Effects of invasive alien plants on riparian vegetation and their response to environmental factors.

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Statement of Originality

I hereby confirm that this PhD thesis is an original piece of work conducted independently by the undersigned and all work contained herein has not been submitted for any other degree.

All research material has been duly acknowledged and cited.

Signature of candidate:

Zarah Pattison

Date:

"…*these plants are common, conspicuous, pestiferous, beautiful, edible, and otherwise useful or harmful*."

Clive A. Stace and Michael Crawley, *Alien Plants* (2015).

Invasion front © Nigel Willby

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General abstract

Biological invasions are reportedly one of the major contributory factors to biodiversity loss worldwide. The impacts of invasive alien plant (IAP) species on native communities are widely documented in the scientific literature, however, there is still a lack of detailed information on their impacts within the most vulnerable habitats. Riparian habitats are highly dynamic systems and naturally disturbed, making them particularly vulnerable to invasion. Climate change, directly or indirectly, is also predicted to adversely impact river systems, which may subsequently alter invasion rates and the impacts of IAPs. However, the interactions between climate and IAPs and their combined effects on vegetation have rarely been examined. To address these knowledge gaps, this thesis investigates: (1) the role of environmental variables, such as sediment loading or climate-related changes to river flow regime, on the abundance of IAPs within riparian zones; (2) how variation in IAP abundance impacts native vegetation, relative to the effects of native dominant plant species and (3) some of the mechanisms underlying the effects of IAPs in riparian habitats.

Historic and recent field survey data were used to investigate changes in riparian vegetation on British rivers during the last 20 years. Analyses indicate that IAPs had a negative but small effect on native plant diversity. Overall, changes in land use and differences in flow regime between recording periods were the most important predictors of plant community change. Specifically, IAPs had a greater probability of being present along lowland rivers that experienced increased frequency of high flow events. On a local scale across rivers in Scotland, the abundance of IAPs was constrained by greater soil moisture in summer, whilst greater abundance was associated with tree-lined banks. Both native dominant species and IAPs negatively affected subordinate species abundance to a greater extent than species richness, although this effect varied spatially with bank elevation.

Artificial turf mats were used to quantify viable propagules within riverine sediment deposited over-winter along invaded riverbanks. The data indicate that there is a legacy effect of IAP abundance, with the most invaded sites being associated with higher sediment loading the following year, though, contrary to the general pattern,

sediment associated propagules were scarcer at invaded sites. Moreover, lower above-ground native diversity was associated with sites which had been previously invaded. Plant species composition in the propagule bank and above-ground vegetation were highly dissimilar, particularly closest to the water's edge at highly invaded sites. This suggests that mono-specific stands of IAPs proliferate best under *less* disturbed environmental conditions, although fluvial disturbance events may be required to create opportunities for initial establishment. The propagule bank contributed very little to the above-ground vegetation, nor did it limit invasion, suggesting that above-ground plant composition is largely dictated by competitive interactions.

The findings presented in this thesis suggest that invasion by IAPs is an additional stressor for native vegetation within riparian habitats, modifying above-ground plant communities via competition and suppressing recruitment from the propagule bank. However, native dominant species common in riparian habitats also negatively impact, subordinate species via competition, in some cases equalling the effect of IAPs. Native dominant and IAP species are differently affected by environmental factors operating in the riparian zone, which may provide future opportunities for reducing and managing invasions.

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Chapter 1: General introduction

1. Overview

The following brief review presents some of the key research questions in the field of invasive plant ecology within riparian habitats. The first section of this chapter discusses general issues of invasion and the impact invasive alien plants may have on native, riparian plant communities. Thereafter, the potential mechanisms via which invasive alien plants have become successful invaders within riparian systems are discussed. Subsequently some of the various aspects of riparian habitats which could potentially promote or limit the success of invasive alien plants, such as changes to flow regime and increased sediment deposition, are presented. Finally, some of the key remaining research questions within the scientific literature and how this thesis aims to address these are highlighted.

2. Nomenclature

An alien species is an organism that has been introduced either directly or indirectly, via human transportation, to an area outside of its native range that it could not have reached on its own (Richardson *et al.* 2000). The term ‘invasive’ focuses on the impact, generally negative, of a species (Ricciardi & Cohen 2007). With no universally accepted definition of an invasive alien species, the terminology applied to biological invasions tends to be complex and often confusing (Richardson & Pyšek 2012). The Convention on Biological Diversity (CBD) defines the term ‘invasive alien species’ (IAS) as introduced species that threaten biological diversity (Brunel *et al.*2012). Invasive species can also be defined as alien species that sustain self-replacing populations at a greater distance from the initial site of introduction (Richardson & Pyšek 2012). Following the terminology of Richardson *et al*. (2000):

Alien plants - those that are present in an area as the result of human-mediated transport. The term ‘alien’ is interchangeable with ‘non-native’ or ‘introduced species’.

Naturalised plants - alien plants which sustain populations, year on year, without the influence of humans.

Invasive plants - a subset of naturalized plants that produce reproductive offspring, often in large numbers, at considerable distances from parent plants, and thus have the potential to spread over a large area.

Introduced range - an area where a species has spread with the assistance of humans, from where it would otherwise have been restricted due to geographical barriers.

Native range – a region where a species naturally occurs without direct or indirect human intervention.

Throughout this thesis I use the term invasive alien plant (IAP) to describe species that are not naturally occurring and are spreading in population size at an expansive rate. However, the term invasive does not automatically denote a negative impact on native species (Ricciardi & Cohen 2007). Native species may also be considered invasive, (for example *Urtica dioica,* forms dominant stands in many habitats throughout Britain (Taylor 2009), without automatic assumption of negative ecological impacts on other plant species. Other definitions used throughout this thesis include:

Dominant native – a plant species with mainly or wholly competitor growth strategies (sensu Grime 1974) that also commonly form mono-dominant stands alongside rivers in Britain.

Subordinate native – a plant species with a wholly or partly ruderal or stress tolerator growth strategy (sensu Grime 1974), which often occur at low abundance and tend to be outcompeted by native dominant species.

Propagule – encompasses both seed and vegetative fragments, unless stated otherwise.

3. Invasive alien species

Human-aided dispersal via global travel and trade has enabled animals and, particularly plants, to colonise new habitats over great distances (Vitousek 1990), with well-known cases including *Impatiens glandulifera* (Himalayan balsam) and *Fallopia japonica* (Japanese knotweed) having been transported from Asia to Europe (Beerling & Perrins 1993; Beerling, Bailey & Conolly 1994). This form of long distance dispersal has changed the pattern of species distribution globally (Niggemann *et al.* 2009) and is sometimes viewed as a distinguishing characteristic of the so-called Anthropocene. There is still much uncertainty as to which species will present a problem once naturalised, therefore IAS represent a growing threat to biodiversity on a global scale (Brunel *et al.*, 2012). Many studies have focused on the mechanisms that underlie invasion success and substantial progress has been made in understanding the drivers of invasion (Hejda *et al.* 2009), such as propagule pressure (Lockwood, Cassey & Blackburn 2005) and a greater tolerance to disturbance (Richardson *et al.* 2007). IAS tend to be defined in terms of negative impact on native biodiversity which is often difficult to quantify and qualify, particularly at a habitat or regional scale, and individual case studies may not be amenable to generalisation (Maskell *et al.* 2006). However, of the many species transported to new environments, only a small portion of these spread and become invasive (Williamson & Fitter 1996) yet this small subset can have major impacts on the economic and environmental well-being of a country (Hulme 2003).

3.1 Invasive alien plants

Invasive alien plant (IAP) species are a well-represented group within the invasion ecology literature. IAPs are often characterized as having rapid growth rates, enabling them to outgrow, over-shadow, or quickly crowd out native plants (Daehler 2003). Reported ecological impacts include loss of native biodiversity and changes in ecosystem processes, such as nutrient cycling (Brunel *et al.* 2012). IAPs also pose a major threat to both agricultural and natural ecosystems, as they compete with crops and natural vegetation, potentially reducing food quality and quantity (Westbrooks 1998). Woody invasive species have been best documented and are known to alter soil nutrient levels and fire regimes, as well as affecting water quality and availability (Hejda, Pyšek & Jarošík 2009). An important example of this is the extensive invasion of *Tamarix* spp. in North American riparian systems, which has led to reduced groundwater levels due to the high intake of water by this species in comparison to native vegetation and consequently reduced flows (Di Tomaso 1998). Tamarix spp. has also dramatically altered the geomorphology and composition of species in riparian zones (Stomberg *et al.* 2007). Changes to ecosystems due to invasion by IAPs can range from severe to negligible. For example, invasion by *Acacia saligna* in the South African fynbos increases rates of N cycling to the extent that even once this species is removed, N levels in the soil remain high enough to allow invasion by weedy grasses, such as *Ehrharta calycina* (Yelenik, Stock & Richardson 2004). Alternatively, Meffin et al. (2010) found that *Hieracium lepidulum* co-existed within montane communities, with no discernible impact on native species over a six year period post colonisation. The detrimental impacts of IAPs are predicted to increase as the global plant trade increases, the global climate changes and land uses adjust to both changing climate and growing food demands (Byers *et al.* 2002).

3.2 IAP impact on native flora

A major concern is the impact of IAPs on native flora, which can be displaced due to the potential dominance IAPs attain. Large-scale invasions can lead to the dominance of monospecific stands, through rapid growth and large seed production, which can suppress the growth of native species (Beerling & Perrins 1993). By reducing species richness and abundance of native biota and decreasing local species diversity, IAPs reduce the distinctiveness of biological communities at various spatial scales (Pyšek *et al.* 2012). However, the extent to which IAPs affect native plant communities has long been an issue of debate among both policy makers and the scientific community. A key example is the variation in impact of *Impatiens glandulifera* on native vegetation. Hulme and Bremner (2005) found that invasion by *I. glandulifera* reduced native species diversity along the River Wear, England. In comparison, Hejda and Pyšek (2006) found negligible effects of *I. glandulifera* on native diversity along six rivers in the Czech Republic. Whilst the British study recorded *I. glandulifera* cover varying from 80% to 100% (Hulme & Bremner 2005), *I. glandulifera* only reached on average 43% in the Czech sites, although results from the second year were obtained where the average cover of *I. glandulifera* in sampled plots was as high as 74%. Pyšek et al. (2012) attempted to quantify the impact of IAPs on native communities using an extensive database from the scientific literature. They found that IAPs reduced species richness and altered native plant communities, a finding concurrent with previous studies that addressed mostly impacts on resident species richness and diversity. However, the majority of their data came from temperate grassland and woodlands of North America and Europe, with the authors suggesting that significant impacts were context dependent and a greater knowledge base is needed to refine general statements relating to impact. Similarly, Hejda *et al.* (2009) assessed the impact of a variety of notorious IAPs, including *I. glandulifera*, *F. japonica* and *H. mantegazzianum*, and found impacts on native species richness to also be species-specific.

Impact can also be scale-specific (geographic and temporal), with studies conducted at small scales (<100 m) or over long periods (>5 years) generally revealing stronger impacts of invasion than those undertaken at large spatial scales and over short periods (Gaertner *et al.* 2009; Powell, Chase & Knight 2011). While there is a wealth of scientific studies reporting negative impacts of IAPs, a recent analysis by Thomas and Palmer (2015) found no impact of IAPs on native vegetation, adding support to Gurevitch & Padilla (2004) who suggested that, regardless of studies designed to assess impact on native plant communities, there has yet to be a native species driven to extinction by an IAP. Nevertheless, Hulme (2012) suggests that more studies are needed which focus on the impact of communities in vulnerable habitats.

3.3 Invasive alien v dominant native species

IAPs (and other IAS) are frequently considered superior competitors (MacDougall & Turkington 2005). Competitive ability can be assessed through various indicators, such as standing biomass, height, leaf area or reproductive output (Gioria & Osborne 2014). Indicators of strong competitive ability may enable IAPs to reduce the ability of native species to maintain or increase population size (Manea & Leishman 2011). However, there are relatively few studies that have measured competitive ability of dominant native and invasive alien species in parallel (Manea & Leishman 2011). An IAP that outcompetes co-occurring dominant natives is expected to increase in relative abundance over time, and abundant IAPs are expected to have significant impacts on co-occurring subordinate native species (Daehler 2003), over and above those of dominant native species. This has important consequences for conservation. Daehler (2003) showed that overall, dominant native plants were equivalent competitors to IAPs, however, this relationship varied with environmental conditions. For example, decreased water availability increased the competitive performance of the native *Glyceria australis*, relative to the alien *Juncus articulatus* during periods of low inundation in a shallow Australian wetland (Smith & Brock 1996). Conversely, Manea and Leishman (2011) found an increase in IAP performance, based on 14 native and invasive alien plant species-pairs, compared to dominant natives under experimentally elevated CO_2 concentrations. However, disturbance events tend to favour IAP colonisation and potential persistence, especially in freshwater systems (Richardson *et al.* 2007). Fluctuating environmental conditions, such as changes in river flood frequency, have been shown to increase competitive ability of species such as *Tamarix* along the Gila River and Lower Colorado drainage basins of Arizona, USA, compared to the dominant native tree species *Populus fremontii* and *Salix gooddingii* (Stromberg *et al.* 2007). Again, evidence shows that superior competitive ability is context- and species-dependent, and prevailing environmental conditions serve to regulate the competitive relationship between dominant native and invasive alien species. Although the significance of impacts was context-dependent, few studies have included environmental variables such as site characteristics to make predictions (Daehler 2003). However, most of these studies are experimental or lab based, which can be non-reflective of dynamic field conditions. Field based observations are needed to test these experimental findings in order to better advise future research, as well as management decisions.

4. Riparian habitats

Riparian habitats are particularly vulnerable to invasion by IAPs as they are naturally dynamic and frequently disturbed. Riparian zones form the interface between aquatic and terrestrial ecosystems, often supporting a unique plant community, which can differ from adjacent habitats (Richardson *et al.* 2007). Riparian vegetation is important in ecosystem functioning and plays a role in the stabilisation of river banks, nutrient uptake and sediment movement, shading and temperature modification, as well as providing a corridor for dispersal of biota (Richardson *et al.* 2007). Riparian vegetation also contains disproportionately high species richness (Stokes, Ward & Colloff 2010). This may be due to regular disturbance events, such as flooding, which can create newly disturbed habitat for colonisation, as well as heterogeneous microhabitats that can support a larger diversity of species (Hood & Naiman 2000), plus ease of dispersal. Riparian habitats are also heavily impacted by agriculture, urban development and recreational activities, representing a unique blend of stressors on this ecosystem (Capon *et al.* 2013).

