwanderungen unter dem Einfluß des Menschen. Beibl Bot
    Jahrb 3/5:37–66
Tyser RW, Worley CA (1992) Alien flora in grasslands adjacent to road and trail corridors
    in Glacier National Park, Montana (USA). Conserv Biol 6:253–262
Vilà M, Pujadas J (2001) Land-use and socio-economic correlates of plant invasions in
    European and North African countries. Biol Conserv 100:397–401
Wace N (1977) Assessment of dispersal of plant species – the car-borne flora in Can-
    berra. Proc Ecol Soc Austral 10:167–186
Willerding U (1986) Zur Geschichte der Unkräuter Mitteleuropas. Wachholtz, Neumün-
    ster
Williams DG, Baruch Z (2000) African grass invasion in the Americas: ecosystem conse-
    quences and the role of ecophysiology. Biol Invasions 2:123–140
Williamson M (1996) Biological invasions. Chapman & Hall, London
Zobel BJ, Wyk GV, Stahl P (1987) Growing exotic forests. Wiley, New York