

Chapter 5

Aliens on the Move: Transportation Networks and Non-native Species

Fernando Ascensão and César Capinha

Abstract Biological invasions are a major component of global environmental change, threatening biodiversity and human well-being. These invasions have their origin in the human-mediated transportation of species beyond natural distribution ranges, a process that has increased by orders of magnitude in recent decades as a result of accelerating rates of international trade, travel, and transport. In this chapter, we address the role that overland transportation corridors, particularly railways, have in the transport of non-native species. We focus specifically on the role of rail vehicles in dispersing stowaway species, i.e. species that are moved inadvertently and that are not specific to the commodities being transported; we also focus on the natural dispersal and establishment of non-native species along railway edges. We place these processes in the context of biological invasions as a global phenomenon and provide examples from the literature. We also list general management recommendations for biological invasions highlighting the particularities associated with their management in railway transport systems. Following previous studies, we briefly outline four possible management approaches: (1) “Do nothing;” (2) “Manage propagule supply;” (3) “Manage railway environments;” and (4) “Act over the invasive populations directly”. These approaches are not mutually exclusive, and they range from an expectation that natural processes (e.g. ecological succession) will drive the invaders out of the ecosystems, to the application of

Fernando Ascensão and César Capinha have contributed equally to this chapter.

F. Ascensão

CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal

F. Ascensão

CEABN/InBIO, Centro de Ecologia Aplicada “Professor Baeta Neves”, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

C. Capinha (✉)

Global Health and Tropical Medicine Centre (GHTM), Instituto de Higiene e Medicina Tropical (IHMT), Universidade Nova de Lisboa, Lisboa, Portugal
e-mail: ccapinha@cibo.up.pt

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measures to extirpate the invaders directly (e.g. manual removal). We highlight that best practices for the management of invaders in railway-related systems may be difficult to generalize and that they may have to be considered on a case-by-case basis. We end by stressing that research on railways in the context of biological invasions remains scarce, and that fundamental knowledge for understanding the relative importance of this transport system in the dispersal of species and on how this process should be dealt with remains largely lacking.

Keywords Biological invasions · Stowaway species · Verges · Invasibility

Introduction

Nowadays non-native species are widespread around the world. These species, which have been moved beyond the limits of their natural ranges by human activities, include not only most farm animals and plants, forestry species and pets, but also many unwanted organisms such as mosquitoes, weeds, fungus and bacteria. Although most of these species perish soon after arriving at the new area, or once humans cease to care for them, a few do form wild populations and become part of the ecosystems (Williams and Newfield 2002). These species, often called as “invasive,” are now one of the most important causes of global change, being responsible for the decline and extinction of native species, economic losses, and human health problems (Simberloff et al. 2013).

Humans have been moving species since pre historic times (Di Castri 1989), but the number of biological invasions and the magnitude of their impacts in the last few decades is unprecedented (Ricciardi 2007). This is to a great extent the result of the recent large scale expansion of the transportation network and of the increasing exchange of commodities to a nearly global coverage (Hulme 2009). Because of this, most of the earth’s surface is now within reach of non-native species. Moreover, the volume and diversity of the cargo and number of passengers now being transported is also much greater than in any period in the past (Hulme 2009). This allows for a greater diversity of species being introduced in new areas as well as a greater number of their propagules, which increases both the number of potential invaders and their ability to establish (Lockwood et al. 2009). Finally, the latest technical advances in transportation allow species to move much faster. Even the least suspicious species, e.g. those that are more environmentally sensitive, may become invasive in remote regions of the original distribution (Wilson et al. 2009). In summary, as the extent, volume, and efficiency of the transportation of people and freight increase, the burden of biological invasions should also increase (Bradley et al. 2012).

