Chapter 18 – Alien plant invasions in Australia's riparian zones

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Introduction

Biological invasions have been identified as one of the main components of global environmental change (Millenium Ecosystem Assessment 2005) and are considered the second largest threat to biodiversity after habitat destruction (Sala *et al.* 2000). Invasive plant species can alter ecosystem structure and function (Richardson and Pyšek 2006), compromising the services that ecosystems provide. Accounting for 13% of Australia's flora, there are currently over 3,000 alien plant species growing wild in Australia, with a further 6,000 species predicted to naturalize in the future (Randall 2007). Alien plants cost more than $4 billion each year in Australia (Sinden *et al.* 2004) and put native biodiversity directly at risk: of 1,302 plant species listed under Australia's Environment Protection and Biodiversity Conservation Act, more than two-thirds are threatened by alien plants (Department of Sustainability Environment Water Population and Communities 2012). The extent and effects of alien plant invasion are particularly apparent in riparian zones.

Riparian zones often experience high levels of invasion compared to other ecosystems (Fig. 1; Stohlgren *et al.* 2002; Richardson *et al.*, 2007; Catford *et al.*, 2012b). For example, of 24 habitat types examined in Catalonia, Spain, riparian ecosystems were among the four most invaded habitat types with respect to alien species richness (Vilà *et al.* 2007). Based on the proportion of the alien species pool that invades a given vegetation type, Catford and Jansson (2014) found that riparian scrub was the third most invaded of 20 vegetation types in Victoria, Australia, mirroring global trends. As well as having significant cultural and socio-economic values, riparian zones are crucial for nutrient processing, water purification and for the provision of resources for native plants and animals. Although these ecosystem functions may be compromised by plant invasions, traditional weed control techniques may further erode them, presenting a dilemma for natural resource managers.

In this chapter, we focus on aspects of alien plant invasion most relevant to Australia's riparian zones. We discuss the primary mechanisms and pathways of invasion, the functional characteristics of invading species, impacts of alien species, management options and key knowledge gaps. Though some authors contend that native species should be included in discussions of biological invasions (Valéry *et al.*

2013), we focus on species that are alien (exotic, foreign, non-indigenous, non-native, introduced) to Australia. We note that there are both invasive and non-invasive alien species. Though definitions vary (Colautti and MacIsaac 2004), alien species are generally considered invasive when they spread beyond the area where they were initially introduced and become dominant in a community (Richardson *et al*. 2000).

Stages and mechanisms of plant invasion

Plant invasion is the result of three interdependent factors, all of which must be accommodating, if not favourable, for invasion to occur (Catford et al. 2009). The first is propagule availability or propagule pressure, defined as the number of individuals introduced per event multiplied by the frequency of introduction events (Eppstein and Molofsky 2007). Propagule pressure is a prerequisite for invasion and the greater the number of propagules introduced, the greater the likelihood of successful invasion (Simberloff 2009). Second, the physical, or abiotic, characteristics of a habitat must be within the environmental tolerance range of an alien species for invasion to occur. Third, invasion outcomes are affected by the biological characteristics of, and interactions among, the invaders and the recipient community. The relative importance of these three factors varies in space and time.

Propagule transport and introduction

Invasion of alien species requires the transport, either intentional or unintentional, of plant propagules (adult plants, seeds, spores or vegetative fragments) to a new location. Alien species may be imported as a commodity, arrive with a transport vector, or may spread from another invaded region (Hulme et al. 2008). Global patterns suggest that the majority of terrestrial and aquatic plants (both of which invade riparian ecosystems) escape into natural ecosystems after being intentionally introduced, most often for ornamental purposes or use in aquaria (Hulme et al. 2008). In Australia, most alien plant species have been introduced for domestic gardens, agriculture and pastoralism (Randall 2007). Pond apple (*Annona glabra*), for example, was originally imported as a rootstock for custard apples, while gorse (*Ulex europaeus*) was introduced as an ornamental hedge, and blackberry (*Rubus fruticosus*) for its fruit. All of these species have since escaped and represent significant problems in riparian or wetland systems (Anon 2008). The Weeds of National Significance (WoNS) ranks problematic species according to invasiveness, potential for spread, impact and ecological and socio-economic values of species (Anon 2008). Fifteen of the 32 WoNS are known to be successful in riparian or aquatic systems and were introduced into Australia intentionally (AWC 2012). However, only a few were deliberately introduced into riparian zones (e.g. *Hymenachne amplexicaulis* for ponded pasture: Smith 1995; *Salix nigra* for soil stabilisation: Ladson 1997).

