Journal of Environmental Management 293 (2021) 112871

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Invasive species in the Anthropocene: Help or hindrance?

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ARTICLE INFO

Keywords:
Refugia
Willows
Thermal maxima
Ectotherms
Shading
Ecosystem engineers

ABSTRACT

Under predicted climate change scenarios many parts of the world will be hotter. Higher temperature extremes present significant physiological challenges to ectothermic freshwater species that cannot regulate body temperature. Willows (*Salix* spp.) are highly invasive deciduous northern hemisphere shrubs and trees that have colonised riparian zones of southern hemisphere streams. Non–native willows are criticised for their high consumption of water and their capacity to form dense monostands along the margins and within waterways that limit light to streams in summer, alter the timing and quality of allochthonous inputs and modify ecosystem function. As such, governments invest heavily in the removal of willows from streams in order to preserve ecosystem integrity. Although detrimental effects of non–native willows are well documented, little attention has been focussed on consideration of potential ecosystem services that non–native willow infestation may provide under predicted climate warming. Here, we use a case study to illustrate that shading by non–native willows can provide thermal refugia for temperature sensitive endemic taxa and we provide a holistic approach to non–native willow removal that may provide benefits to aquatic species amid changing climate. We present a simple decision matrix for prioritising willow removal activities that may be applied to other invasive species and we discuss traditional views of invasive species management and river restoration and their relevance in a rapidly warming world. The concepts we discuss are of immediate relevance to environmental managers challenged with maintaining and restoring ecosystems that are rapidly changing in structure and function in response to climate warming.

1. Introduction

Globally, 2019 was the second hottest year on record and some parts of the southern hemisphere recorded their warmest and driest year to date (Bureau of Meteorology, 2020). For much of the world, the future will be hotter and drier (e.g. Grose et al., 2019), and climate change will affect freshwater ecosystems by warming water temperatures, altering stream flow patterns, and increasing storm events (Poff et al., 2002). Inhabitants of streams are particularly at risk from climate change due to their comparative isolation and the dendritic spatial arrangement that constrains dispersal of species as temperatures increase (Woodward et al., 2010).

Some aquatic ectotherms are already approaching the limits of their thermal tolerance (e.g. crayfish; Stoffels et al., 2016). Riverine ectotherms that reach their thermal maxima are ultimately left with two options and can either 1/adapt to warmer conditions or 2/migrate upstream to cooler water. For many taxa, the former option is not possible due to the rapid rate at which habitats are warming (e.g. limited thermal tolerance plasticity; Gunderson and Stillman, 2015). The latter option presents difficulties for taxa that inhabit modified ecosystems (e.g. rivers with dams and weirs) or that contain natural barriers to movement (e.g. waterfalls), taxa with poor dispersal traits, and taxa that inhabit rivers that rise from modest elevations.

Preservation of existing refugia, defined by Dobrowski (2011) as ‘places where local climate is decoupled from regional climate’ will play a critical role in aquatic species conservation under predicted climate scenarios. Thermally sensitive species may seek refugia under extreme conditions, endure until conditions alter and then potentially expand again when severe conditions abate (Keppel et al., 2012). Sentient ecosystem conservation planning must carefully consider changing climate as a driving factor and should incorporate the protection of climatic or thermal refugia into future restoration programs for

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https://doi.org/10.1016/j.jenvman.2021.112871
Received 13 July 2020; Received in revised form 20 May 2021; Accepted 21 May 2021
Available online 29 May 2021

freshwaters (*sensu* Groves et al., 2012).

Due to accidental and unintentional anthropogenic introductions, species invasions are widespread globally. Governments invest large sums of money and effort to control and remove invasive species from a diverse range of ecosystems. The dynamic nature of riverine floodplains (e.g. flooding and drying disturbance sequences) and anthropogenic modifications to hydrological patterns, render riparian habitats particularly susceptible to non–native plant invasions (Richardson et al., 2007). Riparian ecosystems have become a focus of invasion ecologists globally, with a wide variety of invasive plants impacting streams via shared mechanistic pathways (e.g. altered shading, changes to organic matter inputs), both in the northern and southern hemisphere (e.g *Tamarix* spp. in the U.S.A. (Shafroth et al., 2005), *Rhododendron* spp. in Europe (Hladyz et al., 2011) and *Eucalyptus* spp. in South Africa (Holmes et al., 2005).