4.1 Influence of flow regime on riparian vegetation

Human mediated activity is increasing pressure on riparian zones (Tickner *et al.* 2001), with anthropogenic disturbance facilitating invasion and natural disturbance creating opportunities for spread of invasive propagules (Stokes *et al.* 2010). Hydrochory (seed dispersal by water), as well as propagule transportation, can facilitate invasion, providing an opportunity for competitive and/or ruderal species to establish (Tickner *et al*. 2001). Hydrological and geomorphic processes are key drivers of vegetation communities therefore changes in water levels, and timing of high flow events can affect vegetation dynamics by changing competitive interactions and favouring species with different life history traits (Stromberg *et al*. 2007). For example, using two decades of data from the Vindel River, northern Sweden, Renöfält, Jansson and Nilsson (2005) showed that species richness varied temporally depending on flood disturbance magnitude. Species richness increased in the middle reaches of the Vindel River following a decade of low to moderate flooding. However, following large flood events species richness continued to decrease downstream (Renöfält, Jansson & Nilsson 2005).

While longitudinal connectivity can disperse propagules downstream, variations in lateral connectivity in river floodplains can generate bare substrate, stress established vegetation and alter nutrient supply (Tockner, Malard & Ward 2000). Whilst these conditions may promote the establishment of native species, they also favour establishment of IAPs and may explain the co-occurrence of native and non-native species in riparian systems (Predick & Turner 2008). Riparian plant communities comprise flood-adapted species that may be more resistant to invasion by IAPs, due to their stress tolerance during flooding (Predick & Turner 2008). However, changes in flow regime, for example due to regulation by dams, abstraction, or climate change, can alter historical patterns of flow to which native vegetation are adapted. Therefore, flood tolerant species may lose their competitive advantage over IAPs and changes in flow regime may limit the recruitment of native species (Predick & Turner 2008).

Anthropogenic alterations to flow regime are a common feature on rivers worldwide (Nilsson *et al.* 2005). However, less is known about the effect of climate change on flow regimes and the consequential impact on riparian vegetation, particularly on invasions. Predick and Turner (2008) found that flooding decreased the presence and abundance of two IAPs, *Lonicera* spp. and *Rhamnus* spp., along the Wisconsin River, USA, yet increased the presence and abundance of the dominant native *Zanthoxylum americanum*. *Lonicera* spp. and *Rhamnus* spp. are flood intolerant species, in comparison to *Z. americanum* that is able to reproduce vegetatively, suggesting that the varied response between these species is most likely due to different life history traits. Other studies have shown an increase in IAPs in relation to flow regime. Catford et al. (2011) modelled pre- and post-regulation flows along the River Murray, south-eastern Australia, and found that reduced flood frequency negatively affected weedy native species and increased cover of terrestrial IAPs (including *Hypochaeris radicata* and *Cynodon dactylon*). Other well-known examples include *Tamarix* spp. being favoured by river flow regulation and drought periods along rivers in the USA (Everitt 1998; Beauchamp & Stromberg 2007).

4.2.1 Riparian propagule banks

The highly connected and disturbed nature of riparian zones can promote dispersal of propagules from upstream sources, whilst variation in flow regime (e.g. increased flood frequency) can increase opportunities for dispersal and sediment deposition along river banks (Gurnell *et al.* 2006). Seed banks play an important role in the regeneration and structuring of the vegetation community within riparian zones, harbouring a temporary or permanent store of propagules in the soil or its surface (Gioria & Pyšek 2015), or within channel sediments (Gurnell *et al.* 2008). In general, the soil propagule bank and established plant communities show closer resemblance under more disturbed conditions, such as those encountered within riparian habitats (Abernethy & Willby 1999). Along the Wannon River, Australia, Casanova (2015) found that highest similarity between the seed bank and extant vegetation occurred after exceptional floods had passed along the river. This led to germination of annual species from the seed bank. In contrast, during a drought period diversity of aboveground vegetation declined and consisted mainly of long-lived perennials germinating from vegetative fragments (Casanova 2015). Although we have advanced our understanding of the contribution from riparian propagules to the above-ground riparian vegetation, there is still a lack of knowledge as to how this relationship will change within heavily invaded sites.

4.2.2 IAP impacts on propagule banks

IAPs can add additional pressure, alongside environmental drivers, on propagule bank and aboveground vegetation dynamics. Changes in the seed bank associated with plant invasions include reduced diversity and abundance of native propagules, as well as changes in the propagule bank composition (Gioria & Pyšek 2015). The mechanisms by which IAPs alter the soil propagule bank include the formation of a novel propagule bank which differs in density and persistence, as well as indirectly, by altering aboveground vegetation and the competitive interactions that occur at various stages of plant development within and between populations (Gioria & Pyšek 2015). Studies from Europe show that negative effects on seed banks are particularly pronounced for invasions by *F. japonica*, *Gunnera tinctoria*, and *H. mantegazzianum*, which are among the largest herbaceous species in the world (Gioria, Jarošík & Pyšek 2014). Seed banks of both native and alien species are remarkably reduced in areas invaded by these species, with the exception of a small pool of species that are capable of coexisting with the invader and setting persistent seed (e.g. *Urtica dioica*) Gioria, Jarošík & Pyšek (2014). Comparing invaded and uninvaded sites in Ireland, Gioria and Osborne (2010) found reduced species richness and abundance, as well as changes in species composition in the seed bank, within areas invaded by *F. japonica*, *G. tinctoria*, and *H. mantegazzianum*. Seed banks of invaded communities contained less native grass species and a reduced abundance of species occurring naturally within uninvaded habitats such as *Achillea millefolium* and *Cardamine flexuosa*. Seed banks within invaded areas had a greater abundance of ruderals such as *Stellaria uliginosa*, *Stachys sylvatica* and *Spergula arvensis*, which are known to produce large, persistent seed bank (Gioria & Osborne 2010). However, Kundel, van Kleunen & Dawson (2014), working in Germany, found no significant reduction in species richness, abundance or diversity in the soil seed bank in areas invaded by *Solidago gigantea* and *Solidago canadensis*, compared to uninvaded areas. Interestingly, total seed bank size was lower in uninvaded compared to invaded sites at greater soil depth. This could have been due to greater immediate germination rates in uninvaded areas due to reduced competition, which depletes the soil seed bank (Kundel, van Kleunen & Dawson 2014).

Assessing propagule bank characteristics in invaded communities is important in predicting potential recruitment of vegetation from the soil propagule bank (Gioria *et al.* 2014) and how, for example, this may respond to invasive species management. Alternatively, there may be features of the propagule bank that either promote or prevent invasion by IAPs. To date, the impact of IAPs on plant communities has been mainly examined with respect to changes in the aboveground vegetation. In contrast, the impact on the soil seed bank has received comparatively little attention (Gioria & Pyšek 2015). These studies illustrate the importance of taking into account the processes that maintain riparian vegetation development, as well as acknowledging the sources of environmental variability that shape vegetation through propagule dispersal and recruitment. However, there is still a need to assess impact by IAPs across a gradient (low to high abundance of IAPs) of invasion rather than using sites that are either invaded or uninvaded. Much information may be missed from removing the variation in IAP cover by focusing on a general characterisation of sites.

4.2.3 Sediment and propagule dynamics

There are also many physical processes that affect the quantity and quality of vegetation and propagule banks. Variations in river flow, particularly during major flood events, mobilize, transport and deposit organic matter, as well sediment (Goodson *et al.* 2002). Floods erode riparian banks, entraining sediments, vegetation debris and propagules, depositing them at different locations downstream (Goodson *et al.* 2002). Over-winter deposition is particularly important for recruitment of propagules (Goodson *et al.* 2002).

Deposition of sediment has been shown to affect the pre-existing vegetation and seedling germination in relation to sediment depth, ranging from the minimal impacts of a light covering of sediment to complete burial of the vegetation and thus creation of fresh sediment patches for colonization (Nilsson *et al.* 1993). Where sediment deposition occurs and where local conditions are not detrimental to colonisation (Dittmar & Neely 1999), ideal sites are provided for seedling germination. Therefore the ability of propagules to reach newly created sediment patches by hydrochory could have a major influence on subsequent vegetation development (Gurnell *et al.* 2006).

One of the most important physical functions of riparian vegetation is their ability to trap and buffer the transfer of sediment and associated nutrients (Steiger, Gurnell & Goodson 2003). Along the Garone River in France, Steiger, Gurnell & Goodson (2003) found that sites under natural riparian vegetation experienced higher sediment deposition. Greater density of natural riparian vegetation at sites may therefore increase entrapment of sediment. Cockel & Gurnell (2011) found that a greater abundance of propagules were associated with greater sediment deposition along urban rivers in London, UK. Gurnell (2007) also found an association between sediment deposition and vegetative fragments along rivers in the UK and in the Italian Tagliamento River, particularly at a catchment scale. Other studies, such as Chambert & James (2009), confirm that seed characteristics influence the effectiveness of hydrochory and sediment entrapment. Non-buoyant seeds were strongly influenced by entrainment and transport processes whilst buoyant seeds types were trapped within vegetation (Chambert & James 2009).

5. Scotland’s changing climate

Climate change scenarios and empirical evidence suggests that climate is changing in response to anthropogenic activity and that this is translated into effects on river flows (Werritty 2002). Riparian ecosystems have been identified as being particularly susceptible to climate change impacts, at least partially because they are among the world’s most transformed and degraded ecosystems (Tockner & Stanford 2002). Although variation in flooding is a regular feature of riparian zones, changes to flow regimes as a result of climate shifts or flow regulation may affect these historic flow processes (Nilsson & Svedmark 2002). Potential climate change effects include changes in flood frequency and potential summer drought periods (Capon *et al.* 2013), with potentially major ecological consequences for riparian habitats (Morecroft *et al.* 2002). Scotland's climate has become more variable, particularly in terms of precipitation, which has increased in the winter months across the north and west. In contrast, the east of Scotland has become drier, experiencing reduced summer precipitation over the same period (Critchlow-Watton *et al.* 2014). Rivers in the west of Scotland have increased in mean flow and experienced a greater frequency of high flow events since the 1970's. It is predicted that average river flows and the frequency of high flow events will continue to increase across Scotland (Truscott *et al.* 2006). From previous studies we know that changes in flow regime can be both advantageous (e.g. *Tamarix* spp. (Stromberg *et al.* 2007)) and disadvantageous (e.g. *Lonicera* spp. and *Rhamnus* spp. (Predick & Turner 2008)) to IAPs. However, little is known about how IAPs interact with abiotic variables, such adjacent land use and nutrient levels alongside climate related changes to flow regime.

6. Study species

The focal species are all currently listed in Europe's top 100 most invasive plant species by DAISIE (Delivering Alien Invasive Species Inventories for Europe) (http://www.europe-aliens.org/ 12/06/16). These species have been well documented within the literature and are known to negatively impact riparian ecosystems (Hulme & Bremner 2006; Gerber *et al.* 2008; Pyšek *et al.* 2012).

*6.*1 *Impatiens glandulifera*

Impatiens glandulifera Royle (Balsaminaceae), commonly known as Himalayan balsam, is currently ranked in the top 20 most invasive plants in the UK (Tanner *et al.* 2008). This species is native to the Western Himalayas and was first introduced to Europe as an ornamental plant in the early 19th century (Beerling & Perrins 1993). *I. glandulifera* has successfully colonised much of the UK, forming dominant stands along riverbanks and in woodlands (Ammer *et al.* 2010). Its success can be attributed to many factors. *I. glandulifera* reproduces sexually via seeds. Each plant can produce up to 2,500 seeds that are released from exploding seed pods over a range of up to 3-5m and remain viable within the seed bank for up to 2 years (Tanner *et al*. 2008). Synchronous germination of a large seed bank, with fast growing seedlings, allows the formation of dense stands potentially out-competing native species for light and space (Beerling & Perrins 1993). Die-back during winter can leave invaded areas bare and river banks prone to soil erosion, which may result in localised flooding (Greenwood & Kuhn 2014). Stems can persist as litter the following spring, possibly altering soil characteristics such as nutrient content (Beerling & Perrins, 1993). *I. glandulifera* is tolerant of shading and of a variety of soil types, including nutrient-poor gravels, and climatic conditions, enabling it to persist and spread in many areas of the UK (Tanner *et al.* 2014).

Fig 1 From left to right: *Impatiens glandulifera* flowers show a wide variation in colour. Assessing root depth of *I. glandulifera* along the River Earn.

6.2 Fallopia japonica

Fallopia japonica (Houtt.) RonseDecraene (syn. *Reynoutria japonica* Houtt.) (Polygonaceae), commonly known as Japanese knotweed, is native to Japan, China and parts of Taiwan and was introduced into Britain from Japan in the early 19th century as an ornamental plant (Beerling *et al.* 1994). This species is now naturalised throughout most of Europe, colonising disturbed habitats such as waste ground, roadside verges and riparian zones throughout Britain (Barney *et al.* 2006). *F. japonica* is a rhizomatous perennial geophyte, reproducing solely by vegetative fragments in Britain (Beerling *et al.* 1994). This species can grow up to 1 metre per month, reaching heights of up to 4 metres in a single growing season. *F. japonica* can form persistent, dense stands potentially outcompeting native species for light and space (Hejda *et al.* 2009), influencing macrofaunal assemblages (Kappes, Lay & Topp 2007), as well as altering physical characteristics (Maurel *et al.* 2010) of the invaded habitat (Barney *et al*. 2006). A recent estimate revealed the economic cost of *F. japonica* invasion in the UK to be £165.6 million per year, hence many studies have focused on both the genetic and biological control of this species (Shaw *et al.* 2011). Other species of *Fallopia* found along UK river banks include *Fallopia sachalinensis* F.Schmidt and *Fallopia x bohemica* Chrtek & Chrtkova.

Fig 2 From left to right: *Fallopia japonica* in flower. Large stand of *F. japonica* along the Black Cart Water, Scotland.