Alien species may escape into riparian zones because human activities often concentrate in and around rivers (Fig. 1). Riparian systems, being effectively linear, have a large edge to core ratio, which makes them particularly vulnerable to species invading from surrounding ecosystems (Cumming 2002). Towns are frequently located near rivers, as are areas of agriculture, which benefit from the fertile soil and proximate water supply. Organic waste from gardens and agriculture may be dumped in riparian zones, and alien species used in aquaria may be released into waterways. Centres of human activity thus provide a ready source of propagules.

Colonisation and establishment

After arriving at a site, introduced plants must colonise and survive. Native and alien species undergo the same colonisation process (Meiners et al. 2004) and both need space to obtain resources. Riparian ecosystems typically have high availability of the resources (especially nutrients and water) that are necessary for the establishment and persistence of plants. Resource availability in riparian zones fluctuates because river systems are temporally and spatially dynamic (Richardson et al. 2007). Pulses in resource availability may provide an opportunity for alien species to colonise and establish (Davis *et al.* 2000). Riparian zones experience high levels of disturbance from floods and human activities, such as logging and grazing. By reducing the uptake of resources (e.g. via removing standing vegetation) and increasing resource supply (e.g. through the deposition of nutrient-rich alluvium), such disturbance events can increase overall resource availability, providing space and opportunities for colonisation (Bornette and Amoros 1996).

Invasion typically occurs more frequently during the early stages of succession, which are characterised by high resource availability and low competition (Catford *et al.* 2012a). Accordingly, many invasive species are early successional species adept at colonisation (Rejmanek and Richardson 1996), although this may also reflect a bias towards good colonisers in the introduced species pool (Colautti *et al.* 2006). By reaching reproductive maturity quickly, invading species can exploit fluctuations in resource availability and become naturalised. For species to become naturalised, pioneer populations must be self-sustaining and not rely on continued input of propagules.

As transition zones between aquatic and terrestrial habitats that are subject to frequent flood disturbance, riparian habitats have high levels of environmental

heterogeneity. As a consequence, riparian zones can also host species with a wide range of life histories and environmental preferences (Catford and Jansson 2014). If alien species are functionally distinct from native species, they may be able to inhabit an "empty niche" unoccupied by resident species (Hierro *et al.* 2005). The potential for unoccupied niches is greater in heterogeneous environments such as riparian zones (Melbourne *et al.* 2007).

Although disturbance is a leading explanation for invasion (Moles *et al.* 2012), native riparian species would presumably be well adapted to frequent disturbance from floods (Catford *et al.* 2014). As such, individual disturbance events may not be a key driver of invasion in riparian ecosystems. Instead, changes to disturbance regimes may be more important in facilitating invasions (Moles *et al.* 2012). Human activities can alter nutrient levels, geomorphic processes and light availability in riparian ecosystems, but the flow regime is arguably the most important force structuring riparian ecosystems (Merritt *et al.* 2010).

Modification of the timing, duration, frequency, magnitude and predictability of flooding and drying may alter the environmental conditions and the types of niches available in riparian zones (Catford *et al.* 2011). If native species are adapted to the historical flow regime and unable to tolerate the modified conditions, invaders may benefit from reduced competition and an increase in resource availability (Catford *et al.* 2011). Invasion will be enhanced if alien species are pre-adapted (or adapt rapidly) to the modified conditions (Mack 2003). For example, the success of alien *Tamarix* species in riparian zones of regulated rivers in western USA, can be at least partly attributed to their greater tolerance of modified flood regimes compared with native riparian tree species (Stromberg *et al.* 2007). Along the regulated River Murray in south-eastern Australia, modification of wetland flooding regimes appears to have inhibited native species adapted to historical conditions and facilitated alien plant invasion (Catford *et al.* 2011). Trait-based analyses suggest that alien species are not specifically adapted to the modified conditions; rather, alien species may indirectly benefit from a decline in competition from native species that are poorly adapted to the new conditions (Catford *et al.* 2014).