Assessments of the influence of climate change on invasive species in have focussed on theoretical and conceptual frameworks to improve our understanding of interactive effects on changing distributions and persistence, along with suggestions for invasive species management plans (e.g. Hellmann et al., 2008; Rahel and Olden, 2008). Broadly, the spread of invasive species is expected accelerate with changing climate due the wide-ranging climatic tolerances and large geographic ranges of many invasive taxa (Pyke et al., 2008). However, less attention has been directed at the exploration of potential beneficial services that invasive species may be able to provide to endemic species as ecosystems change with climate.

Many invasive taxa share common traits (e.g. fast growth rates (Grotkopp and Rejmánek, 2007), strong dispersal capacity (Alex Perkins et al., 2013), and wider niche width (Olsson et al., 2009)) that have facilitated their successful colonisation of new habitats. Some invasive species can regulate resource provision to other species by causing physical state changes in biotic or abiotic constituents and have thus been termed 'ecosystem engineers' (Emery-Butcher et al., 2020; Jones et al., 1994). It is such characteristics that place invasive taxa in a unique position with changing climate; in many cases they may be capable of enduring changing conditions better than endemic taxa, and in some cases, they may even modify existing ecosystems to improve the chances of persistence of more vulnerable endemic taxa by creating new refugia. Here, we use non–native willows, a recognised 'ecosystem engineer', as a case study to explore how the biological characteristics of invasive species might be harnessed by policy makers and managers of natural resources, to provide ecological and ecosystem service benefits (e.g. Riis et al., 2020) under predicted climate scenarios. We present a decision matrix to help prioritise willow removal activities in light of predicted changes to climate.

2. Invasive willows

Willows comprise trees and shrubs belonging to the genus *Salix*. They are deciduous plants with native distributions confined almost entirely to the northern hemisphere where they are widely recognised as disturbance specialists (Meikle, 1984). Willows are highly successful invaders of temperate southern hemisphere riparian zones and are now extensively distributed in South Africa (Henderson, 1991), South America (Budde et al., 2009), Australia (Cremer, 2003) and New Zealand (Wilkinson, 1999). The bulk of invasive willows research in the southern hemisphere has examined their water use in comparison to native riparian plants (Doody and Benyon, 2011; Doody et al., 2011, 2014b), their effects on in–stream macroinvertebrate communities and comparisons of leaf leaching rates with leaves from endemic riparian plants (e.g. see review by McInerney et al., 2016a). More recently, invasive willow research has shown how willows alter trophic dynamics and species compositions within aquatic ecosystems (McInerney et al., 2016c) and that they can modify microbial communities via co–invasion of non–native symbionts (McInerney and Rees, 2017).

One of the primary criticisms of willows, is their tendency to form dense monostands on banks and within stream beds that prevent light penetration, restricting establishment of other riparian species (Greenwood et al., 2004) and reducing standing stocks of benthic algae in aquatic ecosystems (Lester et al., 1994), with the latter shown to have cascading effects on in-stream food webs (McInerney et al., 2016c). But it is this tendency to form dense stands on the margins that lend willows to be a potentially useful tool in the fight against temperature driven species extinctions. Although a large body of literature describe the ways in which invasive willows can modify their invaded ecosystem, to date, the authors are unaware of any evidence that willows have been directly responsible for the extinction of a species. The evidence for willows decreasing taxa richness of stream invertebrates is inconsistent between studies and highly context dependent (e.g. Table S1), and when compared to climate change, this could make invasive willows the lesser of two evils.

3. Case study

Willow removal from riparian zones of Australian temperate streams is an ongoing management activity funded by governments. Happy Valley Creek in north east Victoria, Australia is a small first order stream where willows were mechanically removed from a 1 km mid-catchment reach in 2009 following widespread bushfires that destroyed large sections of riparian vegetation. To assess instream effects of willow removal, temperature loggers (along with other metrics not discussed here) were placed in three locations in Happy Valley Creek: 1/At the willow removal site mid-catchment with all riparian vegetation removed, 2/A site at the top of the catchment inside state forest with a native forest riparian zone, and 3/a site at the bottom of the catchment with a dense invasive willow over story (see Fig. 1). Loggers (HOBO Pendant® Temperature/Light 8 K Data Logger, www.onsetcomp.com) were attached to metal stakes and submerged in the stream to a depth of 20 cm in flowing water and recorded temperature every 10 min from February 2013 to December 2014.

