

Riverbanks as Battlegrounds: Why Does the Abundance of Native and Invasive Plants Vary?

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ABSTRACT

The abundance of invasive alien plants (IAPs) can vary dramatically over small spatial scales for reasons that are often unclear. Understanding these could offer key insights for containing invasions, accepting that eradication is often no longer feasible. This study investigated determinants of IAP cover on riverbanks, a well-known hotspot of invasion, using *Impatiens glandulifera*, a prolific invader across the Northern Hemisphere, as a model species. Within this framework, we included the potential for dominant native vegetation cover, mediated by favourable environmental conditions, to resist invasion by *I. glandulifera* through negative association. Our analyses, using structural equation modelling, showed that *I. glandulifera* is more sensitive to environmental conditions than dominant native vegetation. High soil moisture was a key determinant of *I. glandulifera* cover, having negative effects across the riparian zone. Spatially,

I. glandulifera and dominant native vegetation responded differently to environmental conditions. Sites with steeper banks had less dominant native vegetation at the water's edge, potentially favouring *I. glandulifera* cover through reduced competition. In general, greater abundance of dominant native vegetation presented a more invasion-resistant community. Maintaining dominant native vegetation at high abundance is thus key to preventing large monospecific *I. glandulifera* stands from forming. Our findings highlight the opportunities to indirectly limit plant invasions in general via targeted environmental management and restoration, as well as understanding future risks from long-term environmental change.

Key words: competition; community dynamics; environmental effects; flow regime; Himalayan balsam; invasive species; plants; river restoration.

HIGHLIGHTS

- Invasive plant growth is controlled by the local environment more so than natives.
- Within riparian zones, wetter soil conditions reduce invasive plant abundance.
- Native dominant plant abundance increases resistance to invasion.

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Author Contributions ZP, NW and MVM developed the research question and designed the experiment, ZP and NW collected the data, ZP analysed the data, and ZP led the writing with the assistance of NW and MVM.

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INTRODUCTION

Invasive alien species represent a major threat to biodiversity that is exacerbated by increasing global travel and trade (Vilà and others 2011), hybridization (Vallejo-Marín and Hiscock 2016) and climate change (Bellard and others 2013). Riparian habitats are among those most prone to invasion by invasive alien plants (IAPs) (Strayer 2010) due to their transitional nature, connectedness and history of fluvial and human disturbance (Tockner and Stanford 2002). Success of an IAP depends on a combination of propagule availability, local environmental conditions and interactions between the IAP and recipient plant community (Catford and others 2014). Knowing the relative importance of abiotic factors and competition is therefore crucial in assessing invasion risk and efficiently managing invasions within riparian habitats.

Experimental studies confirm that native plants and IAPs often perform differently under a given change or difference in some abiotic variable, for example, increased salinity (Borgnis and Boyer 2016) or increased nutrients (Dassonville and others 2008), under controlled conditions. However, Daehler (2003) found that studies comparing growth of a native plant and IAP under one altered condition disproportionately favoured IAP performance, while natives performed better when multiple environmental conditions were evaluated simultaneously. This suggests that in situ studies under naturally varying environmental conditions are needed to better understand the relative performance of native plants and IAPs (Daehler 2003; Kuebbing and Nunez 2015), although disentangling cause and effect can be difficult in a multifaceted system (Catford 2016).

In riparian zones, floods scour or deposit sediment and associated nutrients, creating gaps in established vegetation (Richardson and others 2007), which can promote colonization by IAPs. Riverbanks represent a gradient of fluvial disturbance that diminishes with bank elevation. Areas closest to the water's edge can experience frequent and prolonged inundation, potentially affecting plant germination and establishment, whereas droughts may cause prolonged low flows, favouring terrestrial species (Stokes and others 2010). At the top of the bank, where conditions are more stable, dominant native plants or IAPs often form large monodominant stands and interspecific-competition replaces hydrogeomorphic factors as the main influence on vegetation. Upper elevations are also likely to be influenced by adjacent land

use, particularly in urban and agricultural settings (Greet and others 2013). Environmental influences and competitive interactions between dominant native and IAPs are therefore expected to vary spatially across the riparian zone. Pyšek and others (2012) showed that at high abundance IAPs have the potential to negatively affect native plant communities. Therefore, identifying the environmental conditions that most affect IAP abundance and, conversely, those which benefit native plants is a priority for those attempting to manage or restore riparian habitats. Understanding the drivers of invasion will also improve our understanding of how both native and alien plants will respond to future environmental changes (Kuebbing and Nunez 2015).