Invading species may become established at a site because of favourable biotic interactions. Regardless of the type of ecosystem, invaders can lose and gain biotic relationships on entry into a new range (Mitchell et al. 2006). While the loss of mutualisms can impede alien species establishment, the loss of pathogens and

herbivores may be of benefit (Keane and Crawley 2002). "Enemy release" can reduce mortality and enable alien species to reallocate resources from defence to growth and reproduction (Joshi and Vrieling 2005). Factors that facilitate naturalisation may enable invaders to outcompete native species, shifting the relationship from coexistence to invader dominance.

Population spread

Although localised dominance by an alien species can be ecologically important (Colautti and MacIsaac 2004), species are only considered invasive when their populations spread beyond the site where first introduced. There is commonly a lag phase between introduction and spread (Kowarik 1995). The lag phase is typically attributed to the time required for alien species to genetically adapt to the conditions of its 'new' region (Joshi and Vrieling 2005) or for propagule pressure to increase and environmental conditions to become more suitable for the invading species (Keane and Crawley 2002; Richardson and Pysek 2006). However, it may simply reflect exponential population growth where population growth is initially slow, later increasing at a rapid rate (David Tilman, personal communication, April 2014).

Riparian zones offer an additional method of dispersal for plants in the way of hydrochory, or water-borne dispersal. Although many alien species are not specifically adapted to hydrochory (Stokes *et al.* 2010), they may opportunistically use this dispersal method, increasing the chance of their success (Eschtruth and Battles 2011). Based on monthly surveys of seeds caught in drift nets along two regulated and two free-flowing rivers in Victoria over the course of a year, Greet *et al.* (2012) found that more exotic species used hydrochory in summer and autumn, whereas native seeds were mostly found in the drift in winter and spring, reflecting the time at which they produce and release seeds. In the two regulated rivers, the timing of peak flows has changed from winter-spring to summer-autumn. Given that most propagules are dispersed during peak flows, Greet et al. (2012) concluded that plant phenology (i.e. timing of seed release), hydrochory and flow regulation may jointly facilitate increased dominance and spread of alien plants in regulated rivers.

As well the initial transport and introduction of alien species, humans can facilitate spread of alien species by acting as additional dispersal vectors and by increasing their abundance in the landscape through planting in horticulture and agriculture (Hodgkinson and Thompson 1997; Catford *et al.* 2012a). The frequent use

of rivers and riparian zones by humans increases the chance of alien species spread. At least half of the riparian WoNS benefit from secondary anthropogenic dispersal (e.g. *Alternanthera philoxeroides* can be dispersed in mud attached to machinery or in turf; Parsons and Cuthbertson 1992). Aside from enabling geographic spread, higher dispersal success and propagule rain can increase the success and dominance of alien species simply by flooding the seed bank (Catford *et al.* 2012a). With high numbers of propagules and frequent disturbance, invaders can become established and dominant based on numbers alone.

In summary, riparian ecosystems may be subject to disproportionately high levels of invasion compared to other ecosystems because they have high edge-to-area ratios, high rates of introduction because of their proximity to human activities, additional dispersal opportunities provided by water and human vectors, and they experience frequent flood disturbance that increases resource availability and maintains high habitat heterogeneity (Richardson *et al.* 2007; Eschtruth and Battles 2011; Catford and Jansson 2014). Alteration of flow regimes and other environmental conditions can prompt a decline in native species and may directly and indirectly facilitate the establishment of alien species better adapted to the modified conditions (Catford *et al.*, 2011).

Traits of invasive plants

Since Baker (1965) first suggested the profile of an "ideal weed" the search for plant functional traits associated with invasive species has been the focus of much research (Pysek and Richarsdon 2007; van Kleunen *et al.* 2010). Isolating a syndrome of traits associated with successful invaders is seen as a practical alternative to compiling an exhaustive list of potentially invasive species. Although a single invasive syndrome has proved elusive (Pysek and Richardson 2007; Moles *et al.* 2008), invasive alien species tend to have higher performance than non-invasive aliens and native species, as indicated by growth rate, plant size, leaf-area allocation, shoot-allocation, fitness and physiology (van Kleunen *et al.* 2010).

Many of the characteristics associated with invasiveness are particularly advantageous in frequently disturbed ecosystems with high resource availability, like riparian zones. For example, vegetative reproduction, persistent seed banks and an annual life history help plants cope with flood disturbance (Catford and Jansson 2014), and many of these traits are common among invasive species (Pysek and Richarsdon 2007; van Kleunen *et al.* 2010). Rather than being riparian-specialists, it seems more likely that most invasive species opportunistically invade riparian ecosystems. Indeed, of the 170 plant species in the Global Invasive Species Database (http://www.issg.org/database) that invade riparian ecosystems, only two invade riparian ecosystems exclusively (Catford and Jansson 2014). Patterns in Victoria, Australia are similar: of 518 alien plants that invade riparian scrubs, only 10 species invade this vegetation type exclusively – most species have a much broader range (Catford and Jansson 2014). We briefly describe some of the plant traits likely to facilitate invasion in riparian ecosystems. A more complete review of plant adaptations to riparian environments is provided in Catford and Jansson (2014).