The Happy Valley Creek catchment provided a rare opportunity to track the influence of riparian cover on stream temperature, since there are no major inflows between the willow removal site and the willow invaded site, altitude difference between sites are small (<200 m, catchment length approximately 30 kms) and all aspects of stream

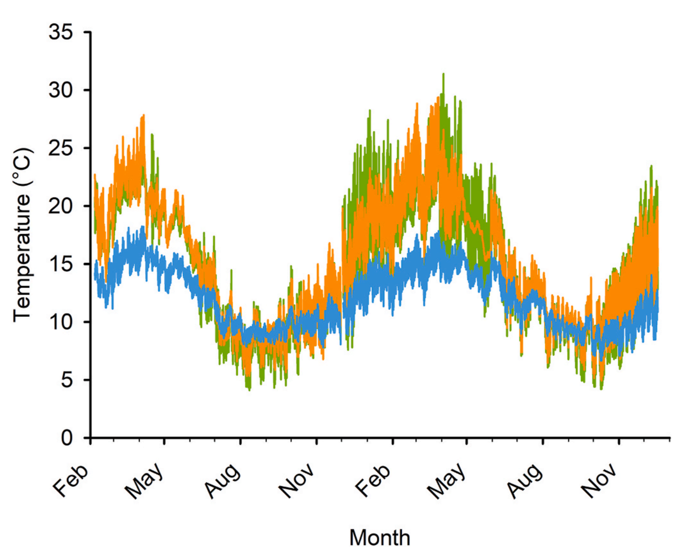

Fig. 1. Happy Valley Creek water temperature in the native riparian zone upper catchment (blue), willow removed mid catchment (green) and the willow invaded lower catchment (orange). Raw data, logged at 10 min intervals from February 2013 to December 2014. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

morphology are similar (e.g. stream direction, substrate) save riparian cover. We expected that stream temperature would gradually rise as water moved down the catchment (e.g. Vannote et al., 1980), but we hypothesised that dense shading by willows may buffer the rate of temperature increase, consistent with reported effects of riparian shading on stream temperature (e.g. Beschta, 1997). Our results require cautious interpretation due to an absence of replication at the stream level, but are nonetheless clear, and surprising. We found that rather than buffer, dense shading provided by willow infestation had the capacity to cool stream temperature by up to a few degrees relative to reaches immediately upstream with no riparian cover, particularly during extreme heat periods in summer (Fig. 1). A number of studies report such daytime stream cooling gradients under forest canopies located downstream of open land–use (e.g. Garner et al., 2014; Rutherford et al., 1997; Story et al., 2003) and the importance of riparian vegetation for mediating stream temperature is well documented (e.g. Dan Moore et al., 2005; Malcolm et al., 2008; Roth et al., 2010). However, cooling gradients have rarely been explored in the context of an invasive species providing ameliorative ecosystem services (Emery-Butcher et al., 2020) and more work is required to test if the observed willow example is consistent among other catchments and over larger spatial scales. Nonetheless, these results have important implications for catchment planning and policy settings for temperature sensitive aquatic species.

4. Implications

Currently willow removal policies vary (e.g. between states or countries), but broadly there is little holistic consideration of potential existing ecosystem services provided by willows or their capacity to provide multiple ecosystem functions (e.g. Giling et al., 2019). The detrimental effects to ecosystems of invasive willows are well studied (e.g. Table S1), but little attention has been paid to potential benefits. Ecosystem restoration has traditionally focussed on returning degraded ecosystems to a perceived 'natural state' (e.g. Dufour and Piégay, 2009). This is problematic for two reasons; 1/often the 'natural state' might not be known with any degree of certainty and can be 'surmised' and 2/the 'natural state' may not be achievable or sustainable under predicted future climate. The latter point is of particular concern, since appreciable effort and expense can be outlaid for minimal environmental return, and more worryingly, because while attention is focussed on recreating quasi 'natural habitats', native ectotherms that have thus far endured under temperature moderated willow monostands, may be extirpated following a return to the open canopy typical of many endemic riparian plants.

