UDK 631.963:581.524.2
Pregledni rad – Review paper

The role of riparian areas in alien plant invasions

Ana Anđelković[1], Snežana Radulović[2]
[1] Institute for Plant Protection and Environment, Department of Weed Research, Teodora Drajzera 9, 11040 Belgrade, Serbia
[2] Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Trg Dositeja Obradovića 3, 21000 Novi Sad, Serbia
e-mail: ana.andjelkovic21@gmail.com

ABSTRACT

Biological invasions represent one of the defining features of the Anthropocene, causing major problems and incurring significant economic losses worldwide, which are only projected to increase in the future. Riparian zones, as critical transition zones, despite providing numerous ecosystem services, are exposed to a multitude of human pressures, making them highly vulnerable to plant invasions. In fact, in Europe, riparian areas are considered to be among the most vulnerable habitat types. As foci of invasive plant species richness, they play an important role in the process of their spread into nearby terrestrial ecosystems. Various disturbance events, both natural (i.e. floods) and artificial (e.g. hydro-morphological alterations), in addition to a strong propagule pressure these areas are subjected to, increase the invasibility of these vulnerable zones. Given their ecological importance and susceptibility to plant invasions, the preservation and restoration of riparian zones is especially important in light of climate change. In order to preserve and restore the ecosystem services and biodiversity of riparian areas, invasive alien plants have to be managed. The success of restoration measures and control activities can be affected by many variables, such as the invasive plants' residence time and their legacy effects. Furthermore, different environmental factors and drivers of invasion must also be considered, as they could potentially impair the restoration measures. Finally, a successful restoration effort depends on the inclusion of all the relevant stakeholders and their understanding of the importance of preventing and managing plant invasions.

Keywords: invasive alien plants, riparian zone, invasibility, restoration.

INTRODUCTION

Biological invasions are among the key characteristics of the Anthropocene (Kueffer, 2017), due to the ever-increasing human-mediated transport of species outside of their native range (Hulme, 2009; Seebens et al., 2015). They are considered to be among the key consequences of global climate and land use change (Davis et al., 2000), affecting human well-being, economy, and biodiversity worldwide (IPBES, 2019). Moreover, with no saturation of their numbers in sight (Seebens et al., 2017), it is expected that their effects will only be exacerbated in the northern temperate regions over the coming years (Pellegrini et al., 2021).

The most recent assessment states that the accumulated costs incurred by biological invasions overall (for the period 1960-2020) have reached 140.20 billion US$ for Europe (Haubrock et al., 2021). Majority of these costs relate to damage and loss (60%), with agriculture being the most impacted sector, with 36 billion US$ in incurred costs (Haubrock et al., 2021). Globally, the economic impacts of biological invasions have been estimated at cca. 2.3 trillion US$, which is still not the full price, keeping in mind that the true economic costs remain underreported across regions and taxonomic groups (Zenni et al., 2021). In fact, a single invasive alien plant (common ragweed) was estimated to cost the European economy in a range between 2.95 and 9.02 billion Euros per year (Bullock et al., 2012). Bearing all this in mind it becomes clear that the science of biological invasions, i.e. invasion ecology, finds itself at the „interface between nature and society", encompassing both fundamental and applied research (Heger et al., 2021).

Davis et al. (2000) highlight that the naturalization and invasion processes depend on three critical factors: the number of incoming propagules, i.e. propagule pressure (Colautti et al., 2006), inherent characteristics of the invasive species itself (Rejmánek, 2011) and susceptibility of the habitat to invasion, i.e. invasibility (Lonsdale, 1999). Invasibility represents an emergent characteristic of a certain environment, resulting from a multitude of factors, including climate, disturbance regimes, and competitive ability of the native biota (Lonsdale, 1999). Several large-scale studies have shown that habitat type is a good indicator of invasion levels in Europe (Maskell et al., 2006; Vilà et al., 2007; Chytrý et al., 2008), with high invasion levels being particularly characteristic of low-lying regions (Chytrý et al., 2009). In this sense floodplains of large lowland rivers are especially important, as shown by a multitude of studies (Pyšek and Prach, 1993; Planty-Tabacchi et al., 1996; Naiman and Décamps, 1997; Tickner et al., 2001; Richardson et al., 2007; Schnitzler et al., 2007; Anđelković et al., 2022a, b).