Propagules and dispersal

High fecundity, where a large number of propagules are produced per plant, increases the probability of colonisation and is therefore key to facilitating invasion. *Sagittaria platyphylla*, a macrophyte native to North America that invades wetlands, riverbanks and irrigation channels in south-eastern Australia, produces 6900 seeds per infloresence and seeds float for seven days (Fig. 2, Adair *et al.* 2012). The species can also reproduce from vegetative fragments, which are buoyant, and can spread laterally

via ramets and tubers at the terminal end of tubers (Adair *et al.* 2012). Its high rate of seed production, capacity for clonal spread and resprouting ability makes its populations very difficult to control and contain.

The capacity for asexual reproduction is an important trait for invasive species in riparian systems (Boedeltje et al. 2003; Lake and Leishman 2004). This is because clonal spread and reproduction from vegetative fragments are independent of flowering and fruiting, can enhance dispersal downstream (especially as most fragments are buoyant; Catford & Jansson 2014), and enable quicker recovery following burial (Xiong et al. 2001). Many invasive willows (*Salix* species) cannot reproduce sexually in Australia because they are dioecious and only a single sex was introduced to the country (exceptions include *S. cineara*, Grey sallow, and *S. nigra*, Black willow: their seeds can spread 50-100 km from parent plants; Holland-Clift & Davies 2007). Instead, most willows spread via vegetation fragments (e.g. twigs, branches), which can disperse great distances downstream (Holland-Clift & Davies 2007).

Long distance dispersal typically facilitates rapid colonisation of the landscape and allows species to disperse far enough to avoid localised disturbance, ensuring the persistence of the genotype at the landscape level (Pausas and Lavorel 2003). The capacity for long distance dispersal is therefore important for plant invasions. Compared to other dispersal vectors, a large proportion of hydrochores, especially when buoyant, can disperse long distances (Andersson *et al.* 2000; Catford and Jansson 2014). Humans, wind and animals also act as important dispersal vectors of invasive plants (Lake and Leishman 2004, Taylor *et al.* 2012).

Rapid growth

Factors that influence capacity for rapid growth have been associated with increased invasive success among alien species. Rapid population growth enables a population to reach reproductive maturity quickly, providing an additional source of propagules that will accelerate rates of spread, especially when the population is at the frontier of the species' current range. Rapid growth also helps individuals to complete their life cycle while environmental conditions are suitable. As riparian zones have high resource availability and are temporally dynamic, they are particularly suitable for species with high growth rates. High growth rates are also important in riparian systems because they allow plants to grow to sufficient size to withstand the physical

stresses associated with flooding. Characteristics often associated with rapid population growth include high relative growth rates, rapid maturation, short generation times and lifespans, high fecundity, small seeds, fast leaf economics (e.g. high specific leaf area, low leaf dry matter content) and low root biomass (Grime 1977).

Within Australian riparian systems, alien species have been found to have a higher specific leaf area (SLA) than native species (Lake and Leishman 2004; Kyle and Leishman 2009; Catford *et al.* 2014). SLA is a measure of investment in leaf production, with a higher SLA indicating lower leaf production cost and faster return on investment, and is associated with faster growth. Similarly, species with an annual or biennial life history colonise, establish and reproduce within one or two growing seasons, and therefore tend to have much faster growth rates than perennial plants. Unlike native riparian species, the majority of alien species invading riparian zones are often annual or biennial, not perennial (Catford *et al.* 2011). This has led some authors to posit that the faster life histories of alien annuals may facilitate their dominance in riparian zones after floodwaters recede (Lunt *et al.* 2012). However, a trait-based test of this hypothesis in River Murray wetlands found no support for it (SLA did not distinguish the distributions of exotic and native species either, Catford *et al.* 2014).