Hulme et al. (2008) distinguish three main mechanisms by which human-activities cause the dispersal of non-native species: (1) through importation as a commodity or with a commodity; (2) as stowaways, i.e. through a direct influence of a transportation vehicle; and (3) by means of natural dispersal along artificial infrastructures, such as water canals, roads, and, especially relevant for our

concerns, railways. The first mechanism arises directly from trading activities, where the traded commodity may itself be the non-native species. In these cases, the “importation” of the species is deliberate, because some of its attributes are desired in the area of destination. The reasons behind the importation of species are varied, and include farming, forestry, livestock, ornamental plants and pets, laboratory testing or biocontrol. In some situations, the goal is purposely the formation of wild populations, as is the case of gaming and fishing or biocontrol agents. In other cases, the imported species are to be stored in enclosed environments, but they often escape from captivity. For instance, the American mink (*Neovison vison*) has invaded many European countries due to accidental escape or deliberate release from fur farms (Vidal-Figueroa and Delibes 1987; Bonesi and Palazon 2007). It is worrisome that a great number of problematic invaders is still actively marketed today, including freshwater macroinvertebrates and fish (Capinha et al. 2013; Consuegra et al. 2011) and plants (Humair et al. 2015).

Trading activities may also lead to the arrival of non-native species as an accidental “by-product” of a commodity, such as a commensal, a parasite or a disease. These species can remain undetected for long periods of time and may benefit from measures towards the establishment to their hosts in the wild. An illustrative example of such by-products of a traded commodity is the crayfish plague (*Aphanomyces astaci*) in Europe. This fungus-like disease is hosted by several North American crayfish species that were introduced in European wetlands in order to boost the wild stocks of this food item. However, unlike for North American species that co-evolved with the disease, the crayfish plague is deadly to European species and has already caused numerous extinctions of local populations (Capinha et al. 2013).

Stowaway species can be associated with trading activities or any other activity that involves a transportation vehicle. In other words, a non-native stowaway species is not specific to a particular commodity, and it can be any organism that at some point is displaced by a vehicle or its load. This occurs more often with species that are difficult to detect, such as those that are small or stealthy. Known examples of these stowaway species include land snails attached to trains or their cargo (Peltanová et al. 2011), plankton in ship’s ballast waters (Hulme et al. 2008), or seeds in soil attached to automobiles (Hodkinson and Thompson 1997). Centers of human and commodity transportation and nearby areas (e.g. seaports and railroad stations and yards) often provide the first records of non-native stowaways (e.g. Noma et al. 2010) and can host diverse communities of invasive species (Drake and Lodge 2004).

Finally, transport infrastructures may also act as “corridors” for the natural dispersal of non-native biodiversity. These infrastructures facilitate the dispersal of non-native organisms by allowing their movement across physical and environmental barriers (e.g. a mountain range now crossed by a tunnel), or by supplying suitable habitat for expanding invasive populations. Concerning the latter case, a few characteristics of the areas managed by transportation companies (e.g. road and railway verges) are considered beneficial to the establishment of non-native species, particularly the regular occurrence of disturbance that gives rise to “vacant” niches

and low biological diversity, reducing the number of potential competitors for space and resources (Catford et al. 2012).

In this chapter, we focus on the role of terrestrial transportation systems, particularly railways, in dispersing stowaway fauna and flora and in facilitating the natural dispersal of non-native species, i.e. the second and third mechanisms identified above. We start by providing a contextual overview of the impacts of invasive species in a global context, in order to better familiarize readers with the significance of the problem. We then focus on the role of railway traffic in transporting non-native stowaway species and describe some of the best-known examples. Finally, we discuss and provide examples of natural dispersal of non-native species along transportation corridors and conclude by discussing some of the management actions that could be taken to help reducing the spread of those species in railways.

Why Care about Invasive Species? An Overview of Their Global-Scale Relevance

In natural environments, invasive species compete, predate and hybridize with native species, and alter community structure and ecosystem processes, ultimately leading to irreversible changes on the diversity and distribution of life on earth (Simberloff et al. 2013; Capinha et al. 2015). Examples of mass extinctions precipitated by the introduction of non-native species include nearly every native bird species on the Pacific island of Guam after the arrival of the invasive brown tree snake (*Boiga irregularis*) (Wiles et al. 2003), or the extinction of more than 100 terrestrial gastropods due to the introduction of the predatory rosy wolf snail (*Euglandina rosea*) in tropical oceanic islands worldwide (Régnier et al. 2009). The Nile perch (*Lates niloticus*) is another paradigmatic example of the negative impacts of invasive species on native species. In the 1950s, this predatory freshwater fish was intentionally introduced in Lake Victoria, Africa, to boost the lake's fish stocks, which were becoming severely overfished. In the decades after its introduction, the Nile perch density grew massively leading to the extinction of nearly 200 endemic species of cichlid fishes (Craig 1992).