Acknowledging the overall importance of riparian areas in the process of biological invasions, and the multitude of impacts of plant invasions, this review aims to provide some insight into the general characteristics and importance of riparian areas, their invasibility, and some restoration implications.

RIPARIAN AREAS – CHARACTERISTICS AND ECOLOGICAL VALUE

Riparian zone forms an interface between the terrestrial and aquatic ecosystems. It is an open and hybrid ecotone, where the fluvial system and its underlying processes are influenced by and in turn influence the surrounding land. At the same time its hybrid nature is driven by a mixture of natural and anthoropogenic processes (Dufour and Rodríguez-González, 2019; Dufour et al., 2019). Riparian vegetation can be defined as „a co-constructed complex of vegetation units along the river network, regardless of physiognomy or origin, that is functionally related to the other components of the fluvial system and surrounding area" (Dufour and Rodríguez-González, 2019, p. 16). Overall, riparian zones are of a highly limited spatial extent, occupying only around 2% of the European land area (Clerici et al., 2013).

Nevetheless, Riis et al. (2020) highlight that, despite their limited area, owing to their ecotone nature and numerous ecological functions of the riparian vegetation (*see* Dufour et al., 2019), riparian zones provide numerous ecosystem services of critical value (Naiman and Décamps, 1997; Rinaldo et al., 2008; Gundersen et al., 2010; Jones et al., 2010; Clerici et al., 2013; De Sosa et al., 2018; Riis et al., 2020). These ecosystem services can be dividided into provisioning services, regulating and maintenance services, and cultural services (Riis et al., 2020), with the provisioning and regulating services being mostly driven by the processes that depend on the biophysical structure of the vegetation (Fonseca et al., 2021).

In this sense, riparian zones represent a meta-ecosystem which ensures the functioning of the carbon cycle in the freshwater ecosystems, as a result of its carbon sequestration processes (Dybala et al., 2019). They also control the flow of matter and energy in the surrounding landscape (Ewel et al., 2001), influence nutrient (nutrient sink; Rosenblatt et al., 2001) and sediment retention (Jones et al., 2001), regulate water temperature by shading (Studinski et al., 2012), perform bank stabilization and flood control (Chaimson et al., 2020), and improve the quality of water (Mander et al., 2005). Moreover, riparian zones are important as habitats and corridors for the movement of biota (Naiman and Décamps, 1997; Ringold et al., 2008; de la Fuente et al., 2018), and safeguarding biodiverisity (Naiman et al., 1993; Wagner et al., 2020; Montejo-Kovacevich et al., 2022). Finally, riparian areas also ensure opportunities for cultural and recreational activities (Riis et al., 2020).

Despite their critical importance, riparian zones experience a range of pressures, e.g. pollution, damming, changes in the disturbance regime, land-use changes (Richardson et al., 2007), resulting in severe degradation of these fragile areas worldwide (Riis et al., 2020) and the disapperance of an estimated 80% of riparian habitats in Europe (Naiman et al., 1993; Riis et al., 2020).

INVASIBILITY OF RIPARIAN AREAS

The Convention of Biological Diversity (CBD) recognizes six routes of alien species introductions. Of the two pertaining to the spread of alien species in recipient ecosystems, corridors are defined as a route which underlies „unintentional introduction via human infrastructure linking previously unconnected regions" (Asth et al., 2021, p. 2). In this sense, linear infrastructures (i.e. roads, railways, rivers, and canals) decrease the landscape connectivity, thus creating habitat breakages and affecting the plant and animal communities (Asth et al., 2021). Additionally, these linear corridors can also be instrumental in the introduction and dispersal of alien species (e.g. Anđelković et al., 2016, 2020, 2021, 2022; Follak et al., 2018;

Rinaldo et al., 2018; Živković et al., 2018; Wagner et al., 2020; Asth et al., 2021; Lemke et al., 2021; Gašparovičová et al., 2022).