Tolerance of stressful conditions

Longer-lived alien species that inhabit riparian zones would need traits that allow them to persist through the challenges presented by riparian environments. Through a number of physiological adaptations, successful riparian invaders such as willows (*Salix* spp.) are capable of tolerating prolonged periods of inundation (Kozlowski 2002), allowing them to colonise frequently inundated zones along the river edge. The ability to tolerate highly saline soils has allowed athel pine (*Tamarix aphylla*) to invade hyper-saline environments where river red gum (*Eucalyptus camaldulensis*) cannot survive (Griffin *et al.* 1989).

To sum up, invasion success is context depenent and the functional traits associated with alien species cannot be considered in isolation from the ecosystems they invade. In riparian environments, traits associated with invasiveness may include rapid growth and resource acquisition, vegetative reproduction, high propagule

output, tolerance of burial and inundation. Unsurprisingly, these characteristics are similar to those possessed by native riparian species. A point of differentiation may occur when environmental conditions are modified such that native and alien species' adaptations differ in their suitability.

Ecological impacts of invasive plants

The vast majority of alien species do not impact the ecosystems they invade, but just add to species richness. However, invasive alien species can alter ecosystem structure and function, reduce biodiversity and compromise ecosystem resilience. They can also threaten human health, reduce visual amenity and cost the economy billions of dollars (Sinden *et al.* 2005; Richardson and Pyšek 2006). Impacts of alien species are conceived as being a function of their abundance, range and per-capita (or per-biomass) effects (Parker *et al.* 1999). While abundance and range can be quantified relatively easily, effects take many different forms and are often hard to attribute to just one cause. Indeed, invasion may be a result or a cause of environmental change (MacDougall and Turkington 2005), and invasion by some species can be both. Plant species that alter the environmental characteristics of an ecosystem, typically to their own advantage, are referred to as transformer species (ecosystem engineers in the case of animals) (Richardson *et al.* 2000). It is often difficult to determine whether invasive species are drivers, passengers or transformers of environmental change, yet the management responses to each of these differ.

We acknowledge that alien species can have positive, neutral and negative impacts on the ecosystems they invade (Shackelford *et al.* 2013), but here we focus on some of the negative ecological effects of invasive alien species in riparian zones because these are typically the focus of management actions.

Abiotic effects

Invasive plants can affect riparian or wetland systems through alteration of the physical environment, including changes in light levels, soil and water chemistry, hydraulics and sedimentation rates. Willows (*Salix* species) have been found to cause a reduction in sedimentation, leading to scour in extreme cases (Ladson 1997), whereas other species increase sediment deposition rates (e.g. *Sagittaria platyphylla*, a Weed of National Significance) by slowing the velocity of stream flow and increasing the capacity to trap sediment (Malanson 1993). In the Australian context, both athel pine (Griffin et al. 1989) and para grass (*Urochloa mutica*: Bunn et al. 1998) have been implicated in increased sedimentation rates. In the Northern Territory, increased sedimentation following the invasion of para grass has been shown to decrease channel capacity by upto 85% (Bunn et al. 1998). This has resulted

in a substantial increase in the frequency of overbank flows and may have important implications for the spread and colonisation of para grass propagules from the river during these events.

Invasive species can also alter the chemical characteristics of an environment through a number of pathways including the addition or consumption of resources, such as nitrogen or oxygen (Richardson et al. 2000). Within wetland systems the consumption of large amounts of oxygen by invasive macrophytes can produce highly anoxic conditions with flow-on consequences for aquatic biota. For example, the removal of water hyacinth (*Eichhornia crassipes*) from the Burdekin delta in Northern Queensland resulted in significantly improved levels of dissolved oxygen, dramatically improving the capacity of the lagoons to support fish species (Perna and Burrows 2005). Invasive plants are also capable of altering the chemical composition of the soil. Salt exudates from the leaves of athel pine can be up to 50 times the concentration of the ground water (Berry 1970). This is believed to have been a contributing factor to the increase in abundance of salt tolerant chenopod and grass species in athel pine invaded regions along the Finke River in central Australia (Griffin et al. 1989).

Biotic effects

Invasive plant species can have numerous effects on the ecological components of riparian systems, including profound changes in community composition. In the Northern Territory, invasive species have had a significant impact on the composition of native wetland plant communities. Mono-specific infestations of mimosa (*Mimosa pigra*) have replaced native sedgelands and have prevented the re-establishment of *Melaleuca* seedlings along watercourses (Waldon *et al.* 2004). Similarly the control of water buffalo has allowed para grass to successfully outcompete *Phragmites karka*, forming mono-specific swards (Finlayson et al. 1997). The invasion of para grass also has implications for the fire regime of the region with larger fuel loads promoting hotter fires (Finlayson et al. 1997). These fires represent a significant threat for neighbouring *Melaleuca* wetlands and fire sensitive monsoonal rainforest communities. Over time, alien plant invasion may lead to the extinction of native species (Gilbert and Levine 2013).