Strategies for managing IAPs to reduce their impact on native communities within riparian zones involve prevention (for example, awareness campaigns and enforcing legislation to prohibit entry or spread), eradication (generally not feasible within riparian zones due to connectivity of watercourses) (Hulme 2012) and control (Culliney 2005). Controlling IAPs using mechanical and chemical methods can be expensive and may not be viable due to the requirement for repeated treatment (Clewley and others 2012). The most effective method for controlling IAPs thus far is herbicide spraying (Kettenring and Adams 2011), but native plants can be impacted disproportionately and there are collateral risks to water quality and aquatic biota from herbicide run-off (Rasmussen and others 2015). Classical biological control offers a less damaging alternative for riparian zones (Pratt and others 2013), but the lag phase before IAP abundance is reduced may be considerable, such as *Aphalara itadori* psyllid released to control *F. japonica* (Shaw and others 2011). Targeted manipulation of abiotic conditions could also potentially equip practitioners with a further tool for managing IAP populations (Nilsson and others 1997), as riparian vegetation is sensitive to hydrologic alteration, particularly to changes in minimum and maximum flows (Naiman and Decamps 1997).

The aim of this study was to determine the relative importance of biotic and abiotic drivers of *I. glandulifera* abundance across the riparian zone and identify whether environmental conditions affect dominant native and IAPs differently. Specifically we ask (1) what are the environmental drivers of local (100 m reaches) scale variation in the abundance of *I. glandulifera* and dominant native plants; (2) does greater abundance of dominant native plants, mediated through specific environmental conditions, confer resistance to *I. glandulifera*.

era invasion (that is, cover of *I. glandulifera* is less when dominant native plant cover is high); and (3) do these patterns vary spatially within the riparian zone (that is, from top of the bank to the water's edge)? We hypothesized that along rivers which have greater cover of dominant native plant species, mediated through favourable environmental conditions (Inderjit and others 2017), *I. glandulifera* would be less abundant (conferring a resistance to *I. glandulifera* via reduced opportunity for recruitment) closest to the water's edge. However, less fluvially disturbed areas at the top of the riparian zone (Bottollier-Curtet and others 2013) could favour IAP cover, increasing competitive interactions between dominant native and IAPs.

MATERIALS AND METHODS

Collection of Vegetation Data

Vegetation surveys were conducted over 2 weeks in August 2014 (summer), along 20 lowland rivers in central Scotland, UK (ESM Figure S1). Rivers ranged between 10 and 75 m in channel width and 5–40 m in elevation. *Impatiens glandulifera* commonly forms near-continuous monocultures along such rivers in the UK (Seager and others 2012; Pattison and others 2017), and initial site searches confirmed its widespread extent relative to other IAPs. Invaded sites were selected that varied in their level of invasion by *I. glandulifera* (as quantified by % cover) and were close to the most downstream accessible point on each river. Other IAPs recorded at study sites included *Fallopia japonica*, *F. sachalinensis*, *Heracleum mantegazzianum*, *Claytonia sibirica* and *Mimulus guttatus*, but these species combined accounted for less than 10% of total IAP cover. To compare the response of dominant native plant species and *I. glandulifera* to common environmental variables, uninvaded sites were also surveyed on each river, when available ($n = 9$). All sites varied in the extent of dominant native plant cover, determined by summing the individual % cover of such species at a site. Native dominant plant species were defined a priori from expert judgement, as being species with mainly or wholly competitor growth strategies (sensu Grime 1974) that also commonly form monodominant stands alongside rivers in Britain. These species comprised *Aegopodium podagraria*, *Epilobium hirsutum*, *Filipendula ulmaria*, *Glyceria maxima*, *Petasites hybridus*, *Phalaris arundinacea*, *Phragmites australis*, *Rubus fruticosus*, *Symphytum officinale* and *Urtica dioica*, all of which are deep rooted perennials. On average, two dominant native plant species oc-

curred per site, their identity varying with bank elevation (for example, *P. arundinacea* dominated closest to the water's edge typically being replaced by *U. dioica* at the top of the bank).