Invasibility of riparian areas seems to be caused primarily by the landscape structure at the local scale and the regime of site disturbances (Planty-Tabacchi et al., 1996). Natural disturbances can be frequent, e.g. flash floods or beaver dams on mountain streams, or reccur every 50 or 100 years, as in the case of windstorms and major flood events on lowland rivers (Tabacchi et al., 1998). Overall, riparian areas are subject to frequent flooding episodes. Richardson et al. (2007) highlight that a 1-in-50-years flood can change the riparian vegetation structure for a period of several decades. Such flood events result in nutrient pulses (i.e. increased productivity on site) and can result in release from light competition with native trees (Slezák et al., 2022), thus favouring the growth of invasive alien plants (IAPs). In this sense, the susceptibility of riparian areas to invasion can best be explained by the theory of fluctuating resources (Davis et al., 2000), which accounts for the effects of resource availability, disturbance regime and fluctuating environmental conditions. It posits that a plant community will be made more susceptible to invasion if there is an abundance of unused resources, coupled with reduced competition. Higher richness of alien species is characteristic for riparian sites with higher ratios of nitrogen in the soil (Stohlgren et al., 1998; Menuz and Kettenring, 2013). The resulting increase in the abundance of IAPs then leads to further changes in the structure and functioning of riparian areas (Richardson et al., 2007). Notable examples are the Japanese knotweed (*Reynoutria japonica* Houtt.) and giant knotweed (*Reynoutria sachalinensis* (F. Schmidt) Nakai) which drastically reduce the diversity and structure of native riparian communities (Urgenson et al., 2009; Aguilera et al., 2010). The riparian vegetation stands outside the *R. japonica* have between 1.6 and 10 times more species (Aguilera et al., 2010), while giant knotweed reduces the regeneration of native pioneer tree species (e.g. *Alnus rubra*, *Salix* spp., *Populus trichocarpa*), and the litter mass of native species by 70% (Urgenson et al., 2009). Similarly, Radovanović et al. (2017) have shown that riparian vegetation stands show a significant decline in the total number of species with an increase in the total cover of IAPs.

Hydromorphological alterations, i.e. man-made changes to the flow regime and natural channel configuration (e.g. damming, flow diversion, channel incision, groundwater pumping, flow regulation) affect the composition and cover of the riparian vegetation (Stromberg et al., 2007; Aguiar et al., 2016; Cubley et al., 2022). Riparian vegetation along dam-regulated and watercourses with an intermittent flow regime is (co-)dominated by more stress-tollerant alien *Tamarix* species (Stromberg et al., 2007). Similarly, Aguiar et al. (2016) have shown that highly altered riparian landscapes (e.g. post-dam contruction) are characterized by vegetation patches which, despite a consistent increase in total area, have a lower edge density and are less complex in shape. On the other hand, post-restoration on the Upper Arkansas River in USA, Cubley et al. (2022) have documented an increase in riparian vegetation cover and height, as well as an increase in structural complexity and habitat heterogeneity. Consequently, heavily modified and regulated rivers are especially prone to plant invasions (Aguiar et al., 2001; Catford et al., 2011; Slezák et al., 2022). This can result from a reduction in the frequency of strong floods and an increase in propagule pressure, caused by channelization works (Aguiar and Ferreira, 2013). The same is true of artificial canals, which can be highly invaded and serve as very effective conduits for the spread of IAPs (Anđelković et al., 2020; Asth et al., 2021). Land transformation required for the construction of artificial canals facilitates the colonization of alien species, by creating new habitats (Asth et al., 2021). Similarly, bank erosion can also lead to an increase in IAPs density, as such eroded banks simultaneously provide a source of propagules and an open space for their establishment (Navratil et al., 2021).

Another important aspect of the invasibility of riparian areas is propagule pressure. On the one hand, dense stands of invasive plants found along the riverbank can serve as a seed pool for further propagule dispersal downstream (Aronson et al., 2017). Floods can be a critical asset in the downstream dispersal of propagules, leading to increased density of some IAPs, e.g. Japanese knotweed (Navratil et al., 2021). Additionally, urban areas can act as propagule hubs for the spread of IAPs down rivers and canals flowing through them (Säumel and Kowarik, 2010). In this sense, both the proportion of urban habitats and population density in the vicinity positively affects the presence of some invasive tree species, e.g. *Acer negundo* and *Ailanthus altissima* in riparian areas (Wagner et al., 2020). Pabst et al. (2022) have also shown that the proportion of urban zones is positively correlated with the richness of IAPs in riparian areas of Portugal, with the highest values observed around Lisbon and Porto, as the two major cities.