It is important to clarify that we are not suggesting that a wholesale cessation of willow removal programmes should be considered; willows remain an invasive pest that require control to meet legislative requirements and to prevent further widespread invasion. However, a strategic approach to willow removal that considers potential refugia benefits, could offer some assistance to temperature sensitive taxa that are walking a fine line as we enter a warmer future (Fig. 2). When

	Criteria score	Does the stream contain rare or endangered temperature sensitive species that may be persisting only because of willows?	Can willows be removed from the upstream extent of the catchment?	What is the likely endpoint for the willow removed site?	Has the horse already bolted?	How big is your stream?
Do not remove willows (1-5)	1	Endangered and thermally sensitive	No funding for follow–up riparian management	Poor condition – highly modified stream from reference	Willows extend from headwaters to estuary of catchment	4th order stream – willows have small functional effect relative to water volume
* Discreet willow removal (6-10)	2	Vulnerable and thermally sensitive	Unlikely funding for follow–up riparian management	Average condition – some aspects of riparian-stream interaction retained	Willows in most reaches of catchment	3rd order stream – willows have relatively small functional effect relative to water volume
* Catchment–scale willow removal (11-15)	3	Near Threatened and thermally tolerant	Likely funding for follow–up riparian management	Good condition – strong likelihood of maintaining terrestrial/aquatic functional attributes	Willows in some reaches of catchment	2nd order stream – willows have moderate functional effect relative to water volume
Remove all willows (16-20)	4	Least Concern and thermally tolerant	Highly secure funding for follow–up riparian management	Reference condition – returned to pre-modern hydrological, riparian and terrestrial/aquatic functional attributes	Willows in isolated patches of catchment only	1st order stream – willows have large functional effect relative to water volume

* Not all invasive willows are created equal – know your target: When scores fall between 6-15 a further overlay should be applied that considers removal of in-channel growing willows preferentially over willows growing on stream margins to reduce water consumption and to ease flow restriction while maintaining shading for thermally sensitive taxa

Fig. 2. Decision matrix for determining the appropriate level of willow removal. Criteria score are summed for each column to determine management action.

planning for implementation of willow removal activities there are some key considerations that should to be taken into account:

4.1. Does the stream contain rare or endangered temperature sensitive species that may be persisting only because of willows?

In small streams or those subjected to very low summer flows, extreme temperatures can pose a greater threat to thermally sensitive taxa than those that inhabit large water bodies, particularly in reaches where all vegetation is removed (e.g. Quinn and Wright-Stow, 2008). Before willow removal occurs, practitioners should ensure that by removing willows they are not removing critical thermal refugia that is locally absent elsewhere. In some cases, this may include rare or endangered regionally endemic species that would not have occurred locally without the presence of willows, but that now persist due to willows. Removing willows from multiple linked reaches of the one stream at one time, could elevate water temperature, lead to fragmentation of populations, loss of connectivity and in extreme cases, local extinctions. In cases where temperature sensitive rare or endemic species are present and willows are providing clear thermal benefits, it may be best to focus willow removal efforts elsewhere. Although there is strong evidence for a number of negative impacts of willows to aquatic ecosystems (Table S1), such impacts may be preferable to potential multiple species extinctions. We do not propose that willows should replace endemic plants during riparian restoration activities, but as climate warms, reaches that are already densely shaded by willows may become increasingly important refugia for a broad range of native fauna.

4.2. Can willows be removed from the upstream extent of the catchment?

Most invasive willows can reproduce vegetatively; some species such as *Salix fragilis* have evolved in northern hemisphere as disturbance specialists in braided river systems (Meikle, 1984), and any branch or limb that is broken off and carried downstream during a flood can take root and form a new tree. As such, there is little point removing trees from downstream reaches if it is not possible to first remove them from the top of the catchment, since eventually they will recolonise in the absence of on–going control. Capacity to remove willows in a top–to–bottom format can be constrained by site access and approval from adjacent land owners, and the efficacy of an entire willow removal program can be eroded if a single tree remains in the upper catchment. Catchments with a high certainty of longitudinal continuity of willow removal may offer greater environmental rewards than streams where only sporadic willow removal is possible.

4.3. What is the likely endpoint for the willow removed site?

Adjacent land–use strongly influences our capacity to return compromised riparian habitats to a hypothesised pre–modernised state (e.g. reduced floodplain–channel connectivity, altered hydrological regimes). Invasive willows have primarily infested waterways that are bounded by areas agricultural land–use, and in many cases, only a very narrow and restricted riparian zone may be achieved during restoration efforts. Such streams may also display elevated nutrient profiles from agricultural fertilisers and are often constrained within reinforced river banks to prevent agricultural land being impacted from floods. In this case, a fully functioning pre–Anthropocene endemic riparian zone is unlikely to be truly be achieved, and perhaps a sensible question to ask is, "What is the anticipated ecological endpoint for the stream and associated riparian zone?" In some circumstances abiotic drivers such as river regulation and reduced water volume in streams caused by climate change may render restoration to a perceived 'natural state' unobtainable, and ultimately, not sustainable in the long–term. There are also some ecosystem services that willows provide that endemics cannot that are preferable to land managers in agricultural areas; 1/they are not fire promoting like many endemic plants and may even offer better protection to steams during fire than endemics 2/they can inhibit colonisation by less desirable weeds via light suppression (e.g. blackberries) and 3/they provide a potential fodder option for stock during drought. Before removing willows from agricultural zones, careful consideration of a realistic endpoint for the riparian zone from an ecosystem services perspective is required.