6.3 Heracleum mantegazzianum

Heracleum mantegazzianum SOMM. et Lev. (Apiceae), commonly known as Giant hogweed, is native to the Caucasus and was introduced into Britain in the 19th century as an ornamental plant (Tiley, Dodd & Wade 1996). *H. mantegazzianum* is a monocarpic perennial species, which reproduces sexually via seeds. This species has been recognised as a prominent example of an IAP with a wide distribution, enabled by a copious seed bank which benefits from downstream dispersal via hydrochory, as well as wind dispersal (Collingham *et al.* 2000). *H. mantegazzianum* is the largest herbaceous plant in Europe growing up to 6m tall, is highly competitive and is considered a noxious weed due to the furocoumarins in its sap which can cause a skin reaction known as phyto-photodermatitis in humans (Tiley *et al.* 1996; Collingham *et al.* 2000). *H. mantegazzianum* is well adapted to areas where soil moisture is maintained throughout the year, particularly riparian habitats (Tiley *et al.* 1996), although it is by no means restricted to riverbanks.

Fig 3 From left to right: Large leaves of *Heracleum mantegazzianum* along the Bannockburn, Scotland. *H. mantegazzianum* in flower along the Endrick Water, Scotland.

6.4 Other alien species

Beside the key IAPs mentioned above, there are other common alien riparian plants found along UK riverbanks that are not necessarily invasive. *Mimulus guttatus* L. (Phrymaceae), commonly known as the monkey flower, was first introduced into the UK from North America in the early 19th century. *M. guttatus* is a perennial herb found in wet habitats such as rivers and damp meadows (Truscott *et al.* 2008) and, unlike *I. glandulifera*, *F. japonica* and *H. mantegazzianum* has the ability to reproduce by both seed and vegetative fragments. This species has a high dispersal capacity, with the potential to expand its range in a short period (Truscott *et al*. 2006). Seeds can be transported downstream by water and upstream by wind and animals. Vegetative fragments can survive for up to 6 weeks, occurring year round with a high survival rate (Matthews *et al.* 2012). Therefore there is a high risk factor associated with the dispersal of *M. guttatus*, particularly with climate change, as this species has the potential to disperse continuously all year round. Other IAPs seen at the study sites include *Claytonia sibirica* L. and *Epilobium brunnescens* (Cockayne) P. H. Raven & Engelhorn found within the soil propagule bank.

Fig 4 From left to right: *Claytonia sibirica*, *Mimulus guttatus* and *Epilobium brunnescens*.

6.5 Dominant native species

Dominant native species were assigned on the basis of their potential to form monospecific stands and outcompete subordinate species, similar to that of the IAPs assessed in this study. Seven common native dominant species were considered in these studies: *Petasites hybridus* L. (common butterbur) is a dioecious rhizomatous perennial herb, spreading mostly vegetatively from rhizome fragments. The leaves of this species are large (diameter of 40–70 cm) and can outcompete other species for light. *Phalaris arundinacea* L. (reed canary grass) is a rhizomatous perennial that grows especially well on riverbanks where water levels fluctuate. *Urtica dioica* L. (stinging nettle) is a dioecious herbaceous perennial growing up to 2 m tall in the summer and dying down to the ground in winter. This species spreads via rhizomes and stolons. *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), is a large perennial grass found in wetlands, growing up to 4m tall. *Rubus fruticosus* L. (bramble) is a deciduous shrub, spreading via sexual reproduction of seeds. *Aegopodium podagraria* L. (ground elder) is a perennial plant spreading via underground rhizomes. Seed dispersal also occurs but is limited by self-shading. *A. podagraria* is highly competitive in disturbed areas where it is a pernicious weed. *Glyceria maxima* (Hartm.) Holmb. (reed sweet grass) is a highly competitive rhizomatous perennial of inundated habitats, growing up to 1 m tall. All other native species found at the study sites are regarded as subordinate native species, although some of these species are known to behave as dominants in non-riparian habitats.

Fig 5 From left to right: Dominant stand of *Petasites hybridus*. Stands of *Impatiens glandulifera* and *P. hybridus* along the river Almond, Scotland.

7. Research questions

Riparian habitats are among the most dynamic and economically important landscape features worldwide. Riparian zones form the aquatic-terrestrial interface and are characterized, naturally, by high biodiversity and productivity (Naiman & Decamps 1997). Rivers are also of great economic importance as flood plains tend to be focal points for agriculture and human settlement, alongside recreational activities and providing aesthetic value (Tockner & Stanford 2002). Riparian habitats are vulnerable to increasing human-induced pressures such as flow regulation, climate change and invasion by alien species (Capon *et al.* 2013). Invasion by IAPs are a prominent threat to native riparian biodiversity, and are also notoriously difficult to control and reverse once established (Strayer 2010). High species plant richness associated with riparian zones should, in theory, reduce invasibility (Levine 2000), although in systems where abiotic factors such as soil moisture, fertility and flow regime, dominate over biotic interactions, this may hold less true (Hood & Naiman 2000). Much work has been done to understand patterns or trends within riparian zones, such as flow regime shifts on riparian vegetation communities (Nilsson *et al.* 2010), and processes, mechanisms which may regulate community patterns such as seed bank studies (Gurnell *et al.* 2006). However, there are still key questions that need to be answered.

7.1 Theme: long term temporal and coarse scale spatial community changes

There is still disparity among scientist as to the type and generality of impacts IAPs have on native species. There is a particular need to focus on long term data sets, predominantly data which has been collected using standard methods from vulnerable habitats such as riparian zones, to assess turnover in species composition and relative effect size of IAPs alongside other changing environmental variables. Where other long term datasets have been used, such as Maskell *et al.* (2006) and Thomas and Palmer (2015), riparian habitats are strongly under-represented. Alongside changes in land use over the last two decades (e.g. increased enclosure of livestock, switch from spring to winter cereals), there have been significant changes in flow regime that might directly or indirectly influence community composition and competitive ability of IAPs along river banks. Establishment at a site is influenced by habitat quality that is often characterised by land use history and soil characteristics and in riparian areas, water quality. This theme is addressed in Chapter 2 using survey data collected at a coarse (500 m patch) scale resolution and on a decadal time scale spanning rivers across the UK to assess the dynamics of riparian vegetation and to assess the relative importance of invasive alien plants impact on community change.

Question: What environmental factors affect the occurrence of invasive alien plants (IAPs) over time and what is the relative contribution of IAPs to changes in the native, riparian plant community?

Hypothesis: Changes in environmental variables, such as flow regime, and a previous history of invasion by riparian IAPs will result in an altered native plant community over time.

7.2 Theme: fine spatial scale changes in vegetation communities

Powell *et al.* (2011) made clear the variation in impact on native species at different spatial scales, when assessing invaded and uninvaded areas. Riparian zones are heterogeneous, with the range of river bank elevations creating strongly contrasting conditions for vegetation development. The relative performance of native and invasive species is influenced by fluvial disturbance (including duration of inundation, or sediment erosion and deposition) or surrounding land-use (Capon *et al.* 2013). There are very few studies comparing the performance of co-occurring native and invasive plants, particularly within riparian zones. Therefore chapter 3 assesses how invasive alien and dominant native species vary with local environmental conditions and how the cover of these species impact subordinate native vegetation along the riparian bank, relative to local environmental variables.

Question: To what extent do local environmental factors regulate the effect of an invasive alien plant species on subordinate plant species, relative to the effect of dominant native plants?

Hypothesis: The dominance of riparian IAPs is greater under more stable flow conditions and they will therefore then have a greater impact on the native plant community. However, IAPs and dominant native species are expected to impact the subordinate native community equally under such conditions.

7.3 Theme: short term temporal mechanisms of community change

Understanding the various pathways and mechanisms that control IAP success within riparian habitats can enable managers to better identify vulnerable zones along rivers or manage conditions within restoration projects or newly designed channels so as to constrain IAPs. Flooding is a common disturbance in riparian systems and increased flood frequency has been correlated with the percentage cover and number of IAPs found at a site (Hood & Naiman 2000). However, changes in flow regime on British rivers over the last 20 years offer increasing opportunity for dispersal of propagules and sediment. Research shows that sediment and seed dispersal are controlled by similar fluvial and geomorphological processes, and that sediment has a propensity for transporting a greater amount of propagules which are deposited along river banks (Goodson *et al.* 2003; Gurnell *et al.* 2006). What is less clear is how increased sediment deposition along riparian zones that vary in IAP cover can impact aboveground vegetation communities over a short temporal scale. Whether or not sediment deposition can disrupt the dominance of IAPs in heavily invaded sites is still unknown. Chapter 4 assesses interannual variation in community composition and species richness of native plant communities, and whether local levels of invasion and over-winter sediment deposition drive these changes. A large amount of data was collated from both soil cores and AstroTurf mats for this thesis. This chapter deals specifically with answering questions pertaining to the dynamics of propagules directly deposited over winter. The majority of this data used were from the Astroturf mats.

Question: Does inter-annual change in riparian vegetation vary with the level of dominance of riparian IAPs and sediment deposition?

Hypothesis: Rivers that have a high level of invasion by riparian IAPs and experience higher sediment deposition will have lower, short term stability in terms of species composition and richness.

7.4 Theme: dispersal and establishment of vegetation communities

Mechanisms underlying the relationship between the soil propagule bank and above-ground vegetation are still obscure. General statements have been made regarding the similarity of soil propagule banks and aboveground vegetation, which can indicate the level of reliance of above ground vegetation on deposited propagules (Tabacchi *et al.* 2005). However, such relationships have yet to be assessed under varying environmental conditions along sites that have a gradient of IAP and dominant native coverage. As colonising vegetation is often reliant on replenishment from propagules, understanding the dynamics of this relationship can better aid restoration efforts along degraded river corridors. Chapter 5 aims to assess how the similarity in community composition between the soil propagule bank and above-ground vegetation varies under different environmental conditions, such as flow regime, and bank and channel characteristics, at a local site scale. Another important and related aspect of propagule dynamics that has yet to be answered is whether aspects of the propagule bank, such as species richness and abundance, can create resilience to invasion by IAPs. This will also be addressed in chapter 5. Propagule bank data incorporates soil core and AstroTurf mat data with a focus on whole community comparisons across seasons.

Question: What is the relationship between the extant vegetation and the soil propagule bank and does this vary predictably with local environmental conditions?

Hypothesis: There will be greater similarity between the extant vegetation and the soil propagule bank under disturbed conditions due to greater deposition of propagules derived from upstream sources and their recruitment. Greater supply of subordinate species will reduce the colonisation potential of invasive alien and dominant native species in the above-ground vegetation.

7.5 Discussion of results and future research

Globally, freshwater habitats are under immense pressure from land use and climate change. Where countries have sought to provide recommendations for management of riparian systems to prevent, remove or control invasions (for examples see Holmes 2005; Esler *et al.* 2008), a clearer understanding of how IAPs interact with the dynamic environmental conditions that characterise riparian habitats is crucial to make informed decisions (Hulme *et al.* 2012). Scotland's rivers provide a variety of conditions that are applicable to many temperate river systems worldwide, particularly in the face of increased flooding and drought. Therefore applying the knowledge gained from the research presented here could assist land managers and policy makers worldwide. Chapter 6 discusses the findings of this thesis, any limitations of the study design and suggest ways forward to improve our understanding of invasions within riparian systems.

Chapter 2. Twenty years of change in riverside vegetation: what role have invasive alien plants played?

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2.1 Abstract

Invasive alien plants (IAPs) are a pervasive feature of disturbed environments. We asked which environmental factors most influenced the occurrence of IAPs in riparian habitats and how much IAPs affected native vegetation compared to other environmental variables. We quantified change in river bank vegetation based on surveys undertaken approximately 20 years apart and assessed how much major IAPs (*Impatiens glandulifera*, *Heracleum mantegazzianum* and *Fallopia japonica*) contributed to these changes alongside factors such as flow regime and land use. Comparing data from pre- and post-1990 surveys revealed that IAPs occurred mainly on lowland rivers (altitude < 200 m) regardless of time period and that their probability of occurrence increased over time with rising flood frequency. Native species diversity declined over time with increasing IAP cover, along lowland rivers, and along all rivers experiencing extended low flows during the growing season. These conditions particularly favoured native dominant species, whereas native subordinate species responded both positively and negatively to increased flood frequency depending on time period. Over time, an increase in woody *Salix* spp. and larger hydrophilic species, such as *Sparganium erectum*, occurred along lowland rivers at the expense of smaller ruderal species, driving a shift towards increased shade tolerance. Smaller compositional changes occurred in the uplands and lacked a clear environmental signature. National scale changes in native riparian vegetation are likely driven primarily by environmental changes and land-use effects, rather than invasion by IAPs. However, as potential beneficiaries of such changes, IAPs may exert important secondary effects on native riparian vegetation. The trend towards reduced diversity, increased shade tolerance and increased dominance of both native species and IAPs is likely linked to a set of interacting factors including drier summers, wetter winters, increased riparian tree cover, reduced livestock access to river banks and increased fine sediment input. Determining ecological responses to land use, IAPs and climate-related changes in flow regime over decadal time scales is important for predicting how vulnerable habitats will respond under future disturbance scenarios.

2.2 Introduction

Riparian habitats are dynamic and frequently disturbed (Tickner *et al.* 2001). Hydrological connectivity between the river channel and its floodplain increases the spatiotemporal heterogeneity of these habitats, leading to their characteristically high biodiversity (Stokes *et al.* 2010). Riparian vegetation in particular, is important in ecosystem functioning such as stabilising river banks from erosion, modifying shade and providing a corridor for the dispersal of biota (Richardson *et al.* 2007). Despite their widely acknowledged importance, riparian zones remain among the most threatened of all ecosystems, under increasing pressure from anthropogenic and environmental stressors, with elevated risk of invasion by alien species (Baattrup-Pedersen *et al.* 2013b).