Invasive plants may affect native fauna directly and indirectly by altering habitat and food availability, environmental conditions and community interactions

(e.g. changes in abundance of predators and mutualists). Griffin et al. (1989) documented a reduction in bird and lizard abundance and diversity in athel pine infestations compared to neighbouring river red gum. These differences were attributed to structural differences such as reduced woody debris and tree hollows, inadequate food supply due to smaller flowers, and increased salinity. Structural differences and insufficient resource provision were also implicated in the avoidance of riparian infestations of rubber vine (*Cryptostegia grandiflora*) by native lizards (Valentine et al. 2007). The abundance and diversity of native birds (Holland-Clift *et al.* 2011) and terrestrial arthropods (Greenwood *et al.* 2004) were lower in Victorian riparian zones dominated by invasive white-crack willow (*Salix* x *rubens*) than in those dominated by native vegetation. These findings were thought to reflect changes in habitat characteristics and food availability, including seasonal availability of resources (Greenwood *et al.* 2004; Holland-Clift *et al.* 2011).

Management of invasive plants

Preventing the introduction of invasive alien species will be the most effective strategy for minimising their impacts (Pheloung *et al.* 1999). Once invasive alien species are established though, their negative impacts can be ameliorated by reducing their population size and limiting spread. Weed control methods include mechanical or hand removal, mulch or weed mats, shading, fire and flame guns, biological control agents, slashing, ring barking, controlled grazing, native plant competition, and manipulation of environmental conditions. Ideally, potentially harmful alien species will be detected early, and eradicated while their populations are still confined and in the lag phase (Hobbs and Humphries 1995). Different control measures will be suitable depending on the stage and extent of a weed incursion, the target species, characteristics of the site, and resources available. For example, densely vegetated riparian zones can be hard to access, making manual and mechanical control challenging. Because of the sensitivity of freshwater ecosystems to chemicals, herbicide use is restricted. In Table 1, we provide a brief overview of the major methods of weed control and list their advantages and disadvantages for use in riparian zones. By targeting alien species with a suite of control measures, integrated weed management will often be more effective than a single approach (Rea and Storrs 1999). Active weed management may need to be sustained to yield lasting ecological outcomes (Harms and Hiebert 2006).

With any form of weed management, the indirect impact of alien species removal, as well as control, should be considered (Flory and Clay 2009). Impacts of weed control include erosion of bare banks, disruption of ecosystem processes, increase in water temperature after removal of vegetation, fouling of water by decomposing vegetation (Ainsworth and Bowcher 2005), loss of faunal habitat (Sogge *et al.* 2008), and disturbance of areas resulting in subsequent invasion by other alien species (Buckley *et al.* 2007). In some cases, mechanical control can result in fragmentation of plant material, resulting in further spread within waterbodies (e.g. *Alternanthera philoxeroides:* Parsons and Cuthbertson 1992).

Non-target impacts can be reduced by removing alien species gradually and revegetating with native species, using herbicides that target certain growth forms but not others (e.g. woody weeds, but not grass), and leaving roots and stems intact to minimise erosion (Ainsworth and Bowcher 2005). In limited cases, it may be

inappropriate to control alien species because they provide an ecological function, such as provision of bird-breeding habitat (Sogge *et al.* 2008) and site colonisation in the early stages of secondary succession (Lee *et al.* 1986). Kyle *et al.* (2008) found that survival and growth of river red gum seedling tubestock was significantly higher when grown among alien willow and fennel (*Foeniculum vulgare*) compared to sites that had been slashed prior to planting. As succession progresses, it is expected that later-successional native species will shade and outcompete alien colonisers, reducing the need for specific weed management, though this is not guaranteed (Catford *et al.* 2012a).

Reflecting the myriad ways that alien species may become invasive in riparian ecosystems, riparian weed management is fraught with difficulty. The high frequency of disturbance and ready availability and dispersal of alien propagules means that management needs to be long-term, sustained and catchment-wide. There are currently 2,739 alien plant species classified as invasive in Australia, many of which invade riparian ecosystems (Randall 2007). A species-based approach is clearly neither sustainable nor practical, though alien species that have particularly strong and undesirable impacts can be directly targeted in control.