4.4. Has the horse already bolted?

In some streams willow invasion is well advanced and capacity to remove every last tree is unlikely, constrained by funding and ease of access. In cases where willow invasion extends continuously from upland reaches to estuaries, unless trees are removed from top to bottom, as previously discussed, it makes little sense to remove them sporadically from mid–reaches. Undertaking willow removal at this scale is a complex and difficult process that may require cooperation from multiple governments and multi–year financial commitments. Unless such commitments can be assured, willow removal efforts targeted at catchments with limited existing willow invasion and high ecological values may be more effective and more ecologically constructive.

4.5. How big is your stream?

Although non–native willows are acknowledged for altering a wide array of structural and functional attributes of in–stream ecosystems compared to endemic riparian taxa (e.g. Table S1), the effect size remains context dependent. For example, in a 1st order stream a large pulse of organic matter at one time of year (e.g. deciduous vs evergreen abscission McInerney et al., 2016b) can have a large effect on in-stream organic matter processing and metabolic activity. By comparison, large pulses of allocthonous inputs are likely to affect biotic communities less in a larger 4th order stream, simply due to stream volume and spatial scale. Thus, the detrimental effects of willow infestation in large streams may be less pronounced and removal activities may provide greater ecological benefits in heavily infested small streams.

4.6. Not all non–native willows are created equal – know your target

Willows growing in–stream use more water via transpiration than their bank–dwelling counterparts or than endemic riparian trees (Doody et al., 2011). In small streams where reduced water volume under changing climate may lead to thermal extremes, substantial water savings could be found with removal of in–stream willows (Doody et al., 2014a). Maximising water savings will be especially important as changing climate increases competition for water resources between the environment and human consumption. Retaining bank growing willows and removing those growing in–channel can buffer potential impacts of removing all willows entirely, by maintaining stream shading and still achieving water savings, especially when revegetation activities may not occur as initially intended. Other benefits include bank stability, particularly in catchments subjected to high but intermittent flows, improving in–stream flow and opening up the stream channel for recreational activities (e.g. fishing). The main issue with this approach (as discussed) is ongoing vegetative colonisation downstream of the targeted willow removal zone. However, in cases where the primary objective is to increase water volume and maximise shading to promote refugia for thermally sensitive taxa, this may be a preferred tactic, as continued riparian management will be required in any case. This approach may also be particularly useful in situations where 'the horse has already bolted', since it offers targeted ecosystem benefits recognising that willows are an entrenched invasive species.

5. Conclusions

Ultimately, as scientists and mangers, we need to decide what 'state' we are trying to manage our ecosystems to and what ecosystem services are of highest importance. Currently, attempts are made to return ecosystems to a state perceived as 'natural', 'pristine' or 'reference'. In many countries, pre–modern world ecosystems are unlikely to be attainable if climate changes as predicted. It is human nature to plan for life–time scale changes, but since predicted changes to climate will persist for centuries hence, we need to be realistic about what our ecosystems are going to look like in the future and what we desire them to look like, not what they looked like in the past. For highly degraded catchments with severely compromised endemic riparian ecosystems, there may be more value in promoting them as a 'thermal refuge catchments' where priorities are centred around buffering temperature extremes that are expected (e.g. greater extremes and more days above historical average temperatures). Here, we present a simple decision matrix (Fig. 2) that may also be applied to other invasive species to aid prioritisation of removal efforts, balanced with potential ecosystem services provided by the invader. Willows have the capacity to form an important tool in such planning, and we should not discount their ability to adapt. We also acknowledge the importance of protecting ecosystems with strong endemic values, but we think efforts in this regard should be focussed on catchments that have retained many of their endemic characteristics, and with them, more resilience.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank an anonymous referee for their insightful comments that improved the manuscript. Data presented in this article were supported by the North East Catchment Management Authority, Wodonga, Victoria, Australia.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.112871.

Author statement

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