Anthropogenic alterations to flow regime, channel engineering and adjacent land-use are almost ubiquitous features of rivers worldwide (Stokes *et al.* 2010), especially in the lowlands (Garssen *et al.* 2015), but there is also mounting evidence of the scale of modification in the uplands (Wheater & Evans 2009). Riparian habitats have traditionally been a focus of agricultural activities, due to ease of water availability and high soil fertility. This has led to poor water quality through nutrient enrichment, sedimentation and loss of woodland cover (Casanova 2015). Livestock grazing has also altered riparian vegetation dynamics while land use intensification has reduced the normally high heterogeneity of riparian vegetation (Stockan, Langan & Young 2012). Hence, Méndez-Toribio et al. (2014), for example, found a negative correlation between species diversity of riparian vegetation and increased anthropogenic disturbance alongside the River Duero, Mexico. Extensive physical transformation has also rendered riparian ecosystems more susceptible to anthropogenic changes in climate and associated flow regime (Capon *et al.* 2013).

Intermittent flooding is a defining feature of riparian zones, with hydrological and geomorphic processes such as inundation, erosion and sediment deposition, among key determinants of vegetation growth and survival (Baattrup-Pedersen *et al.* 2013b). Historic changes to flow regimes as a result of climate shifts or flow regulation may affect these processes, thereby altering species diversity and composition of riparian vegetation (Nilsson & Svedmark 2002). The consequences of altered river flows for riparian biota are usually negative (Poff & Zimmerman 2010; Webb *et al.* 2013). However, little is known about the effect of climate-induced changes in flow regime on riparian vegetation (Tickner *et al.* 2001). Changes in the timing, duration and frequency of high and low flow events can affect vegetation dynamics, by changing competitive interactions and favouring specific life history traits (Stromberg *et al.* 2007). Flooding can alter resource availability and affects the frequency of connectivity between channel and floodplain that is critical for the movement of plant propagules within riparian zones (Stromberg *et al.* 2007). Since flooding favours waterborne dispersal of propagules and their recruitment (Richardson *et al.* 2007), riparian ecosystems are responsive to changes in precipitation (Garssen *et al.* 2015). However, flooding not only enables the recruitment of native species, but also invasive alien plant species (IAPs), which may compromise the resilience of riparian vegetation to disturbances (Richardson *et al.* 2007).

Disturbance, whether from natural or anthropogenic sources, can disrupt species interactions, lower competitive ability and favour recruitment of IAPs, which are widely regarded as a major threat to native biodiversity (Richardson *et al.* 2007). Disturbed habitats with heightened potential for propagule dispersal, such as riparian zones, are especially amenable to invasion (Maskell *et al.* 2006), with IAPs developing monospecific stands that can potentially suppress the growth of native species (Beerling & Perrins 1993). Hence there is concern that invasions will lead to the large-scale homogenization of native flora over time (Hulme & Bremner 2006). Nevertheless the precise impact of alien species on native ecosystems is still widely disputed. Of the numerous alien plants in Britain only a few are considered to be invasive. *Heracleum mantegazzianum, Fallopia japonica* and *Impatiens glandulifera* are all currently listed in Europe's top 100 most invasive plant species by DAISIE (http://www.europe-aliens.org/ 23/01/13) and commonly occur in riparian habitats. The ecology and distribution of these three species is well studied, but reported impacts on the diversity of native vegetation are few and sometimes conflicting (Hulme & Bremner 2005; Hejda & Pyšek 2006), and appear to be scale and species-specific (Hejda *et al.* 2009; Powell *et al.* 2011).

Evidence from previous studies and predictive models suggest that rates of invasion and establishment within freshwater habitats will continue to increase (Strayer 2010). The degree to which native riparian vegetation has changed due to a suite of multiple stressors – IAPs, anthropogenic disturbance and climate-related changes to flow regime and their various interactions – at large spatial and temporal scales, is relatively unknown and significantly constrains our understanding of how riparian habitats will respond to future environmental change and management (Hejda & Pyšek 2006). The widespread establishment of IAPs is perhaps the most profound change to have occurred in European riparian habitats in recent decades, but whether this directly influences changes in native vegetation or other less obvious but more potent factors are at play is unclear. Recent studies using UK Countryside Survey (CS) data collected between 1990 and 2007 have concluded that IAPs do not negatively impact native vegetation on a national scale (Thomas & Palmer 2015), or have only weak and likely secondary effects (Maskell *et al.* 2006). Such conclusions are likely to depend on the species or habitats considered and the levels of abundance attained by IAPs. Moreover, the CS datasets do not focus explicitly on habitats of conservation concern, or those IAPs considered to pose the greatest ecological risk (Hulme *et al.* 2015).

In this study we use botanical data from two large-scale surveys of British rivers to assess the contribution of three major IAPs (*I. glandulifera, F. japonica* and *H. mantegazzianum*) to changes in native riparian vegetation over a 20 year period, relative to the effects of flow regime, river type and land use characteristics. The wide geographical coverage of these surveys allows inference to be made about the extent of changes in riparian vegetation on a national scale (Maskell *et al.* 2006). In this analysis we consider (i) which environmental factors most affect the probability of occurrence of an IAP; (ii) how are changes in the diversity, turnover and cover of native species related to IAP cover, flow regime changes and land-use; (iii) what specific changes have occurred within riparian vegetation on a decadal time scale within contrasting river types and how can these best be explained.

2.3 Methods

2.3.1 River Macrophytes Database

The Joint Nature Conservation Committee (JNCC) River Macrophytes Database (RMD) contains records from standardised vegetation surveys of rivers from across the whole UK undertaken by experienced surveyors. Surveys focus on rivers with existing or potential conservation value and almost 4500 surveys have been undertaken since 1977 following the methods described by Boon et al. (1996) and Holmes et al. (1999). Survey sites comprised 500m river stretches, with sites along the same river being located 5 - 10km apart, depending on river size. Plants were recorded using a standardised species checklist to aid recording. Each species recorded was given a cover score of 1-3 corresponding to a range of percentage cover. The entire channel (permanently submerged) and the immediate banks (periodically inundated) were surveyed at each site (Boon *et al*. 1996). The checklist was commonly supplemented by surveyors with records of additional species. Basic locational and environmental data such as substrate type, altitude, distance from source and channel width were either collected in the field or derived subsequently through GIS. Upland rivers were defined as those at or greater than 200m, whilst lowland rivers were less that 200m in altitude.

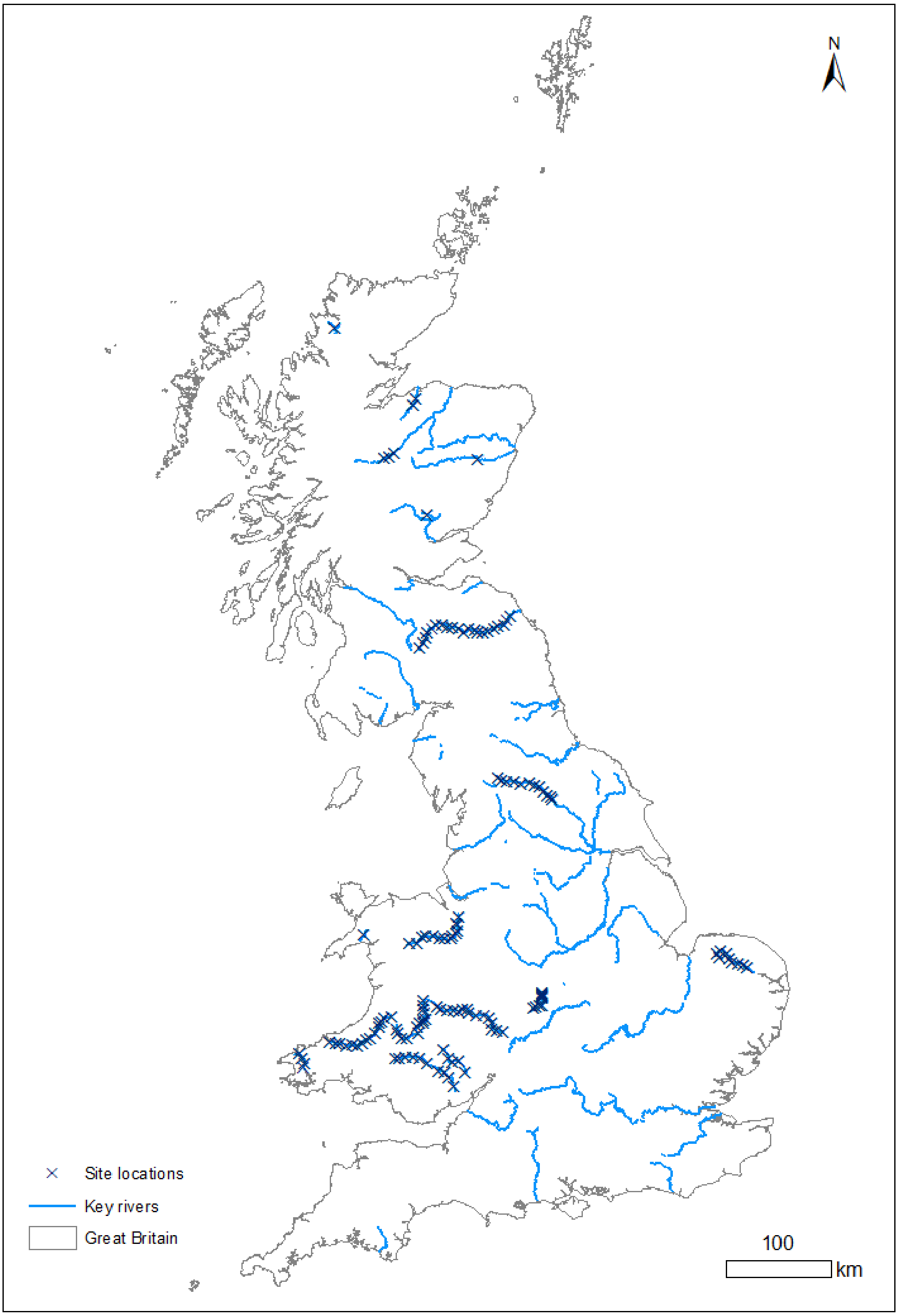

Fig 1. Location of survey sites included in this study (scale and locations approximate).

2.3.2 Data extraction

Sites with repeat surveys separated by at least 10 years were extracted from the RMD. This yielded 271 sites (Fig. 1), first surveyed in the period 1979-1982 (hereafter first survey period) and resurveyed in the period 1992-2009 (hereafter second survey period). The average interval between first and second survey was ~20 years. Although annual survey data are preferable to allow for the effects of short term temporal variation, such data were unavailable and have only been collected exceptionally and at a local scale in the case of riparian vegetation.

All surveyors used a standard species checklist and additional species were also recorded in some instances. All surveys in the first period were undertaken by a single surveyor (Nigel Holmes). However, in the second period seven different personnel conducted surveys. To offset the bias in recording of additional species by different surveyors, a conservative criterion (presence at >2% of sites) was used to obtain a list of species common to both survey periods. A total of 119 angiosperms and bryophytes representing those on the standard checklist, plus additionally recorded species, were used in subsequent analyses. Species excluded from analyses represented <10% of the total cover of all species recorded. Plant species that had an Ellenberg moisture score of 11 and 12 (Hill et al. 1999, 2004) were removed to ensure a focus on riparian vegetation.

2.3.3 Vegetation descriptors

Alien species were defined as those that colonised Britain with the help of humans. We focused on the invasive alien species *H. mantegazzianum, I. glandulifera* and *F. japonica.* Previous studies have associated these species with negative impacts on native riparian vegetation (Hejda *et al.* 2009). *Impatiens glandulifera* was the most frequently recorded of these species, occurring at 70% of invaded sites. The percentage cover of *I. glandulifera, H. mantegazzianum* and *F. japonica* were combined and used to assess the effect of IAP cover on aspects of the native plant community. Commonly occurring riparian alien species that were not considered invasive for the purposes of this study included *Acorus calamus*, *Claytonia sibirica*, *Epilobium brunnescens*, *Impatiens capensis* and *Mimulus guttatus.* Some studies have shown that native dominant species may have a comparable competitive ability to IAPs (Bottollier-Curtet, Planty-Tabacchi & Tabacchi 2013). In order to assess the comparative effect of dominant native species on the associated native vegetation, native species were split into subordinate and dominant categories. Native dominant 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 mono-dominant stands alongside rivers in Britain. These comprised *Angelica sylvestris, Carex acutiformis, Carex aquatilis, Carex riparia, Carex rostrata, Epilobium hirsutum, Filipendula ulmaria, Glyceria maxima, Oenanthe crocata, Petasites hybridus, Phalaris arundinacea, Phragmites australis, Sparganium erectum, Symphytum officinale* and *Typha latifolia.* The percentage cover of native dominant and subordinate species was determined by summing the individual % cover of the species belonging to these groups.

Native species richness was assessed using Shannon's diversity index. Bray–Curtis dissimilarity Index (BCI) was used to quantify temporal change in species composition, calculated using cover (percentage, square-root transformed) of native species. Theoretical values of BCI range from 0 to 1, with 1 indicating no shared species between paired surveys and 0 indicating complete overlap.

To identify specific changes in community composition, while accounting for differences in site attributes, sites were first clustered by altitude, slope, hydrology and location (easting) into homogenous groups using K-Means cluster analysis. The two clusters chosen, 'upland' (n=132) and 'lowland' (n=139) river types, reflected ease of interpretability and the need for a minimum sample number per cluster. Species characteristic of the earlier or later survey periods within each of the two river types were identified using indicator species analysis (IndVal; Dufrene & Legendre 1997) applied to square root-transformed percentage cover data. IndVal is based on specificity and fidelity in different groups with the index ranging from 0%, denoting no presence in a survey group, to 100%, indicating that a species occurs in only one group of samples and is present in all samples within that group. The significance of these values was tested using a Monte Carlo randomisation procedure (Dufrene & Legendre 1997).

To allow a more comprehensive interpretation of environmental conditions, Ellenberg's indicator values for moisture (F), light (L), pH (R) and fertility (N) were compared for the indicator species in each group and survey period (Hill *et al.* 1999). Ellenberg indicator values (Ellenberg *et al.* 1991) that rank plant tolerance to light (L), moisture (F), pH (R) and nitrogen (N) were assigned to all bryophytes and vascular plants using the PLANTATT and BRYOATT databases (Hill *et al.* 2004).