Surveys began at a randomly selected point along a 100 m reach (see ESM Figure S2 for survey design). At the start of each surveyed reach, a transect was established perpendicular to the channel and three plots, each of 1 m², were positioned equidistantly between the water's edge (lower), mid-bank height (mid) and the bank top (upper). A new transect was established every 10 m, with seven transects per site. A total of 21 plots were sampled at each site, with a combined total of 609 plots sampled across all rivers. In each plot, all species were identified and abundance was quantified using a five-point scale (1 = < 2%, 2 = 3–10%, 3 = 11–25%, 4 = 26–50%, 5 = > 51%) adopted by Joint Nature Conservation Committee (JNCC) for river vegetation surveys. Abundance scores were subsequently converted to mid-point percentage cover for analysis purposes (1 = 1%, 2 = 6%, 3 = 18%, 4 = 38% and 5 = 75%).

Collection of Environmental Data

Soil moisture was measured using a hand-held meter (SM150, Delta-T Devices Ltd, Cambridge, UK) at three points within each plot and then averaged to obtain a mean percentage soil moisture per plot. Seven soil cores (depth 5 cm) were taken across each site, combined and used to estimate soil organic matter content by the loss on ignition method (Wang and others 2011). Proximity to the nearest tree (> 5 m high) was used as an estimate of plot scale shading. Riverbank slope was estimated using a clinometer at each transect across all sites. Daily mean flow data from the Centre for Ecology and Hydrology's National River Flow Archive, for the most downstream gauging station on each surveyed river, was used to assess possible fluvial effects on riparian vegetation. Using data from 1990 to 2014, the percentage increase in mean flow over the last 24 years was calculated to characterize the general long-term trend in flow on each of the 20 rivers. The rivers studied showed a gradient of increase in mean annual flow since 1990, ranging from 4 to 28% (ESM Table S1). Water chemistry data were obtained from the Scottish Environment Protection Agency for the closest routine chemical monitoring site on each river for the period 2009–2014. Mean values from this period were calculated from bimonthly sample data for soluble reactive phosphorus as P (mg/L) and suspended solids (ss) (mg/L), as indicators of

catchment pressure from nutrient and fine sediment loading.

Statistical Analyses

The analysis sought to differentiate responses of dominant native plants and *I. glandulifera* to environmental variables and to assess whether greater abundance of dominant native plants, mediated through abiotic conditions, would have a negative impact on *I. glandulifera* cover. We also tested whether the hypothesized effect varied at different bank elevations across the riparian zone. We used piecewise structural equation models (confirmatory path analysis; Shipley 2009; Lefcheck 2016) to test direct (for example, dominant native plant cover influences *I. glandulifera* cover) and indirect (for example, soil moisture influences dominant native plant cover, which influences *I. glandulifera* cover) relationships. Structural equation models (SEMs) are a multivariate technique useful for testing a priori defined models and quantifying the relative importance of explanatory variables. A conceptual model (meta-model) detailing potential cause–effect relationships based on biological relevance in the literature or logical arguments was constructed to guide the modelling process (Figure 1).

To construct the structural equation models (SEMs), linear mixed effect models (LMMs) with a Gaussian error structure were used. River and transect were included as random intercepts to account for pseudoreplication. However, transect did not explain any variation and was therefore excluded from the model to adhere to rules of parsimony. Before fitting SEMs, constituent models were examined for normality and transformed when necessary. Multicollinearity among predictor variables within constituent LMMs was checked, none of which were highly correlated (> 0.60). All predictors were mean-centred and scaled by 1 SD prior to statistical analyses to enable direct comparison of effect sizes between predictors. This SEM was constructed and run separately for data collected at the water's edge, at the top of the riverbank and from a position intermediate to these locations.