Various anthropogenic disturbances affect the vitality of riparian zones, which often results in the spread of IAPs (Richardson et al., 2007). There are different factors affecting the role disturbance plays in facilitating plant invasions in riparian areas. In general, fewer IAPs are characteristic of riparian sites with a more natural land use type (Zelnik et al., 2020), as changes in land use and land cover strongly impact the riparian vegetation structure (Fonseca et al., 2021). For example, the proximity of wetlands to areas with a strong anthropogenic pressure, like agricultural fields, results in a high proportion and cover of IAPs (Stanković et al., 2020). Moreover, the structure of the riparian vegetation and its complexity are negatively correlated with the abundance of IAPs (Zelnik et al., 2020). The abundance of IAPs in a riparian zone shows a longitudinal trend, increasing from the river source to its piedmont (Planty-Tabacchi et al., 1996; Zelnik et al., 2020; Pabst et al., 2022), with the distance from the source being one of the crucial paramteres affecting the IAPs presence and abundance (Zelnik et al., 2020).

Such a trend results from an interaction of a multitude of factors. First of all, riparian corridors in lowlands are more heavily fragmented (Planty-Tabacchi et al., 1996), thus exhibiting a stronger edge effect (Theoharides and Dukes, 2007), incurring greater invasibility of the riparian community. Furthermore, low-lying riparian areas experience stronger anthropogenic pressures and hydrological disturbances, resulting in an abundance of young and disturbed communities, which are more prone to invasion, e.g. river bars (Liendo et al., 2021). Land use adjacent to the riparian zone also plays an important part in the communities' susceptibility to invasion (Zelnik et al., 2020), with proximity of agriculture (Osawa et al., 2013; Anđelković et al., 2022a) and proportion of urban areas (Aronson et al., 2017; Wagner et al., 2020) resulting in higher invasibility of riparian areas. Dominant vegetation on site also affects the invasibility of a riparian area on a local scale (Anđelković et al., 2022a), as the final degradation stages of natural floodplain forests (Radovanović et al., 2017) and riparian sites with dominant shrub vegetation (Anđelković et al., 2022a) tend to harbour the highest proportion and cover of IAPs. Finally, temperature also plays an important part in the susceptibility of riparian areas to invasion, with the areas found at lower elevations exhibiting warmer climates, often favouring alien over native species (Chytrý et al., 2005; Schnitzler et al., 2007). Consequently, open-canopied, dry and hot riparian sites, in proximity of roads, have a higher likelihood of containing more invasive species (Menuz and Kettenring, 2013), compared to riparian areas at higher altitudes.

All of the above has resulted in riverine sites, especially floodplain forests (gallery forests) and riverine scrubs being among the most heavily invaded on the European continent (Schnitzler et al., 2007; Marinšek and Kutnar, 2017; Anđelković, 2019; Kalusová et al., 2021; Lapin et al., 2021; Wagner et al., 2021), with the G1.1 EUNIS habitat type harbouring the highest sum cover of alien plant species (Wagner et al., 2021).

RESTORATION IMPLICATIONS

Riparian areas, despite their limited spatial extent (Clerici et al., 2013), experience a multitude of anthropogenic pressures, making them very challenging for management and restoration (Richardson et al., 2007). Preservation of complex riparian areas can ensure that the introduction and spread of IAPs within riparian zones and downstream are prevented (Zelnik et al., 2020). With climate change, it is especially important to ensure effective conservation and restoration of riparian areas' ecological integrity (Urbanič et al., 2022). Furthermore, restoration measures have been shown to augment some of the key ecosystem services riparian forest patches provide in agricultural landscapes (Castellano et al., 2022).

In order to preserve and restore the ecosystem services and biodiversity of riparian areas, it is necessary to manage IAPs, and their prioritization is critical when defining appropriate management goals (Lapin et al., 2021). Various ecological quality indices used for assessing the general state of rivers and/or riparian zones (e.g. RVI, Kemper, 2001; IMPI, Ferreira et al., 2005; RQI, González del Tánago and García de Jálon, 2006) account for the presence and cover of IAPs.

In order to develop successful management plans, it is necessary to understand the timing of IAPs introduction (Aronson et al., 2017), as the power to detect them early on is essential for their potential eradication or success of subsequent control activities (i.e. early detection and rapid response; Reaser et al., 2020). Moreover, when conducting prioritization and developing management plans, legacy effects must also be taken into account. Legacy effects from previous years of the competition between the native and invasive alien plants have a greater influence on the aboveground vegetation at heavily invaded riparian sites than propagule pressure and sediment deposition (Pattison et al., 2018). Obtaining the long-term success of IAPs management largely depends on the degree to which the native vegetation can recover (Holmes et al., 2005).