2.3.4 Site characteristics

A Principal Components Analysis (PCA) was conducted, following Jeffers (1998), to reduce collinear site characteristics (slope, altitude, distance from source and height of source) to a single axis of variation. Site altitude and slope were expressed mainly through the first axis of the PCA analysis, which explained 55% of the variance. Percentage woodland cover within a 100m radius of a site was determined using the Land Cover Map 2007 (LCM2007) (Morton *et al.* 2011) imported to ArcGIS/ArcMap (v 10). Data on water chemistry (alkalinity and total oxidised nitrogen (TON)) were available for a subset of sites. However, since the variable easting was collinear with alkalinity and was universally available, easting was used as a surrogate for both fertility and intensive agricultural land use that generally increases in Britain from west to east.

To assess the effect of hydrology on riparian vegetation, daily mean flow data were obtained from the Centre of Ecology and Hydrology's National River Flow Archive. Data for the five years prior to the dates of the first and second surveys were used to calculate flow regime indicators, using data from the most downstream flow gauging station on each surveyed river. Flood frequency, expressed as the mean number of days per year on which flows exceeded a threshold of 5 times the median flow (FRE_5), was used as an indicator of fluvial disturbance. The maximum number of consecutive days over the period 1 March to 30 September each year on which flows did not exceed a threshold of 3 times the annual median flow, averaged over the five years prior to each survey period, was used as an indicator of undisturbed growing season length. These indices capture contrasting but ecologically-relevant components of flow variability (Clausen & Biggs 1997).

2.3.5 Statistical analysis and model selection

Our primary focus was on whether the various response variables (IAP presence or absence, Shannon diversity, native subordinate and dominant species % cover) differed between the two survey periods and whether any difference in these values, or the amount of species turnover (BCI) between surveys, was explained by other vegetation indicators or environmental factors (altitude/slope (PC1), easting, woodland % cover, flood frequency and low flow duration). Therefore, in all models (BCI response excluded) a fixed factor survey (with two levels: first and second survey period), was included as an interaction with each predictor. Thus, the significance of an interaction between a given predictor and survey period would indicate that this predictor affects the change in the response between the survey periods. Since sites were nested by river this identifier was treated as a random effect. All predictors were standardised to one standard deviation prior to statistical analyses, in order to be able to assess relative effect sizes of each predictor directly (Nakagawa & Schielzeth 2010). This modelling approach was used to model five response variables with choice of error structure dependent on the type of response: (1) the probability of an IAP being present at a site (generalized linear mixed model (GLMM) with a Binomial error structure), (2) Shannon's Diversity Index (linear mixed models (LMM)), (3) Bray–Curtis Index (BCI), (LMM), (4) native subordinate species cover and (5) native dominant species cover (both %, squared root transformed and LMM). Although BCI is theoretically bounded by zero, data ranged from 0.2 – 0.8 enabling us to model this index within the theoretical constraints of bounded data. Quadratic terms were used to test for non-linear relationships between variables. Quadratic predictors within the models were flow variables and invasive and dominant native plant cover. These were chosen a priori and retained within the model when model fit was improved. We checked for multicollinearity among the predictor variables before use in multiple regression analyses, retaining those variables that were not highly correlated ($r = < 0.60$). Models were also run using time between the first and second survey at each site as a continuous predictor. The results from these models were the same as using survey as a factor in the analyses. We therefore continued with the latter choice and present our data accordingly.

Models were ranked using the information theoretic approach (Burnham & Anderson 2002) to select the best combination of interaction effects from the global model. Models were compared using AICc (correcting for small sample sizes), with all possible combinations of predictors identified using the dredge function in MuMIn. Main effects (including quadratic terms) were only considered alongside their interactions, if the effect contributed to model fit. The best fitting models were evaluated based on their ΔAICc, with values < 4 considered to be equally parsimonious (Burnham & Anderson 2002). Akaike weights were calculated for each explanatory variable, in order to compare the relative importance of each variable in the top set (ΔAICc < 4) of models. Model coefficients were averaged across this set (full averaging) and the resulting averaged coefficients were used for predictions and 95% confidence intervals. Confidence intervals were calculated as 1.96* the standard error of the model predictions. Model predictions were plotted holding all other standardised predictor variables at zero. To account for the variation explained solely by the fixed effects, as well as the variation explained by both the fixed and random effects, both the marginal and conditional R^2 values are reported for each model, respectively (Nakagawa & Schielzeth 2013).

All statistical analyses were conducted using R 3.2.2 (R Development Core Team 2015), with the additional R packages vegan (v 2.3-0), labdsv (v 1.8-0), NbClust (v 3.0), MuMIn (v 1.15.1) and lme4 (v 1.1-10).

2.4 Results

2.4.1 Invasive alien species

The probability of IAP presence increased with PC1 scores, equivalent to decreasing altitude and slope. This effect was the same for both survey periods (Fig. 2a). Flood frequency and PC1 (altitude and slope) were the most important variables (interaction terms with survey, (Table 1)) in predicting the probability of an IAP being present at a site, compared to other predictor variables in the model. Both predictors had a relative variable importance (RVI) of 1. The top model within the top set had a marginal R^2 of 0.57 and a W_i of 0.68 (Appendix Table 1). Flood frequency increased the probability of an invasive species being present at a site, particularly so for the second survey (Fig. 2b). IAPs were present at 34% of the 271 sites in the first survey period compared to 47% of sites in the second survey period. The median percentage cover of IAPs in the first survey period was low, ~5%, compared to 15% in the second survey period.

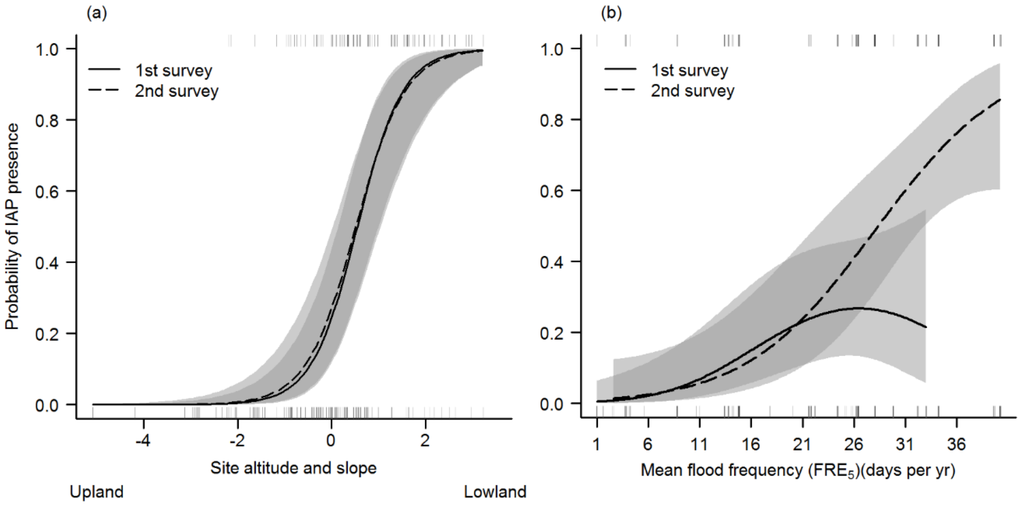

Fig 2. Observed values (dashes) and full model averaged predicted values (lines± 95% CI) from the GLMM analysis of probability of invasive alien plant presence. Interaction effect between a) altitude and slope (PC1) x survey and b) mean annual flood frequency (FRE_5) x survey.

2.4.2 Native species diversity

Across sites as a whole native species diversity declined by an average of 6% between surveys. Along lowland and upland rivers, native diversity declined by 10% and 2.4 % respectively. Interaction terms IAP^2 x survey and easting x survey had the greatest effect on native species diversity. At both lower altitudes (Fig. 3a) and with extended flow periods (Fig. 3b), native species diversity was lower in the second survey compared to the first. In the first survey period diversity was positively associated with low level increases in IAP cover. As IAP cover increased further in the second survey period, this relationship became neutral to negative (Fig. 3c). All predictors except flood frequency had an RVI of 1 (Table 1). The top model had a weighting of 0.87 and a marginal R^2 of 0.27 (Appendix Table 1).

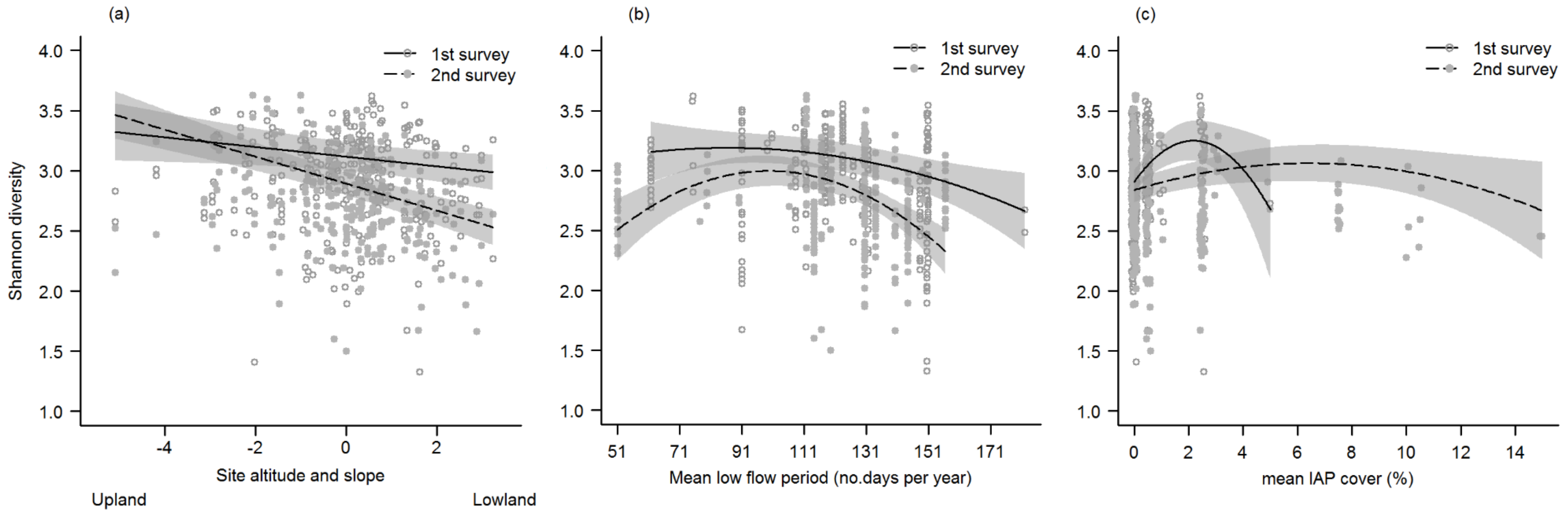

Fig 3. Observed values (points) and full model averaged predicted values (lines± 95% CI) from the LMM analysis of native species Shannon diversity. Open and closed circles represent observed values from the first and second survey respectively. Figure a) shows the altitude and slope (PC1) x survey interaction, b) mean number of low flow days x survey interaction and c) invasive alien plant % cover x survey interaction.

2.4.3 Native species cover

Interaction terms flood frequency^2 x survey, easting x survey and low flow^2 x survey had the greatest effect on native subordinate species cover and an RVI of 1 (Table 1), compared to other predictor variables in the model. In contrast to the first survey period, native subordinate species cover was highest at intermediate flood frequencies in the second survey period (Fig. 4a). There was a negative association between native subordinate species cover and decreasing site altitude and slope in both survey periods, although this effect was strongest in the second survey period. Thus, the difference in native subordinate species cover between the second relative to the first survey period increased from low to high altitude sites (Fig. 4b). All predictors were retained within the top model set. The top model had a W_i of 0.38 and a marginal R^2 of 0.35 (Appendix Table 1).

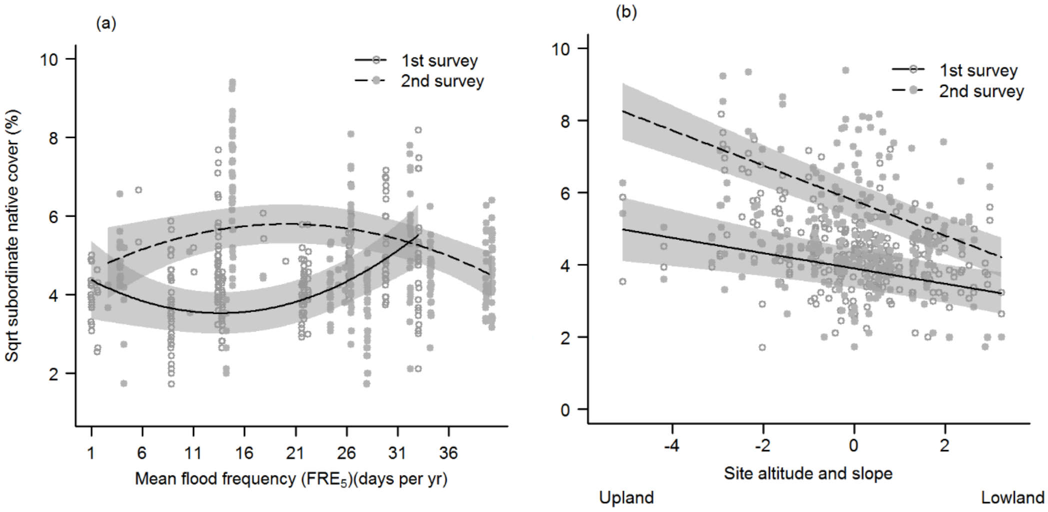

Fig 4. Observed values (points) and full model averaged predicted values (lines± 95% CI) from the LMM analysis of native subordinate species % cover (sqrt transformed). Open and closed circles represent observed values from the first and second survey respectively. Figure a) flood frequency x survey interaction, b) altitude and slope (PC1) x survey interaction.

Although most explanatory variables had a relatively small effect on native dominant species cover, easting x survey and low flow^2 x survey had an RVI of 1, with the largest relative effect sizes (Table 1), compared to other predictor variables in the model. After an initial decline at an intermediate low flow period, an increase in native dominant species cover was associated with a greater number of consecutive low flow days in the second survey period. In contrast, an initial increase and thereafter a decline in native dominant species cover was associated with an increased low flow period in the first survey period (Fig. 5a). There was an overall positive association between native dominant species cover and decreasing site altitude and slope in both survey periods. However, in contrast to the first survey period, there was a reduction in the rate of native dominant species cover increase in the second period, moving from high to low elevation (Fig. 5b). The top model within the top model set had a marginal R^2 of 0.24 and a W_i 0.26 (Appendix Table 1).