Instead of species-specific measures, effort should be directed into maximising ecological resistance and resilience to invasion by rejuvenating native plant communities or manipulating environmental conditions. For example, provision of environmental flows that resemble historical conditions in regulated rivers has the potential to favour native species over alien ones (Catford *et al.* 2011). For ecological restoration, planting native species with similar traits as potential invaders' is likely to increase biotic resistance and reduce the number of colonisation opportunities of alien species (Funk *et al.* 2008). Manipulating abiotic conditions may be a cost-effective weed control technique that yields multiple environmental benefits (Rood *et al.* 2003).

Current knowledge gaps and future research directions

There is considerable knowledge and understanding of riparian plant invasions in Australia. However, knowledge gaps – and research opportunities – nevertheless remain. We outline three of these below.

1.   Identifying and quantifying impacts of invasion

Invasive alien species are primarily of concern because of their ecological and socio-economic impacts. However, it is very difficult to identify, isolate and quantify the magnitude of their impacts, especially when they are indirect, like changes to ecological processes and ecosystem services. Given that management budgets are limited, it is essential that the costs and threats of individual species can be compared so that management priorities can be objectively determined. Species rarely have the same effect though, so measuring these costs in a comparable way is challenging. Although there are some efforts have been made (Catford *et al.* 2012b; Barney *et al.* 2013), this area is ripe for further research. Knowing the efficacy of management approaches in different contexts is also required.

2.   Restoring historical environmental conditions and disturbance regimes

If invasive species are a passenger of environmental change, restoring the historical environmental conditions – or changing them in such a way as to favour natives over invaders – may be an effective way to manage alien species and facilitate native species. However, this requires detailed understanding of the system and the species in question. In the case of flow regulation, it is unrealistic to aim for the complete restoration of the historical flood regimes in most cases because water volumes are limited. Environmental flows can be delivered in such a way as mimic historical conditions, but – to get the most out of these flows – it is essential that the relative influence of flood magnitude, frequency, seasonality and duration on riparian vegetation is better understood (Catford *et al.* 2014).

3.   Managing novel ecosystems

Given global environmental change, including increasing pressure on water resources (Capon *et al.* 2013), it may not be possible to restore or maintain historical environmental conditions of riparian zones; novel ecosystems characterised by new

species assemblages that result from human-induced ecological changes may be more likely (Hobbs *et al.* 2009; Catford *et al.* 2013). In novel ecosystems, dominance by invasive alien species may be inhibited by introducing native (or non-invasive alien) species that are capable of competing with invasive alien species under the modified conditions. Determining the types of species, based on their functional traits, that will be favoured in modified ecosystems will be essential for guiding species selection (Funk *et al*. 2008). If the functional composition of riparian flora shifts, this will likely prompt shifts in the properties, characteristics and functions of riparian ecosystems as a whole (Kominoski *et al*. 2013). It remains to be seen whether maintaining historical ecosystem functions is realistic in novel ecosystems.

Conclusion

Riparian plant invasion is a major issue worldwide. Riparian systems seem particularly vulnerable to invasion by alien species because of their proximity to, and association with, human settlements, their large edge to core ratio, high rates of disturbance and high levels of habitat heterogeneity. Although most alien species do not become invasive or cause harm, a small proportion of alien plants can alter the structure and function of riparian ecosystems and threaten their biodiversity. Riparian ecosystems will never be free of alien species, but a range of management options is available to limit current and future invasions. Given the importance of riparian ecosystems now and in the future, effective understanding and management of invasive alien plant species in these systems is essential.

Acknowledgements

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Figures

Figure 1: Rivers provide great environments for recreation but are very prone to weed
invasion. Much of the River Murray in Barmah National Park, Victoria, is
fringed with invasive Weeping willow (*Salix babylonica*) and Delta arrowhead
(*Sagittaria platyphylla*), pictured here. Source: J.A. Catford.

Figure 2: Many invasive species can reproduce sexually and asexually and use water
as a dispersal vector. Delta arrowhead (*Sagittaria platyphylla*), invasive in
south-eastern Australia, produces 6900 seeds per inflorescence, which help it
to increase in population size and spread downstream starting new, satellite
populations (inset A). It also spreads clonally (inset B). Source: J.A. Catford.