Some of the clonal perennial invasives present in European riparian forests form dense stands reaching up to 3-4 m in height (e.g. stands of *Fallopia* sp.), or even 9 m in the case of *Arundo donax* (Schnitzler et al., 2007). Such IAPs affecting water flow and the flooding regimes are very difficult and expensive to manage. Therefore, planning and implementation of management actions for these invasive plants should be conducted at the watershed scale, requiring a coordinated and concerted effort of all the affected municipalities found along the watercourse (Aronson et al., 2017). Aronson et al. (2017) highlight that such coordinated efforts would ensure the success of IAPs management upstream, thus preventing the creation of invasion foci in these upland reaches and removing a potential source for IAPs propagule spread downstream.

Different factors affecting the river catchment, which might limit and impair the restoration measures conducted at a specific local river section should also be considered (Holmes et al., 2005). Furthermore, when selecting areas of priority for IAPs management, it is critical to consider adjacent land use types and anthropogenic presence (Bellini and Becker, 2021).

In order to ensure successful implementation of restoration projects, achieving a high conservation and ecological potential, it is necessary to identify relevant stakeholders, and effectively communicate the importance of such actions to ensure their continued engagement (Damnjanović et al., 2019; Arsénio et al., 2020). For this to be effective, it is critical to ensure that stakeholders are involved in knowledge exchange and co-creation of relevant policies and management plans (Urbanič et al., 2022). Such a system would ensure that stakeholders (e.g. counties and municipalities) with more expertise would be willing to help indentify the priority areas and ensure the flow of information and knowledge transfer between the affected communities (Aronson et al., 2017). Finally, owing to the dynamic nature of riparian systems, one must be aware that rather than restoring the area to its historical condition, its management and restoration should aim to restore its natural processes which would ensure a desired set of riparian ecosystem structures and functions (Richardson et al., 2007).

ACKNOWLEDGMENTS

The authors acknowledge financial support of the Ministry of Education, Science and Technological Development of the Republic of Serbia (Grants No. 451-03-68/2022-14/200010 and 451-03-68/2022-14/200125).

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Uloga riparijalnih oblasti u invaziji stranih biljnih vrsta

REZIME

Biološke invazije predstavljaju jednu od odlika koje karakterišu Antropocen. Invazivne vrste uzrokuju niz problema i rezultuju velikim ekonomskim gubicima na globalnom nivou, čiji se dalji rast očekuje i u budućnosti. Riparijalne (priobalne) zone, kao kritične tranzicione oblasti, uprkos tome što pružaju niz ekosistemskih usluga, nalaze se pod uticajem brojnih antropogenih pritisaka, što ih čini posebno podložnim prodoru invazivnih biljaka. Na području Evrope, upravo se riparijalne zone smatraju jednim od najinvazibilnijih tipova staništa. Kao žarišta biljnih invazija, riparijalne zone takođe imaju važnu ulogu i u procesu daljeg širenja invazivnih biljaka u obližnje terestrične ekosisteme. Različiti tipovi narušavanja, prirodni (poplave) i veštački (npr. hidromorfološke modifikacije), uz snažan pritisak propagula kome su ove oblasti izložene, povećavaju invazibilnost ovih oblasti. Imajući u vidu njihov ekološki značaj i podložnost prodoru invazivnih vrsta, zaštita i oporavak riparijalnih zona je od posebnog značaja u svetlu klimatskih promena. Kako bi se očuvale i povratile ekosistemske usluge i biodiverzitet riparijalnih oblasti, neophodno je sprovoditi kontrolu stranih invazivnih biljaka. Uspeh mera oporavka i aktivnosti kontrole invazivnih vrsta zavisi od niza činilaca, poput vremena introdukcije invazivnih vrsta i posledica njihovog prisustva u tom periodu. Takođe, različiti faktori životne sredine i faktori koji utiču na uspeh procesa invazije moraju se uzeti u obzir, jer bi mogli narušiti proces oporavka (obnavljanja) datog ekosistema. Na kraju, uspešnost procesa oporavka ekosistema, zavisi i od uključivanja svih zainteresovanihstrana i njihovog razumevanja značaja sprečavanja prodora i rešavanja problema invazivnih biljaka.

Ključne reči: strane invazivne vrste, priobalne zone, riparijalne zone, invazibilnost, oporavak ekosistema.