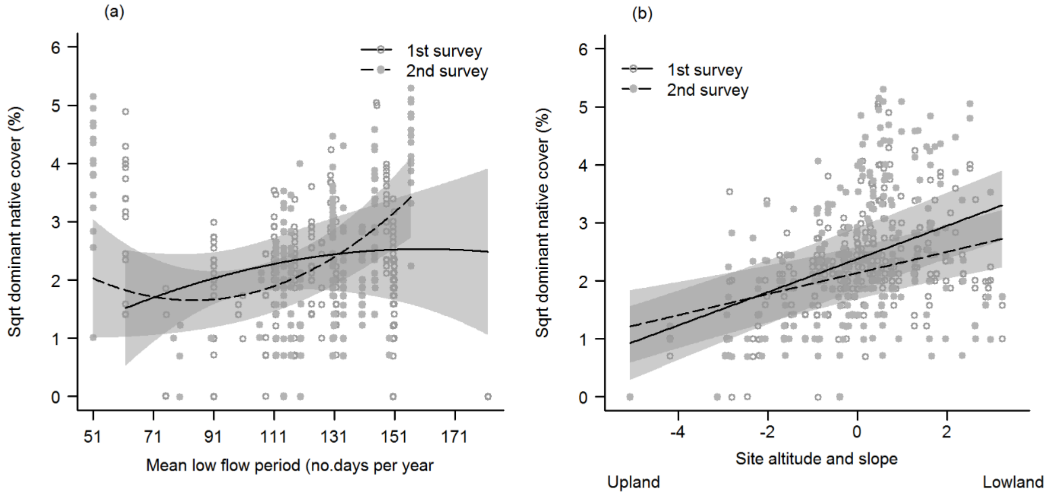

Fig 5. Observed values (points) using full model averaged predicted values (lines± 95% CI) from the LMM analysis of native dominant species % cover (sqrt transformed). Open and closed circles represent observed values from the first and second survey respectively. Figure a) shows the interaction effect between number of low flow days x survey, b) altitude and slope (PC1) x survey for both the first (solid line) and second (dashed line) survey period.

2.4.4 Change in native species composition

Easting, PC1 (altitude and slope) and low flow days had the greatest effect on BCI (Table 1), compared to other predictor variables in the model. Thus sites which showed the least change in native vegetation composition (low BCI) were generally located further east and/or at higher elevations (figure not shown), whilst the greatest compositional change (high BCI) was associated with low elevation (Fig 6), and a greater number of consecutive low flow days. The top model within top model set had a marginal R^2 of 0.23 and a W_i 0.20.

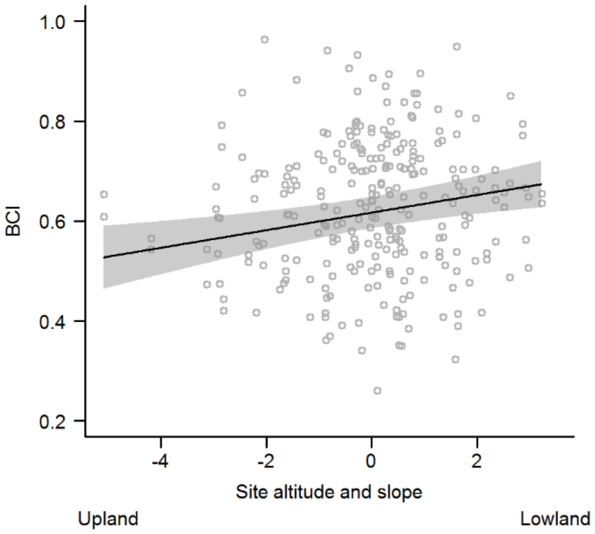

Fig 6. Observed values (points) and full model averaged predicted values (lines± 95% CI) from the LMM analysis of native species Bray-Curtis Dissimilarity Index (BCI) showing the effect of PC1.

Table 1. Full model-averaged parameter estimates for GLMER (invasive presence or absence) and LMER (native species diversity, BCI, native subordinate and dominant species % cover) analyses ±95% confidence intervals. Confidence intervals were calculated using full model averaged standard errors. The estimates for survey are relative to the first survey period. All explanatory variables were standardised to 1SD prior to analyses. Superscript 2 indicates a quadratic term. Relative variable importance (RVI) is also given.

	Invasive Presence/Absence				S-W Diversity				BCI (Turnover)				Subordinate Cover				Dominant Cover			
Predictor	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI
Intercept	-1.13	-2.00	4.35		3.12	3.00	3.24		0.62	0.59	-1.13		3.91	3.37	4.44		2.38	1.85	-3.35	
PC1	2.06	1.27	-2.08	1.00	-0.04	-0.07	-0.01	1.00	0.02	0.01	-0.01	1.00	-0.21	-0.32	-0.10	1.00	0.29	0.21	-0.38	1.00
Dominant Native Sp Cover	-	-	-	-	-	-	-	-	<0.01	-0.01	0.03	0.27	-0.10	-0.32	0.13	1.00	-	-	-	-
Dominant Native Sp Cover^2	-	-	-	-	-	-	-	-	-	-	-	-	0.13	0.02	0.25	1.00	-	-	-	-
Easting	-	-	-	-	-0.08	-0.15	0.00	1.00	-0.05	-0.08	0.17	1.00	-0.39	-0.70	-0.07	1.00	-0.03	-0.20	0.49	0.27
Invasive Cover	-	-	-	-	0.38	0.20	0.55	1.00	<0.01	-0.01	0.02	0.34	0.43	-0.08	0.95	1.00	-0.01	-0.19	0.46	0.51
Invasive Cover^2	-	-	-	-	-0.26	-0.43	-0.09	1.00	-	-	-	-	-0.19	-0.69	0.32	0.49	-	-	-	-
Woodland Cover	-	-	-	-	-	-	-	-	<0.01	-0.01	0.02	0.33	0.01	-0.06	0.07	0.29	-	-	-	-
Flood frequency	0.64	-0.32	1.11	1.00	<0.01	-0.04	0.04	0.13	-	-	-	-	0.97	0.53	1.41	1.00	0.17	-0.23	0.65	0.57
Flood frequency^2	-0.79	-1.56	3.46	1.00	-	-	-	-	-	-	-	-	0.62	0.30	0.95	1.00	-0.08	-0.31	0.73	0.57
Low flow	-0.08	-0.70	1.68	0.32	-0.10	-0.17	-0.04	1.00	0.03	0.00	0.02	0.96	-0.02	-0.35	0.32	1.00	0.20	-0.18	0.55	1.00
Low flow^2	-0.09	-0.51	1.22	0.18	-0.04	-0.08	0.01	1.00	<0.01	-0.01	0.03	0.19	0.18	0.01	0.34	1.00	-0.07	-0.20	0.46	1.00
Survey	0.14	-0.86	2.19	1.00	-0.22	-0.33	-0.12	1.00	-	-	-	-	1.88	1.38	2.38	1.00	-0.24	-0.53	1.18	1.00
PC1 x Survey	-0.15	-0.76	1.79	1.00	-0.07	-0.12	-0.03	1.00	-	-	-	-	-0.27	-0.41	-0.13	1.00	-0.10	-0.19	0.42	1.00
Easting x Survey	-	-	-	-	0.23	0.16	0.30	1.00	-	-	-	-	0.94	0.63	1.25	1.00	0.04	-0.11	0.30	0.27
Dominant Native Sp Cover x Survey	-	-	-	-	-	-	-	-	-	-	-	-	0.55	0.28	0.83	1.00	-	-	-	-
Dominant Native Sp Cover^2 x Survey	-	-	-	-	-	-	-	-	-	-	-	-	-0.26	-0.41	-0.12	1.00	-	-	-	-
Invasive Cover x Survey	-	-	-	-	-0.26	-0.44	-0.08	1.00	-	-	-	-	-0.24	-0.72	0.25	1.00	0.04	-0.16	0.43	0.51
Invasive Cover^2 x Survey	-	-	-	-	0.24	0.07	0.41	1.00	-	-	-	-	0.17	-0.31	0.65	0.49	-	-	-	-
Woodland Cover x Survey	-	-	-	-	-	-	-	-	-	-	-	-	-0.03	-0.17	0.10	0.29	-	-	-	-
Flood frequency x Survey	1.10	0.03	0.48	1.00	-	-	-	-	-	-	-	-	-1.10	-1.47	-0.74	1.00	-0.07	-0.30	0.71	0.57
Flood frequency^2 x Survey	0.75	-0.07	0.54	1.00	<0.01	-0.03	0.03	0.13	-	-	-	-	-1.01	-1.30	-0.72	1.00	0.01	-0.13	0.32	0.57
Low flow x Survey	0.08	-0.74	1.87	0.32	-0.13	-0.23	-0.04	1.00	-	-	-	-	-0.85	-1.19	-0.51	1.00	0.45	0.19	-0.23	1.00
Low flow^2 x Survey	0.11	-0.41	1.06	0.18	-0.10	-0.15	-0.04	1.00	-	-	-	-	-0.76	-0.96	-0.56	1.00	0.29	0.16	-0.26	1.00

Indicator species analyses showed that taxa strongly associated with lowland sites in the first survey period (Table 2) were mostly small ruderal species of inundation zones and livestock grazed margins (including *Agrostis stolonifera, Myosotis scorpioides, Epilobium spp., Juncus bufonius, Equisetum arvense, Persicaria hydropiper, Callitriche stagnalis, Alopecurus genicuatus* and *Ranunculus sceleratus*) or those resistant to grazing (*Deschampsia caespitosa* and *Juncus inflexus*). The second survey period featured *Salix* spp.*, Sparganium erectum* and *I. glandulifera* as the strongest indicators alongside a suite of other tall canopy-forming herbs (e.g. *Angelica sylvestris*, *Stachys palustris*, *Scrophularia auriculata* and *Lysimachia vulgaris*) or their understorey associates. In the upland site group some of the same differences in indicator taxa applied, with *S. palustris*, *Sagina procumbens*, *Leptodyction riparium*, *Galium palustre*, *Pellia epiphylla* and *Lunularia cruciata* and the IAPs *I. glandulifera* and *F. japonica* again being indicative of the second survey period. In the first survey period the indicators *A. stolonifera*, *A. geniculatus* and *E. arvense* were also common to both upland and lowland groups of sites. However, some contrasts were also evident with strong indicators of the first survey period in the lowland sites (*P. hydropiper* and *D. caespitosa*) being associated with the latter survey period in the upland sites.

Table 2. Significant indicator species for the first and second survey period in lowland rivers and upland rivers. Observed indicator values (IV) and their significance are given. An asterisk indicates that species were very highly (***), highly (**) or significantly (*) associated with a particular survey period, based on Monte Carlo permutation tests. Invasive alien plant species shown in bold.

	First survey period (pre 1990)		Second survey period (post 1990)	
River Type	Species	Observed IV	Species	Observed IV
Lowland	*Agrostis stolonifera****	59.1	*Salix spp.***	54.3
	*Myosotis scorpioides***	50.9	*Sparganium erectum**	48.7
	Epilobium spp ***	41.4	***Impatiens glandulifera******	41.9
	*Persicaria hydropiper****	37.5	*Leptodyction riparium****	34.9
	*Equisetum arvense****	29.8	*Stachys palustris****	33.8

	*Juncus bufonius****	28.9	*Conocephalum conicum s.l.**	30.1
	*Callitriche stagnalis***	24.6	*Angelica sylvestris****	26.0
	*Deschampsia cespitosa****	18.3	*Scrophularia auriculata***	25.9
	*Marchantia polymorpha****	16.2	*Galium palustre****	22.9
	*Alopecurus geniculatus****	16.2	*Pellia epiphylla****	21.5
	*Juncus inflexus**	13.9	*Lunularia cruciata***	20.5
	*Hygrohypnum ochraceum****	13.3	*Sagina procumbens****	20.3
	*Ranunculus sceleratus***	12.7	*Equisetum palustre****	17.1
	*Rorippa amphibia***	11.4	*Lysimachia vulgaris****	16.8
	*Carex hirta****	11.2	*Callitriche platycarpa**	15.9
	Jungermannia spp. ***	6.1	*Cardamine amara****	13.6
	*Nardus stricta**	4.6	***Fallopia japonica******	12.9
			*Phragmites australis***	9.6
			*Brachythecium plumosum**	6.5
Upland	*Agrostis stolonifera**	49.8	*Deschampsia cespitosa****	41.8
	*Rhynchostegium riparioides****	42.9	*Persicaria hydropiper**	36.9
	*Equisetum arvense**	27.1	*Filipendula ulmaria***	36.6
	*Chiloscyphus polyanthos**	26.5	*Galium palustre****	33.8
	*Eleocharis palustris****	23.2	*Pellia epiphylla****	33.2
	*Alopecurus geniculatus****	22.2	*Leptodyction riparium****	32.1
	*Fissidens spp.****	14.3	*Senecio aquaticus****	30.7
	*Scapania spp.**	14.0	*Sagina procumbens**	26.0
	*Pohlia melanodon****	13.5	*Stachys palustris****	24.0
	*Cratoneuron filicinum***	13.0	*Brachythecium rivulare**	24.0
	*Carex acuta****	12.3	*Thamnobryum alopecurum**	22.1
	*Carex acutiformis***	11.1	***Impatiens glandulifera******	21.9
	*Glyceria notata***	7.0	*Stellaria uliginosa***	16.3

*Lunularia cruciata**	14.5
*Montia fontana**	13.4
*Rorippa sylvestris****	12.8
Fallopia japonica**	9.4
*Epilobium brunnescens****	7.9

Ellenberg scores of significant indicator taxa, within river types, showed no difference from the first to second survey period for both pH (R) and fertility (N). In the lowland cluster indicator species from the second survey period were associated with shadier conditions than those of the first survey period ($F_{1,34} = 5.803$, $p < 0.05$). At upland sites (Group 2) there was no significant difference in Ellenberg scores for light conditions between the indicator taxa of the first and second survey periods ($F_{1,29} = 0.004$, $p = 0.951$), in line with the lack of tree indicator taxa. Moisture (F) was also not significantly different between the survey periods in lowland ($F_{1,34} = 1.474$, $p = 0.233$) and upland sites ($F_{1,29} = 0.529$, $p = 0.473$). There was however, increased occurrence and abundance of some strongly hydrophilic species such as *S. erectum* in the second survey period in the lowland sites.