The economic costs of invasive species can be striking. It is estimated that invasive species can cost many billions of dollars in the USA and in Europe alone (Pimentel et al. 2005; Davis 2009; Hulme 2009; Marbuah et al. 2014). For example, Bradshaw et al. (2016) recently compiled a comprehensive database of economic costs of invasive insects. Taking all reported goods and service estimates, according to the authors' study, invasive insects cost a minimum of US\$70.0 billion per year globally and the associated health costs exceed US\$6.9 billion per year. These values mainly reflect observable damages, such as those caused on other economically important species, e.g. the cinnamon fungus (*Phytophthora cinnamomi*) on the sweet chestnut (*Castanea sativa* in Europe, and *Castanea dentata* in North America) (Vettrai et al. 2005), or on man-made infrastructures and equipment,

e.g. the zebra mussel (*Dreissena polymorpha*) in water treatment works (Elliott et al. 2005). However, there are also many indirect damages that are difficult to quantify because they would require a deeper understanding of the ecosystem-economy relationship (Bradshaw et al. 2016). Furthermore, many invasive species are also vectors of human diseases, such as malaria, plague, typhus or yellow fever, and their transportation may result in outbreaks of these infections in previously unsuspected areas (Lounibos 2010; Capinha et al. 2014). Also, invasive species may cause ecological or landscape changes that have negative implications for human safety, these can assume multiple forms, such as the promotion of pathogen eruptions (Vanderploeg et al. 2001), or an increase in the vulnerability of landscapes to natural hazards such as fires (Berry et al. 2011).

Importantly, many of the future impacts of non-native species may still remain unknown. For instance, the increased profusion of invasive species may render a cascading effect on the vulnerability of ecosystems, i.e. by making these even more susceptible to future impacts. Climate change is a further source of concern. Changes in climatic patterns altering the geography of the areas that can be invaded may put additional pressures on native biodiversity. Understanding how these processes will interact in the future to determine the impacts of biological invasions is challenging. In fact, many future invasions may have already been set in motion, i.e. many non-native species are currently in a lag-phase, i.e. with little or no increase in species occurrence, to be followed by an increase-phase in which species occurrence and invasiveness rises rapidly before becoming invaders (Aikio et al. 2010; Essl et al. 2011).

Without increased efforts to manage non-native species in transportation infrastructures, including in vehicles, transported cargo and verges, the number of invasive species will likely continue to grow steadily (Keller et al. 2011). Hence, more effective policies to reduce the transport and release of non-native species, and to manage those already established, should become a priority (Pimentel et al. 2005; Keller et al. 2011).

Non-native Hitchhikers: Transportation Vehicles as Vectors of Stowaway Species

The surroundings of transportation infrastructures (e.g. verges and embankments) often host a high diversity of non-native species (Gelbard and Belnap 2003; Hansen and Clevenger 2005), in many cases due to their transportation as stowaways in vehicles. Species can be accidentally moved by a vehicle in many different ways, e.g. snails and slugs clinging to a train, insects flying inside a vehicle, plant seeds in passengers' boots, or any organism that makes frequent use of cargo yards and that is loaded unintentionally with the cargo. Nevertheless, despite the range of possibilities, the movement of stowaway fauna and flora is poorly documented for terrestrial transportation systems. This is in contrast with aquatic transportation, especially maritime, for which there is a large body of research, particularly

regarding the movement of species in ballast waters (Drake and Lodge 2004; Seebens et al. 2016). We speculate that overland transportation of biological stowaways is likely to be less frequent than those by aquatic vehicles; however, we also suspect that the lack of studies for the terrestrial counterpart does not reflect the true contribution of this process for non-native species dispersal. Below we describe a few documented cases where terrestrial transportation had a relevant role on the expansion of biological invaders, with special emphasis on trains.