During model validation, missing paths were evaluated and added if they were considered causal, or otherwise allowed to freely covary. Upon model validation, two significant missing paths were identified and added to the SEM: (1) the direct effect of bank slope on dominant native plant abundance and (2) the direct effect of LOI on *I. glandulifera* cover. Fisher's *C* (Shipley's test of

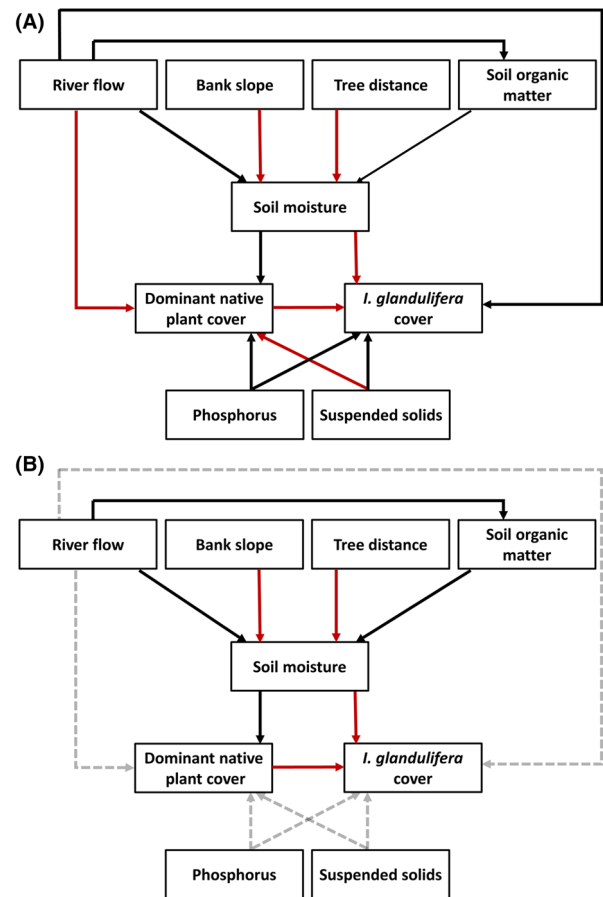


Figure 1. Meta-model used to guide construction of the structural equation models (SEMs). Illustrated are the general hypothesized direct and indirect relationships (ESM Table S3) between response variables (dominant native and invasive plant cover) and environmental variables: % increase in mean annual river flow, distance from sample plot to the nearest tree, riverbank slope, soil moisture and water phosphorus concentration and how this is expected to vary between **A** the water's edge (influenced by in-channel processes) and **B** the top of the riparian zone (influenced by adjacent land and weakly by in-channel processes). Hypothesized causal relationships (based on knowledge of our study sites) are shown by red (negative) and black (positive) arrows. Dashed arrows indicate no expected causal relationship.

directed separation; (Shipley 2009)) was used to evaluate SEM fit, where higher *p* values (> 0.05) indicate that the data support the model. R^2 values (Nakagawa and Schielzeth 2013) are reported for each constituent LMM within a SEM. All statistical analyses were conducted using R 3.2.2 (R Core Team 2017), with the additional R packages vegan (Oksanen and others 2017), nlme (Pinheiro and others 2017) and piecewise SEM (Lefcheck 2016).

RESULTS

The initial model of hypothesized direct and indirect effects of local biotic and abiotic variables on *I. glandulifera* % cover was not significantly different from the observed data for all SEMs: water's edge (Fisher's $C = 9.94$, $p = 0.62$) and top of the riparian bank (Fisher's $C = 10.49$, $p = 0.57$). Details for the mid-bank position SEM can be found in Supplementary Material (ESM Table S2). We hypothesized that both *I. glandulifera* and dominant native plant cover would be differentially affected by environmental conditions; however, in all SEMs *I. glandulifera* was affected more strongly by local environmental conditions than were dominant native plant species.

Water's Edge

Due to greater intensity of fluvial disturbance, we expected a more tightly interactive system closest to the water's edge compared to the top of the riverbank. *Impatiens glandulifera* % cover was negatively affected by greater cover of dominant native plants, as expected (Figure 2A and ESM Table S3). However, besides a negative effect of bank slope on dominant native plant cover, this effect was not mediated through local abiotic conditions. Steeper riverbank slope reduced soil moisture and dominant native plant cover. Greater soil moisture in turn reduced *I. glandulifera* cover, while soil organic matter had the greatest positive effect on cover of *I. glandulifera*.