2.5 Discussion

Directional change in vegetation attributes over decadal time scales, as observed over an almost 20 year period in this study, is likely correlated with underlying changes in key environmental drivers. Overall, our study highlights that native plant diversity of river margins has decreased over time and native community composition has changed, especially in the lowlands. We also observed changes in shade tolerance and the relative proportion of native dominant and subordinate plant species. Candidate drivers for these changes include increased abundance of IAP species, shifts in river flow regime, with reduced grazing and increased fine sediment inputs linked to agricultural and river management practices.

2.5.1 Invasive alien plant distribution

IAP species were found across a greater proportion of sites in the second survey period. *Impatiens glandulifera* was the most frequent of these, consistent with Seager et al. (2012) who reported little change in the distribution of *H. mantegazzianum* or *F. japonica* on UK rivers between 1996 and 2008, whilst *I. glandulifera* became more widespread and abundant. Altitude or its correlates is a major determinant of colonisation success in plants (Nucci *et al.* 2012). We found that regardless of survey period, IAPs had a higher probability of being found along lowland (< 200m altitude) river sites, which can also be reflective of hydrochory. This may be due in part to climatic factors, such as incidence of frost, which is known to restrict germination and establishment of our target IAPs (Funkenberg *et al.* 2012). Disturbance regime can also vary along attitudinal gradients, with lowland rivers typically being more severely modified (Seager *et al.* 2012). This reduces ecological resilience, potentially favouring colonisation by weedy, ruderal species such as IAPs (Richardson *et al.* 2007).

At similar high flood frequencies there was a greater probability of IAP occurrence in the second survey period than the first. Since flooding favours spread of IAPs along rivers (Truscott *et al.* 2006), an increased frequency of high flows has the potential to intensify this effect. Direct effects of high flows include reduced cover of dominant species, and increased species turnover, as well as facilitating establishment of species through reduced competition (Nilsson & Svedmark 2002). Garssen *et al.* (2015), however, showed that increased duration of flooding did not reduce riparian plant biomass, as species tolerant of flooding may already be adapted to frequent inundation. The potential for IAPs to maintain abundance after flood-enhanced colonisation therefore represents an additional pressure upon riparian communities.

2.5.2 Changes in native plant diversity

Our study shows that as IAP cover increases over time, native species diversity is negatively affected at a landscape scale in riparian habitats. There has been much debate regarding the impact of IAPs on native vegetation (Thomas & Palmer 2015). General spatial scale trends reveal stronger negative effects of IAPs on species richness at progressively smaller spatial scales (Powell *et al*. 2011). Maskell et al. (2006) does provide evidence of negative landscape scale effects of IAP cover on native diversity, but this effect was observed across nested plots varying in size within a 1km sample area. However, in our study overall diversity of native riparian vegetation was lower in the second survey period regardless of whether a site was invaded, suggesting that IAPs were not a general causal factor in this change, observed at a coarse 500m spatial scale.

A decline in native diversity in the second survey period was also associated with a longer growing season undisturbed by peak flows. Diversity peaked at ~97 low flow days, suggesting that low flow periods of intermediate length favour colonisation and establishment, but over prolonged periods diversity declined, perhaps because such conditions favour expansion of dominant plant species (either native or invasive), thus increasing competitive exclusion. During the 1990s, areas of southern and eastern Britain in particular, experienced recurrent droughts (Blenkinsop & Fowler 2007). The summer of 1995 experienced the lowest rainfall in England and Wales since recording began, with low flows persisting until 1997 in some areas (Morecroft *et al.* 2002). This would have accentuated low flows within the second survey period and may have subsequently enhanced the sensitivity of vegetation to growing season length. Morecroft et al. (2002) noted that most tree and shrub seedling numbers increased across terrestrial sites in Britain during this drought suggesting that it may have also contributed to the increases in *Salix* cover that we observed. However, it is unclear from our data whether vegetation changes are a short term response to extreme droughts from which vegetation may recover quickly (Holmes 1999), or reflect the general decline in heavy rainfall during the summer that has been ongoing in the UK since the 1960s (Maraun, Osborn & Gillett 2008).

2.5.3 Subordinate and dominant native plant cover

Lowland rivers supported less native plant diversity in the second survey period. Lowland rivers were also associated with less native subordinate species cover overall, with the loss of native subordinate species cover being greater in the second survey period with decreasing site altitude. In contrast, native dominant plants were positively associated with lowland sites, most likely favoured by a combination of higher fertility, finer sediments and lower variation in flows (Tickner 2001). Changes in flow regime had contrasting effects on native subordinate and dominant species cover. Native dominant species cover was less affected by flood frequency, and benefitted more from an increase in duration of low flows than native subordinate species, consistent with the reduced native species diversity observed at lowland sites. Bunn & Arthington (2002) highlight multiple studies linking increased growth of river plants with reduced flow variability and artificially stabilised flow regimes, with dominant species likely to be the main beneficiaries.

There is marked interannual variability in UK rainfall but in recent decades the frequency of high intensity rainfall events has increased, particularly in the autumn and winter (Werritty 2002; Maraun, Osborn & Gillett 2008). Resulting surface runoff is associated with increased high flow events. Native subordinate species cover was most influenced by flood frequency (Truscott *et al.* 2006). This association showed opposite trends in the first and second survey periods. Increasing flood frequency was initially associated with greater native subordinate species cover, after which cover declined in the second survey period. Initially an increase in flood events might have led to increased dispersal and establishment opportunities. However, reduced resilience of vegetation over decades of increasingly intense fluvial disturbance might selectively favour dispersal and recruitment of competitive species with high seed output (e.g. IAPs such as *I. glandulifera*), or that spread via vegetative fragments (many native dominant species), excluding species susceptible to changes in fluvial disturbance or associated processes (Leishman & Gallagher 2015).

2.5.4 Changes in native species composition

Turnover in native vegetation was influenced to a greater extent by environmental and topographical features, as opposed to IAPs. Sites along lowland rivers became more dissimilar over time than those on upland rivers. An increased number of consecutive low flow days were also associated with greater turnover of the riparian vegetation. This reflects reduced native plant diversity and increased native dominant species cover observed at lowland sites, after extended low flow periods.

Sites further east showed less species turnover, retaining similar native riparian communities over time. This is surprising as the east of Britain is generally associated with more intensive agricultural land use, consistent with increased total oxidised nitrogen and alkalinity at survey sites, as well as generally being more prone to summer droughts. Since Britain has a strong historical agricultural legacy (Withers & Lord 2002), replacement by species adapted to higher fertility or agricultural disturbance may have already taken place prior to our surveys, causing these sites to retain a similar composition due to prevailing constraints.

Species-specific changes in the vegetation between survey periods highlight a switch at lowland river sites from small ruderal herbs and grasses or unpalatable species often associated with livestock-disturbed margins and inundation zones (Rodwell 2000) to *Salix* spp. and tall-herbs, including the IAPs *I. glandulifera* and *F. japonica,* and moisture-affiliated, *S. erectum*, plus their understory shade-tolerant associates. Increased cover of IAPs is often associated with lower light due to their taller stature and fast growth (Maskell *et al.* 2006). Seager et al (2012) found a marginal increase in extensive (> 33% of 500 m river length) tree shading of river channels in Britain, using River Habitat Survey data. Trees such as *Salix* spp. are an important feature of lowland rivers as this species is an ecosystem engineers (as well as *S. erectum*), providing habitat complexity and temperature regulation (Gurnell *et al.* 2005). However, increased tree cover might also favour moderately shade-tolerant IAPs, such as *I. glandulifera* (Beerling & Perrins 1993), as well as maintaining canopy gaps and providing a focus for fine sediment deposition, both of which will favour further IAP recruitment (Pattison, Vallejo-Marin & Willby (Ch3)). *Impatiens glandulifera* and *F. japonica* were also indicative of upland sites in the second survey period. Other changes in upland riparian vegetation did not show clear environmental trends with regards to Ellenberg indices. Upland rivers may have been too small or already shaded, thereby reducing sensitivity to change in tree cover. Some indicator species are, however, suggestive of increased water level range (e.g. bryophytes) coupled with greater sediment transport and fine sediment input (*Persicaria hydropiper*, *Sagina procumbens*, *Rorippa sylvestris*) consistent with increased runoff and flow variability.

Land-use changes offer a complementary alternative explanation for changes between the two survey periods, particularly in lowland catchments. The period between 1991 and 2004 saw a ~10% decline in Britain in total cattle numbers (Defra 2015). Since 1986 agri-environment schemes have also subsidised farmers to reduce bankside grazing by stock (Kirkham *et al.* 2006), partly to enhance the effectiveness of riparian buffer zones in lowland catchments, while the fencing of stream margins has been widely adopted in fisheries management (SEPA 2009). Since riparian areas are favourable for cattle grazing due to water access and palatable vegetation (Batchelor *et al.* 2015) these changes are likely to have reduced grazing pressure on riparian habitats. Decreases in both the density and height of woody plants have been documented with grazing activity (Batchelor *et al.* 2015). González et al. (2015) highlighted studies showing positive responses of *Salix* and *Populus* tree species following exclusion of cattle grazing. Previous studies have also shown that excluding cattle from riparian zones can lead to a fourfold increase in rush and willow species, as well as an increase in hydrophytic plant species previously suppressed by grazing (Hough-Snee *et al.* 2013; Batchelor *et al.* 2015). The increases we observed in *Sparganium erectum*, a species that is often targeted by livestock (Willby pers. obs.), and woody *Salix* spp. therefore seem likely to be related, at least in part, to changes in grazing pressure. Alongside changes in livestock management there was a pronounced switch from spring to winter cultivated cereals between survey periods (Barr *et al.*, 1993). Cultivated land is a major source of fine sediment input to rivers (Collins & Walling 2007) and this change in practice, coupled with increased intensity of winter rainfall, is likely to have exacerbated fine sediment inputs. Deposition of fertile fine sediment on river banks creates gaps that are conducive to growth of IAPs such as *I. glandulifera,* as well as some native dominant species (Pattison, Vallejo-Marin & Willby (Ch3)).

2.5.5 Conclusion

The above observations revealed that large, spatiotemporal scale changes in flow regime have increased opportunities for establishment of IAPs and that these IAP species have reduced native diversity along riparian zones. However, environmental factors played a definitive role in the changes seen in riparian vegetation over the last 20 years. IAPs themselves were a prominent feature of changing riparian zones, benefitting from changes in flow regime on lowland rivers, probably reinforced by changes in agricultural practices that reduce bankside herbivory or trampling but increase fine sediment inputs. IAPs across Britain may have therefore benefitted from climatic and anthropogenic changes, with the potential to outcompete native species at a landscape level once established and then promoted further by local conditions. Identifying areas most susceptible to effects of IAPs is important for management and restoration efforts globally (Strayer 2010). Climate change scenarios suggest that summer droughts and wetter winters will become more frequent across NW Europe, with potentially major ecological consequences for riparian habitats (Morecroft *et al.* 2002). The response of species to future climate change has become an important theme of ecological research (Parmesan & Yohe 2003). Piecing together trends from the recent past may enable us to forecast future ecological changes more accurately. However, it is crucial to account for interactive effects between co-occurring environmental changes in order to better predict plant community responses.

Chapter 3. Comparative effects of invasion, competition and abiotic factors on the riparian vegetation of lowland rivers.

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3.1 Abstract

The consequences for native flora of invasion by invasive alien plants (IAPs) and the relative effects of invasive alien and native dominant plant species are the subjects of ongoing debate. Riparian habitats are especially vulnerable to invasion by IAPs, being highly disturbed environments exposed to frequent input of water-borne propagules. An intensive field-based study across 20 Scottish rivers varying in environmental conditions and level of invasion by three key IAPs (principally *Impatiens glandulifera* but also *Fallopia japonica* and *Heracleum mantegazzianum*) was used to identify if invasive alien and native dominant species have contrasting responses to environmental variables and the consequences for native vegetation. Greater cover of IAPs was associated with drier conditions, along low energy rivers with tree-lined banks, while dominant natives were favoured by high soil moisture, fertility and a steeper channel gradient. IAPs and dominant native species both reduced subordinate species cover and richness to a similar extent. Sites invaded by *I. glandulifera* were distinguished by a small suite of other IAPs and native ruderal species, while uninvaded sites had a larger characteristic flora suggesting division into potentially ‘invasion prone’ and ‘invasion-resistant’ states supported by underlying differences in growing conditions. Richness at different spatial scales was a poor indicator of invasion status. Our results reveal how invasive alien and dominant native plant species respond differently to local conditions both temporally (through the growing season) and spatially (across river banks). This finding undermines the validity of using uninvaded sites as a proxy for pre-invasion conditions but also raises the prospect of limiting invasions indirectly via river management and restoration. Eradication of IAPs within riparian zones may be unachievable, but an integrated view of the combined influence of abiotic and biotic factors on both IAP and dominant native species at an appropriate spatial scale will contribute to more effective management of riparian plant invasions.

3.2 Introduction

Invasive alien species are a major threat to biodiversity, exacerbated by increasing global travel and trade (Vilà *et al.* 2011), hybridisation (Vallejo-Marin & Hiscock 2016) and climate change (Bellard *et al.* 2013). Freshwaters are some of the most vulnerable ecosystems to invasion by invasive alien plants (IAPs) (Strayer 2010). Riparian zones are heterogeneous, biodiverse and of economic, cultural and agricultural significance yet their transitional nature, connectedness and history of fluvial disturbance makes them particularly prone to invasion (Tockner & Stanford 2002). An increase in disturbance events, such as high flows, can offer opportunities for dispersal and colonisation by both IAPs and native species (Richardson *et al.* 2007). However, environmental stresses will potentially regulate the relative success of IAPs or dominant natives and hence their effects on native vegetation, by, for example, affecting their ability to form extensive monodominant stands.