The spotted knapweed (*Centaurea stoebe*) is an example of a non-native species dispersed by trains. This plant, native to south east and central Europe, arrived in North America in the late 1800s and by the year 2000 it was already found in most contiguous American states (Sheley et al. 1998). The mechanisms that enabled such a fast dispersal were unclear for a long time, but a recent reconstruction of the patterns of invasion of this plant showed a close agreement between the extent of colonized areas and its velocity dispersal on one side, and the spatial coverage and development of the railway network in the USA on the other (Broennimann et al. 2014). For instance, the wave of invasion was much faster and wider in the eastern states, where a denser and older network exists. In favor of the important role of stowaway transportation of this species in trains, particularly for some long-distance dispersal events, is the plants' known ability to become attached to the undercarriages of vehicles (Sheley et al. 1998).

Trains are known to have been a vehicle of dispersal also for ragwort plant species. One of such cases concerns the South African ragwort (*Senecio inaequidens*), a species introduced in Europe from South Africa in the first half of the twentieth century, and that is now found from Norway in the north to Italy in the south, and from Bulgaria in the east to Spain in the west (Heger and Böhmer 2006). The achene-type fruit of this species is able to stick to trains in movement or to their transported commodities, a characteristic that contributed to the rapid dispersal of the species along railways systems (Heger and Böhmer 2005). Another plant of this group known to "hitchhike" on trains is the Oxford ragwort (*Senecio squalidus*), a hybrid that escaped cultivation from the Oxford Botanic Garden. At the end of the eighteenth century it was established in some parts of Oxford (Harris 2002; Heger and Böhmer 2005), and it currently invades most of Britain. George Druce, an English botanist, described the dispersal of this plant as follows (1927b, p. 241, in Harris 2002): "... the vortex of air following the express train carries the fruits in its wake. I have seen them enter a railway-carriage window near Oxford and remain suspended in the air in the compartment until they found an exit at Tilehurst [about 40 km from Oxford]".

A few records of animal species being transported as stowaways in trains can also be found in the scientific literature and the media. Perhaps the most recurrent cases refer to urban pest species, such as rats and mice (Li et al. 2007), but there are also references to ants (Elton 1958), beetles (White 1973), spiders (Nentwig and Kobelt 2010) and even armadillos (Hofmann 2009). However, in these cases the contribution of train-mediated transportation to the overall process of dispersal remains poorly studied.

Verges as Habitat and Corridors for Non-native Species

Vegetated verges generally border transportation infrastructures, in particular railways and roads. These verges are regularly mowed in order to ensure traffic safety, resulting in open and well-lighted areas. In places where the transportation corridor is wider, intense mowing is applied only to the zone closest to traffic, while the farthest zone is managed less intensively, leading to the creation of a well-developed vegetation structure. These two zones of management regime provide habitat not only for native species but also for many non-native organisms. In Portugal, for example, many kilometers of railway and road verges are dominated by silver wattle (*Acacia dealbata*), one of the most widespread and damaging invasive plants in the country (Sheppard et al. 2006; Vicente et al. 2011). This small tree is native to Australia, and was introduced in Europe in the 1820s. In addition to its great natural dispersal ability, silver wattle inhibits undergrowth species from growing, due to allelopathy, i.e. the ability to produce biochemical agents that the growth, survival, and reproduction of other organisms. Many other examples are referenced in the literature on the presence and sometimes dominance of non-native weedy species in transportation verges (Ernst 1998; Parendes and Jones 2000; Tikka et al. 2001; Gelbard and Belnap 2003; Albrecht et al. 2011; McAvoy et al. 2012; Penone et al. 2012; Suárez-Esteban et al. 2016). Even maritime or wetland species may spread their populations into inland areas along railway and road verges, as found in Finland (Suominen 1970), England (Scott and Davison 1982), or the USA (Wilcox 1989).