Top of the Riverbank

We hypothesized that competitive interactions between dominant native plants and *I. glandulifera* would be the main predictor of invasive alien plant cover in the upper part of the riparian zone, because fluvial disturbance is reduced. However, *I. glandulifera* abundance was lower with greater dominant native plant cover and with greater soil moisture (Figure 2B and ESM Table S3). The competitive effect between dominant native plants and *I. glandulifera* was the strongest effect size, with an almost equivalent negative effect of soil moisture on *I. glandulifera* cover. Other abiotic drivers of *I. glandulifera* cover were not significant at the level of $p < 0.05$, although a marginal negative effect of bank slope ($p = 0.06$) was seen for dominant native plant cover.

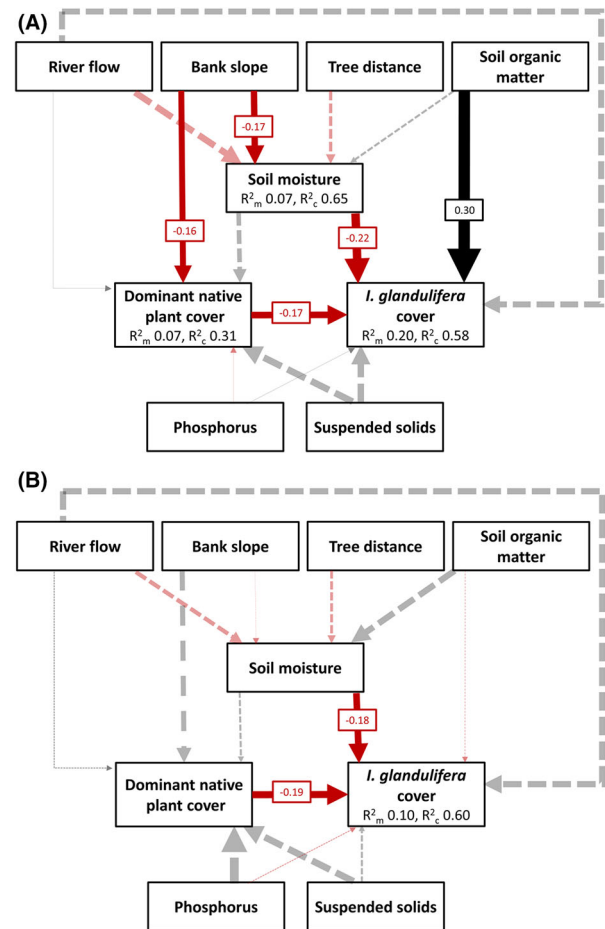


Figure 2. Structural equation model (SEM) path diagrams for biotic and abiotic effects on cover of the invasive plant, *Impatiens glandulifera*, at **A** the water's edge (influenced by in-channel processes) and **B** the top of the riparian zone (influenced by adjacent land and weakly by in-channel processes). Arrows and number on arrows are the standardized effect sizes for significant variables. Black arrows denote positive relationships and red arrows negatives ones. Arrows for non-significant paths ($p > 0.05$) are semi-transparent and dashed. The thickness of the significant paths is scaled relative to the magnitude of the standardized regression coefficient. Both the marginal R^2 (R^2_m) explaining the fixed effect component and the conditional R^2 (R^2_c) explaining both the fixed and random effects are shown for each response variable.

DISCUSSION

Assessing abiotic and biotic interactions in situ can reveal direct and indirect effects of the local environment and resolve how these drive vegetation composition in riparian zones. Our analyses reveal that local conditions are important determinants of *I. glandulifera* cover, but have less influence on dominant native plants, which are perhaps better

adapted to local conditions (Turner and others 2015), or more generalist in their requirements. The environment and the recipient community together determine the success of invasion by IAPs (Catford and Jansson 2014). *Impatiens glandulifera* was less abundant at sites that had a greater cover of dominant native plants, implying a more invasion-resistant community. These findings have implications for understanding vegetation dynamics and managing invasions in riparian habitats. Although invasion by invasive alien plants has the potential to alter the vegetation of riparian zones (Richardson and others 2007), the magnitude of any effect is likely to be moderated by local environmental conditions that, directly or indirectly, reduce the abundance of IAPs or facilitate IAPs indirectly through negative effects on the dominant plant component of the native vegetation.