By facilitating dispersal, railways and roads may lead to homogeneous communities, sometimes dominated by invasive species. For example, Hansen and Clevenger (2005) measured the frequency of several non-native plant species along transects from 0 to 150 m from the edge of railways and highways in grasslands and forests, as well as at control sites away from corridors. These authors found that both transportation corridors had a higher frequency of non-native species than the respective control sites. Also, grasslands had a higher frequency of non-native species than forested habitats, but this frequency did not differ between the highways and the railways. Other studies have described a decline in the presence of invasive species as a function of the distance to the transportation corridor (see Gelbard and Belnap 2003). Interestingly, the penetration of non-native species in areas adjacent to the transportation corridor is likely to vary according to the dominant land cover. In the study mentioned above, Hansen and Clevenger (2005) discovered that the frequency of non-native species in grasslands along railways and highways was higher than at control sites up to 150 m from the corridor's edge, whereas in forested habitats the higher frequency of non-native species was only evident up to 10 m away from the corridor's edge. A similar result was found in forested areas in the Chequamegon National Forest (USA), where invasive species were most prevalent within 15 m of roads but were uncommon in the interior of the forest (Watkins et al. 2003). Hence, it appears that the dispersal of non-native

species in transportation corridors may have a lower impact in forested landscapes than in open areas, such as grasslands.

The importance that verge areas represent for the spreading and fixation of non-native species is therefore clear. In fact, despite their relatively narrow width, verges can be long, creating continuous strips that may extend for many kilometers and occupy considerable areas. Knowing that the global railway and road lengths are, respectively, approximately 1.1 and 64.3 million km (CIA 2016), and using a conservative value of mean verge width of two meters on each side, we realize that more than 262,000 kilometers of the world are occupied by verges. For comparison, this is equivalent to approximately 33% of the terrestrial protected areas of Natura 2000 Network (EU 2016). Therefore, the management of the vegetation of verges is of utmost importance not only for traffic safety, but also for the control of non-native species.

Management of Non-native Species in Transportation Corridors

As discussed, transportation corridors can function as habitats and venues for the dispersal of non-native species, hence they are an important element to consider when managing and preventing the threats caused by biological invasions. On the other hand, verges can also help maintain conservation values and the connectivity among landscapes, particularly in areas that are heavily modified by human activities (see Chap. 4). Because verges provide habitat areas and corridors for both native and non-native species, it creates management challenges, such as how to maintain or increase the conservation value of transportation verges, while preventing non-native animal and plant species from spreading throughout the network and its surroundings. A delicate balance between restricting the arrival and dispersal of non-native species and maintaining or restoring the conservation value of verges is thus needed. This requires specific management actions, as we discuss below.

Identifying the factors that facilitate the arrival of propagules of non-native species and their dispersal along the corridors may render it possible to manage verges in ways that limit the expansion of an invasive species (Fagan et al. 2002; With 2002). Despite the difficulties in identifying such key factors for all organisms, some general management practices are likely to prevent the dispersal of non-native species in most circumstances.

Perhaps the best management option is to avoid setting up the conditions for non-native species dispersal and establishment when a corridor is under construction, being upgraded or under maintenance. Such activities may imply barring soil, clearing of natural vegetation, or drainage, resulting in considerable disturbance of natural communities. In turn, these disturbances underlie ecological processes that often facilitate the colonization by invasive species, as they “remove” any pre-existing advantage of native over non-natives species that could be present in

the area. Hence, reducing the disturbance of the existing communities as much as possible, may be itself a good management practice.

Propagule pressure is also important. Christen and Matlack (2006) suggested that undisturbed areas are generally less invaded precisely because they may receive fewer non-native propagules. Avoiding the introduction of non-native propagules prevents not only the establishment of invasive species, but also offers much greater economic benefits than the management of invasive populations after their establishment (Keller et al. 2007). Equally important, management options available prior to invasion are more numerous and include legislation or quarantine rules (Keller et al. 2011; Buckley and Catford 2016). In this context, the inspection of cargo and their containers is of great importance, particularly for those having an international origin. For example, a recent inspection of international cargo entering the USA by rail enabled the identification of dozens of undeclared organisms, among which were invasive insects, noxious weeds and vectors of human diseases (<https://goo.gl/fJ1uMo>). Following legal rulings, some of the inspected cargo was re-exported to its origin in order to prevent the dispersal of the unwanted pests.

In many cases, however, prevention is not possible as the non-native species are already established in the landscape. In such cases, management actions should aim at containing or eradicating these species. However, the broad range of invasive species and the different ways that humans value the colonized ecosystems mean that few generalizations can be provided for management and policy guidelines. In other words, appropriate management and policies for invasive species is highly context dependent (Keller et al. 2011). However, based on the review provided by Catford et al. (2012), one can consider four not mutually exclusive main approaches for managing transportation corridor verges when attempting to control or eradicate invasive species: (1) “Do nothing;” (2) “Control at the introduction level by managing the propagule supply of non-native and native species;” (3) “Manage environmental conditions;” and (4) “Manage invasive species populations.”

1. *Do nothing*. This is an option when invaders are well established and are successional colonists. Several studies have shown that the proportion of invasive species can decrease with time since disturbance—not only weedy plants (Bellingham et al. 2005), but also larger plants (Dewine and Cooper 2008). Hence, active management by removal of invasive species immediately following disturbance may be unnecessary and counterproductive. For example, tamarisk species (*Tamarix ramosissima*, *T. chinensis*, *T. gallica* and hybrids) have invaded riparian zones throughout western North America, southern Africa, Argentina, Hawaii, and Australia, demanding expensive control efforts. However, as a relatively recent addition to North American plant communities (the 1920s–1960s was the period of main invasion), the competitive and successional processes are still ongoing. In fact, Dewine and Cooper (2008) demonstrated that box elder (*Acer negundo*), a native species found in canyons throughout western North America, is a superior competitor to tamarisk and is capable of becoming established under dense tamarisk canopies, overtopping and eventually killing the tamarisks. Thus, superior shade tolerance appears to

be the mechanism for the successional replacement of tamarisk by box elder. The authors suggest that the preservation of box elder and other native tree populations is probably a better and cheaper means of tamarisk control than traditional control techniques.

As highlighted by Catford et al. (2012), however, there are several arguments against the “do nothing” approach. Firstly, ecosystem functions may be significantly altered by early successional invasive plants colonizing soon after disturbance (Peltzer et al. 2009). Secondly, some invasive species can out-compete functionally similar native species and therefore persist and dominate over long periods after disturbance (Christian and Wilson 1999). Thirdly, non-native species may establish themselves in highly disturbed areas first, and subsequently adapt and colonize nearby areas with different environmental conditions (Clark and Johnston 2011). Finally, most invasive species are not early successional species that will be replaced over time, some of them are even long-lived K-strategists that are highly competitive and able to invade even undisturbed areas (Wilsey et al. 2009).

2. *Manage the propagule supply.* By reducing the propagule pressure of non-native organisms and increasing that of native species, one can increase the dominance of the former. For example, one control action against silver wattle is the use of prescribed fire to favor the germination of the seed bank, therefore reducing it by destroying part of the seeds or by stimulating the germination of the remainders (<http://invasoras.pt>). Applying this or other measures to reduce the seed bank soon after disturbance activities may strongly reduce the propagule pressure and prevent or reduce the success of invasion. On the other hand, native species suitable for direct sowing should also be selected based on their traits and ability to establish and persist under the specific conditions of the transportation verges. This active selection towards native colonists may benefit not only local biodiversity but also regional agricultural areas. Blackmore and Goulson (2014) found that sowing native wildflowers in road verges significantly increased the abundance of native flowering plants and that of pollinator bumblebees (*Bombus* spp.) and hoverflies (Syrphidae), with benefits to agricultural crops. Furthermore, larvae of hoverflies prey on aphids, arthropod pest species that are responsible for enormous crop damages worldwide, every year. Hence, even easy to-implement interventions in verges may result in considerable environmental and economic gains.
3. *Manage the environmental conditions.* In some cases, it may be more effective to target the causes that boost the disturbance and facilitate the spread of non-native species than to attempt to manage their populations directly. For example, some weeds are particularly adapted to severely eroded verges. Rather than applying herbicide to control such weeds, it may be more effective to stabilize the soil (Catford et al. 2012). This option requires excellent knowledge of the ecological requirements of each invader and it may imply conducting experimental ecological work in order to evaluate the effectiveness of distinct management actions. Nevertheless, for some of the species the necessary

information already exists and is available in the various on-line databases that profile problematic invaders, such as the Invasive Species Compendium (<http://sites.cabi.org/isc/>), Invasoras (<http://invasoras.pt>) or the 'Global Invasive Species Database' (<http://www.iucngisd.org/>).