Abiotic Influences on *Impatiens glandulifera* and Dominant Native Plant Cover

Impatiens glandulifera was negatively affected by greater soil moisture across the riparian zone. Tickner and others (2001) found that *I. glandulifera* seedlings were sensitive to early season flooding both during and after germination. Invasive species colonization, particularly by *I. glandulifera*, tends to be associated with damp conditions (Hejda and Pyšek 2006). However, experimental work suggests that *I. glandulifera* grows more vigorously in drier environments (Tickner and others 2001; Baattrup-Pedersen and others 2013), whereas field investigations by Catford and others (2014) also found that alien plants were more likely to germinate on drier soils and alien stands were larger with less standing water. Contrary to their hypothesis that drier conditions would favour perennial alien species, most alien species in their study were annual. This is consistent with our findings, as *I. glandulifera* is an annual, while its native competitors are predominantly perennial. Our results suggest that dominant native plant species have a competitive advantage where growth of *I. glandulifera* is limited physiologically by soil saturation. Traits such as laterally extensive below-ground biomass in dominant native perennials should reduce their sensitivity to waterlogging and increase nutrient uptake (Grime and others 2014), thereby helping to resist competition from the shallow rooted annual *I. glandulifera* in wetter habitats.

Common dominant native plants of riverbanks, such as *U. dioica*, thrive in drier habitats but are also tolerant of winter inundation, while species such as

P. arundinacea and *G. maxima* commonly tolerate permanent saturation (Grime and others 2014). This suggests that dominant native plant species will be less sensitive to flooding during the growing season, but that drought or dewatering of banks via over-abstraction, channel incision or bank aggradation (Catford and others 2011), will favour *I. glandulifera*. Prolonged periods of drought during the 1990s in the UK were associated with a decline in dominant native plant species cover along rivers (Pattison and others 2017), coinciding with an increase in the incidence of various IAPs.

While our study highlights that high soil moisture appears to restrict *I. glandulifera* growth, some physical characteristics of the riparian zone could also promote its abundance. Soils on steeper banks hold less moisture and support lower dominant native plant cover closest to the channel, potentially offering ideal growing conditions for *I. glandulifera* (Catford and others 2014). Steeper banks may also be associated with reduced deposition of seeds or their germination success at higher bank elevations due to scouring, rapid recession of water and reduced fine sediment deposition (Goodson and others 2003; Corenblit and others 2007), leading to less competition with native plant species. Greater soil organic matter closest to the water's edge had a positive effect on the cover of *I. glandulifera* which was unexpected in light of the negative association between *I. glandulifera* and soil moisture and given the normal positive association between soil moisture and organic matter content. This effect was not seen at the top of the bank. However, flood-borne sediment, which may be enriched with organic matter, is most likely to be deposited closer to the channel (Gurnell and others 2008). This pattern may arise coincidentally in low-energy environments if sediment deposited by floods is enriched with both organic matter and propagules of IAPs, or if soil organic matter content is a proxy for levels of retention of locally produced seed. Higher soil organic matter content may also provide a superior seed bed for germination (Richardson and others 2007).

Competition Between Dominant Native Plants and *Impatiens glandulifera*

Within our modelling framework, we hypothesized that dominant native plants and IAPs share biological traits which make them similarly competitive, particularly among wetland species (Houlahan and Findlay 2004). Native dominant plant species might therefore resist invasion where abundant, unless disturbed. The establishment of large mon-

dominant stands of *I. glandulifera* would be even more difficult under adverse abiotic conditions which favour the proliferation of dominant native plants. Our study showed that where dominant native plant cover was high, *I. glandulifera* abundance was significantly reduced across the riverbank. Dense stands of dominant natives such as *P. arundinacea* (closer to the water's edge) or *U. dioica* (top of the riverbank) may hamper opportunities for germination and establishment by *I. glandulifera*, due to fewer gaps for recruitment and strong competition between seedlings and established plants. However, IAPs are opportunistic passengers of disturbance (MacDougall and Turkington 2005; Van Kleunen and others 2010) and may benefit from disturbance events, such as deposition of flood-borne sediment (Steiger and others 2003), that reduce competition with native plants by creating gaps, and increase soil fertility (Richardson and others 2007). Within highly disturbed environments, native plant species poorly adapted to changeable abiotic conditions (whether natural or anthropogenic) may be filtered out, thereby promoting competitive, fast-growing annual IAPs such as *I. glandulifera* (Nobis and others 2018).