4. *Manage invasive species populations.* For some highly problematic invasive species it may be more effective to focus on management techniques that directly target their populations. Traditional control techniques, such as the use of prescribed fire or herbicides, as well as mechanical removal may help to alleviate the competitive effects of some species and limit further spread. However, care should be taken to minimize impacts on native species. If the non-native species, particularly plants, have unrestricted dispersal but infrequent propagule arrival, mapping and removing the individual colonist patches soon after they arise, may achieve effective control. This is most important, as such patches often pose a high risk of becoming sources of subsequent dispersal (Moody and Mack 1988). Conversely, if the invasive species has limited dispersal ability, an effective control may be achieved by creating spatial discontinuities on vegetation types at an extent greater than the seed dispersal range, thereby breaking the continuity of the habitat to the invader (Christen and Matlack 2006).

Currently, railroad companies routinely clear-cut and/or spray with herbicide all vegetation that grows too close to the tracks. However, although this method eradicates most of the vegetation (including native species), it also favors the dominance of species that respond favorably to clear-cutting or resist herbicides. Actually, in some cases, roadside herbicide treatments are known to reduce the cover of some non-native species favoring others (Gelbard and Belnap 2003). Hence, investing exclusively in the direct management of invasive populations should be accompanied by a careful evaluation of trade-offs and probably the best option is often a combination of various management possibilities.

Where to begin the control of invasive species is a major question when managing railway verges. One factor that apparently influences the propagule pressure is the disturbance level of the transportation infrastructure. For example, it is known that older roads typically have higher cumulative levels of traffic and maintenance than younger roads, which might result in an increase in non-native species occurrence near old roads simply due to higher disturbance and therefore of propagule pressure. This was found for earthworms (Cameron and Bayne 2009) and the invasive common reed (*Phragmites australis*) (Jodoin et al. 2008). Likewise, plant communities adjacent to roads that receive heavy traffic might be expected to be invaded more than those adjacent to infrequently used and unpaved roads (Parendes and Jones 2000; Gelbard and Belnap 2003). Hence, the degree of perturbation of the transportation corridor, namely the traffic level, could be used as an indicator of the invasion level of verges in railways, and to identify which corridor should be targeted for management.

During the project phase of new railway corridors, engineers should consider whether some routes might aid the dispersal of non-native species more than others. For example, routes expanding railways that are highly colonized by problematic

invaders should be regularly monitored and managed to avoid the spread of propagules. Additionally, transportation networks can also be set to benefit people while minimizing their environmental and social costs. Integrating transportation verges in landscape connectivity management plans, including ecological corridors, would therefore better enable achieving the conservation goals, in particular to ensure a sustainable co-existence between transportation networks with the conservation of biodiversity.

Conclusions

Invasive species are responsible for many negative impacts on biodiversity and human welfare. What is worrisome is that as the transportation of people and goods around the world increases, so does the number of biological invasions. It is thus increasingly important to identify the role that each transportation system has in dispersing species beyond the limits of their natural ranges and to develop procedures by which this process can be reduced. Railways are responsible for several important invasion events but, in comparison to other transportation systems, their overall contribution to biological invasions remains poorly understood. Likewise, the guidelines for preventing or managing the transportation of unwanted organisms in trains or along railways are poorly synthesized and consist mainly of a hand-full of general principles that can be applied to overland transportation systems in general. Thus it is thus clear that more research must be devoted to this topic. Particularly relevant contributions include the identification or “profiling” of the species that go as stowaways in trains or their cargo, and the identification of the characteristics of railways verges that contribute to the natural dispersal and establishment of invaders over native species. Such knowledge remains vital for assessing the relative importance of railways systems in biological invasions and to helping prioritize which measures to take in order to reduce the human dispersal of unwanted species.

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