The differentiation in growing conditions of dominant native plants and *I. glandulifera* within a small geographical area suggests that some habitats and/or the flora they support are potentially 'invasion-resistant'. This may undermine the widely practiced use of uninvaded plots as a proxy for the pre-invasion state (Sax and others 2005; Thomaz and others 2012) since uninvaded plots located in a region where invasion is widespread might, in fact, be permanently resistant to invasion due to differences in local conditions, rather than simply 'pending invasion'. Because uninvaded or sparsely invaded patches often occur in close proximity to sites that have been invaded for a decade or longer, it would appear that their vegetation is either intrinsically resistant to invasion (for example, high stem densities of grasses might limit recruitment opportunities for annual IAPs) or associated with growing conditions that are less conducive to the growth of IAPs (for example, frequent inundation). Resolving the biotic or abiotic properties that confer invasion resistance would significantly enhance our ability to manage invasions.

Implications for Management

River restoration recognizes the importance of naturalizing flow regimes to assist fluvial geomorphological processes (Holmes and others 2005). The results of the present and other recent studies (Vi-

vian and others 2014) suggest there could also be indirect benefits in terms of controlling invasions. For example, maintaining high spring water levels (for example, via existing flow regulation infrastructure or by restricting water abstraction) could be advantageous in rivers with invaded riparian zones because raised soil moisture negatively affects *I. glandulifera*. This might be especially effective in spring when seeds of *I. glandulifera* are germinating (Tickner and others 2001). Spring targeted management of *I. glandulifera* will also reduce the potential for monocultures to form in summer and may lower the competitive ability or onset of growth of seedlings of annual IAPs such as *I. glandulifera*, compared to flood-tolerant dominant native plant species (Bottollier-Curtet and others 2013). On the other hand, such efforts might be setback in the future by climate-related increases in spring and summer droughts or increased pressure on water resources (Diez and others 2012), thus shifting flow regimes in favour of IAPs.

Reduced engineering of riverbanks particularly in downstream areas could also increase lateral flow, maintaining higher levels of moisture in the riparian zone (Merritt and others 2010; González and others 2015). Riverbank re-profiling to reduce steepness will similarly help to reduce dewatering of banks, as will restoration projects designed to reverse over-deepening of channels. Maintaining the overall integrity of riparian zones is also likely to provide an effective buffer to intercept transfer of fine sediment from adjacent arable land during high rainfall periods (Gurnell and others 2012). Large drapes of fine sediment deposited on riverbanks can contain high densities of IAP propagules (Steiger and others 2003) and are often a focus for IAP establishment (Z. Pattison and N. Willby, unpublished observations). Previous studies have suggested that the cover of *I. glandulifera* needs to be high (> 70%) to have measurable impacts on native communities (Pyšek and others 2012). Containing *I. glandulifera* at lower cover in riparian zones is therefore crucial to avoid a significant loss of species (Hejda and Pyšek 2006; Hulme and Bremner 2006). Manipulation of environmental conditions may be one option to achieve this.

CONCLUSIONS

The invasive alien plant, *I. glandulifera*, and its dominant native plant competitors respond differently to environmental conditions that vary spatially across riverbanks. Invasion by *I. glandulifera* poses an additional pressure on an already dynamic and often degraded habitat, and the sensitivity of

this species to soil moisture is therefore particularly instructive for land management and river restoration. Attempting to eradicate IAPs, such as *I. glandulifera*, from interconnected lowland watercourses is futile. However, improved assessment of invasion risk, combined with management designed to promote environmental conditions that favour native vegetation, could reduce the scale of invasions and hence their impacts on native species.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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