IAPs such as *Impatiens glandulifera* (Himalayan balsam), are able to grow faster and taller than neighbouring plants (Hulme & Bremner 2005; Bottollier-Curtet *et al.* 2013). This can lead to increased competition for space and light, excluding shade intolerant species (Hulme & Bremner 2005). The most serious invaders of riparian zones in Europe include *I. glandulifera* (Balsaminaceae), *Heracleum mantegazzianum*

(Apiaceae) and *Fallopia japonica* (Polygonaceae) (DAISIE 2014). Of these three IAPs, *I. glandulifera* is the most frequently occurring along river banks in lowland Britain (Seager *et al.* 2012; Pattison *et al.* 2017). Growing up to 4 m, *I. glandulifera* is considered the tallest annual in Europe. However, the few studies of its impact on native plant communities reveal contrast findings (Hejda & Pyšek 2006; Hulme & Bremner 2005) suggesting that effects on native species are context-dependent and species-specific (Hejda *et al.* 2009). Consequently there is still much debate and uncertainty regarding the effect of even the most widespread IAPs on native vegetation (Thomas & Palmer 2015).

Detecting an IAP's influence on native communities can be extremely challenging (Hulme 2003). For instance, impacts can be scale-specific with some landscape scale studies often describing small negative effects (Powell et al. 2011), whilst others reveal positive associations between native and invasive alien species richness (Maskell *et al.* 2006; Thomas & Palmer 2015). Studies at smaller spatial scales have found stronger evidence for declines in native species richness linked to the presence of IAPs, particularly when comparing invaded and uninvaded plots of up to 100m2 (e.g. Aguilera et al. 2009). Although many impact studies use species richness to represent native diversity, there is also a need to focus on community level changes in native species (Powell *et al.* 2011). Species richness is a relatively conservative indicator and community changes caused by increasing cover of IAPs are arguably of greater consequence for ecosystem function. Positive associations between invasive alien and native species richness, may be attributed to increased habitat and resource availability in disturbed environments. Flood events can result in sediment deposition and associated nutrient delivery, creating gaps in established vegetation (Richardson *et al.* 2007). Riparian vegetation is sensitive to hydrologic alteration, particularly to changes in minimum and maximum flows (Naiman & Dechamps 1997), with river banks enduring a gradient of disturbance, both spatially and temporally. During spring, riparian zones commonly experience inundation, potentially affecting germination success and growth of established vegetation while summer droughts may lead to prolonged low flows. At higher bank elevations interspecific-competition influences community structure more than hydrogeomorphic factors, as stable conditions allow invasive alien and dominant native plants to attain greater abundance, culminating in the formation of monodominant stands (Richardson *et al.* 2007).

Reduced interspecific competition following disturbance is considered one of the most important processes determining the success of plant invasions (Vilà & Weiner 2004) but once IAPs are established, competitive ability is a primary mechanism in their dominance at a site. However, whether IAPs truly differ from native dominant plant species in their ability to exclude other (subordinate) native plant species is still disputed (Daehler 2003), since both share traits of disturbance tolerance, fast growth and the potential to form monodominant stands (Tickner *et al.* 2001). Evidence from pair-wise and single species experimental studies supports the general view that invaders are better competitors than native dominant species (Vilà & Weiner 2004). Surprisingly, studies comparing competitive abilities of alien and native plants have mainly focused on native species that are intrinsically sensitive to competition (Bottollier-Curtet et al. 2013). Thus, most previous studies have compared the competitive abilities of dominant (invasive) vs subordinate (species having less ability to form dominant monocultures) (native) species, instead of native vs alien species of similar competitive ability (Bottollier-Curtet *et al.* 2013). However, Van Kleunen *et al.* (2010) showed that, when compared to native species which become invasive elsewhere, IAPs do not have distinguishing traits that increase competitive ability, suggesting that they are not intrinsically better competitors than native dominant species. Evidence that IAPs are better competitors than native dominant species remains scarce (Bottollier-Curtet *et al*. 2013) indicating a need for field-based measurement of the effect sizes of both native dominant species and IAPs on native communities (Vilà & Weiner 2004).

Assessing the structure of riparian vegetation across a gradient of disturbance, and how the impacts of IAPs vary with the intensity of environmental stressors, is important for understanding the drivers and consequences of invasion (Kuebbing 2014). More explicit research on how IAP interactions change across stress and productivity gradients will improve our understanding of how both native and alien plants will respond to future environmental changes (Kuebbing 2014). If abundance of IAPs is the main driving force for a decline in native species (Simberloff *et al.* 2013), identifying the environmental factors that most affect IAP abundance will be of particular interest to those attempting to manage or restore riparian habitats.

In this study we use field data from botanical surveys of rivers in central Scotland, to assess how the abundance of three key IAPs (*I. glandulifera, F. japonica* and *H.*

mantegazzianum) associated with negative impacts on native riparian vegetation communities (Hejda *et al.* 2009; Pyšek *et al.* 2012), differs spatially and temporally relative to native dominant species, as well as how the variation in abundance of IAP and native dominant species impacts native riparian vegetation. Specifically we ask (i) what are the environmental drivers of local scale (100m sites along rivers) variation in the abundance of IAPs and native dominant plants on rivers; (ii) what is the relative impact of IAP or dominant native species cover on the richness and cover of subordinate native species and how does this change seasonally and with bank elevation; and (iii) how much of the difference in native riparian vegetation between paired invaded and uninvaded sites is attributable to IAPs? We hypothesize that invasion will have greater effects on native species at higher bank elevations in summer, since there is less fluvial disturbance and IAPs are therefore more likely to achieve monospecific stands.

3.3 Materials and methods

3.3.1 Vegetation data

Vegetation surveys were conducted along 20 lowland rivers in central Scotland, UK (Fig. 1, appendix Table 2). Rivers ranged between 10-75 m in channel width and 5-40 m in elevation. *I. glandulifera* is the most frequently occurring IAP across rivers in Scotland and commonly forms continuous monocultures along lowland rivers (Seager et al, 2012; Pattison, Minderman & Willby (Ch2)) and initial site searches revealed the widespread extent of *I. glandulifera* relative to the other IAPs. Thus sites were selected that contained at least this species and were concentrated near the most downstream accessible point on each river. This meant that all study sites were adjacent to agricultural land or in urban/suburban areas. Sites varied in their level of invasion (quantified by % cover of IAPs) thus affording a gradient of potential invasion impact. Vegetation surveys were conducted over two week periods during May 2014 (spring) and August 2014 (summer), in order to compare effects on plant communities between seasons. Surveys began at a randomly selected point along a 100 m reach. At the start of each surveyed reach, a transect was established perpendicular to the channel and three plots of 1 m^2 plots were positioned equidistantly between the water's edge (Q1), mid-bank height (Q2) and the bank top (Q3). 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 420 plots sampled across all rivers in each field season. In each plot, all species were identified and abundance was quantified using the five point DAFOR 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, allowing for different canopy layers. Abundance scores were then converted to percentage cover for analyses (1= 1%, 2=6%, 3=18%, 4=38%, 5= 75%). In summer additional uninvaded sites were surveyed along nine of the chosen rivers. These sites exhibited high cover of native dominant plant species. This enabled assessment of a gradient of percentage cover in both invasive and native dominant sites. On the remaining 11 rivers IAPs were extensive and no uninvaded sites were located. Due to the pervasiveness of IAPs along rivers in central Scotland, all 'uninvaded' sites were found on closer examination to have a low level of invasion (1-10% cover) but this was considered insufficient to alter stand composition, even at fine spatial scales (Hulme & Bremner 2005). Moreover, the presence of invasive species within these sites demonstrates that these areas were potentially invadable. Uninvaded sites were situated within 200 m of the paired invaded site to ensure that overall habitat conditions in uninvaded and invaded plots were as similar as possible.

Alien species were defined in line with Preston *et al*. (2002) as those that colonised Britain with the aid of humans. We focused on the IAP species *H. mantegazzianum, I. glandulifera* and *F. japonica.* Other IAPs recorded at study sites include *Claytonia sibirica, Fallopia sachalinensis* and *Mimulus guttatus.* Percentage cover of all invasive alien species were combined and used to assess the effect of invasion on aspects of the native vegetation. Species other than *I. glandulifera* were too infrequent to assess effects of specific IAPs. In order to compare the effect of native dominant species on the associated native vegetation, natives were split into subordinate and dominant categories. Native dominant 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 mono-dominant stands alongside rivers in Britain. These species comprised *Aegopodium podagraria, Epilobium hirsutum, Fillipendula ulmaria, Glyceria maxima, Petasites hybridus, Phalaris arundinacea, Phragmites australis, Rubus fruticosus, Symphytum officinale* and *Urtica dioca.* The percentage cover of native dominant and subordinate species was determined by summing the individual % cover of the species belonging to these groups.

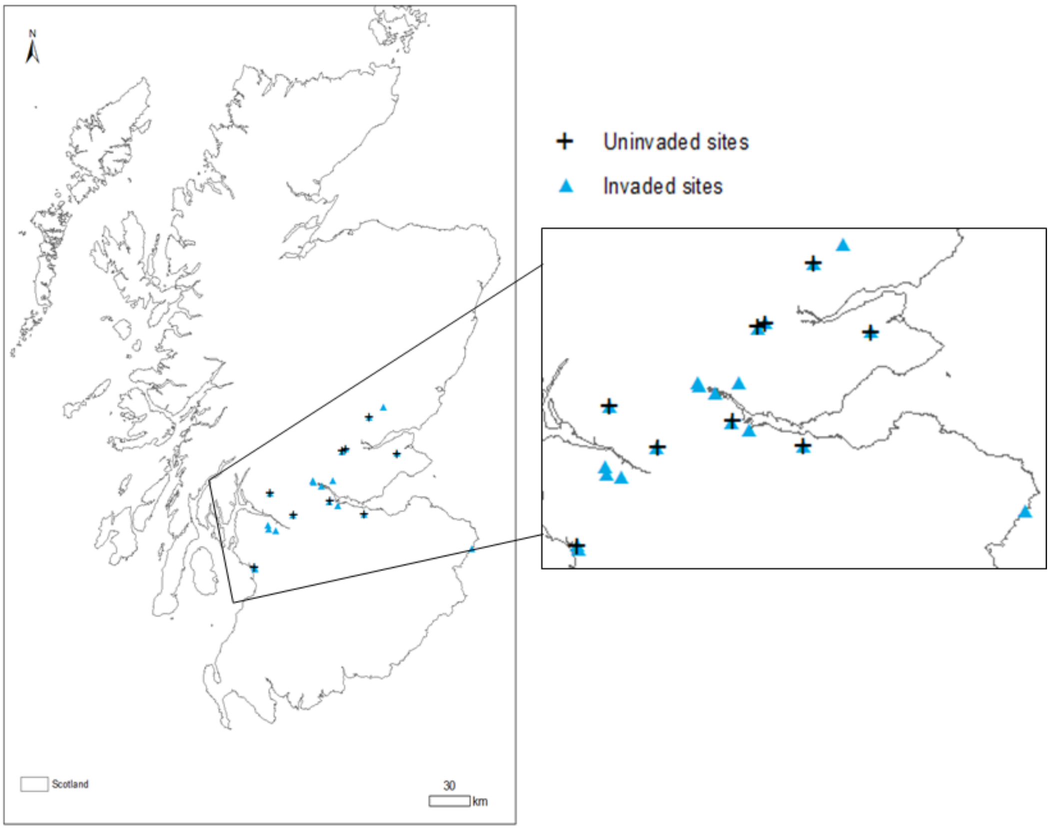

Fig 1. Location of survey sites across the central belt of Scotland included in this study (scale and locations approximate). ▲ indicate sites invaded by invasive alien plant species, predominantly *Impatiens glandulifera*. + indicate uninvaded sites.

3.3.2 Environmental predictors

Soil moisture was measured over the two week survey periods using a hand held meter (SM150, Delta-T Devices Ltd, Cambridge, UK) at three points within each plot and 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 determine bulk density and organic matter content by loss on ignition following the methods of Wang *et al*. (2011). Tree density was inferred from the inverse of the proximity of a plot to the nearest mature tree (> 4 m high) and average slope of the upstream channel (mkm^{-1}) was calculated from the drop in elevation over the distance from the site to the river’s source.

Hydrological regime has been widely recognized as an important factor affecting riparian biota (Clausen & Biggs 1997), with flood frequency and flow variability having been shown to affect the biomass and species richness of macrophytes (Riis *et al.* 2008). To assess the effect of hydrology on riparian vegetation, daily mean flow data were obtained from the Centre for Ecology and Hydrology's National River Flow Archive, for the most downstream gauging station on each surveyed river. Using data from 1990 to 2012, the percentage increase in mean flow over the last 22 years was calculated, to characterise the general long term trend in flow across each of the 20 rivers. The rivers studied showed a gradient of increase in mean annual flow over the last 22 years, ranging from a 4-28% (Appendix Table 3). The coefficient of variation was used to express variability in flow in each river using daily mean flow data. 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 monthly or bimonthly sample data for alkalinity as CaCO3 (mg/L), total oxidised nitrogen (TON) as N (mg/L), total suspended solids (mg/L), soluble reactive phosphorus as P (mg/L) and ammonia as N (mg/L).

3.3.3. Data analyses

A general linear modelling approach was used with different error structures to model response variables within the global models: (1) invasive alien, native dominant and subordinate plant cover (%, squared root transformed, linear mixed effects models (LMM)) and (2) native subordinate species richness (generalized linear mixed effects model (GLMM) with a Poisson error structure).To prevent over-fitting predictor variables were reduced to those with the largest effect size within each family of predictor variables. For example, there were five candidate flow variables describing flow regime. These five variables were modelled as fixed effects against the response and the predictor with the largest effect size was retained for use in the global model.

Fixed effects for invasive alien and native dominant species cover were soil moisture (plot level data), tree cover (plot level data), channel gradient (site level data), coefficient of variation in flow (site level data), mean site water column soluble reactive phosphorus and suspended solids concentrations (site level data). Predictor variables invasive alien and native dominant species cover (plot level data) were used to model native subordinate species richness and cover. Two-way interactions between bank position (Q1, Q2, Q3) * predictor variables and season (spring, summer) * predictor variables were chosen a priori based on biological knowledge of the sites and environment (Appendix Table 4). Site nested within river was included as a random intercept to account for the nested structure of the data. All predictors were standardised to one standard deviation prior to statistical analyses, in order to assess relative effect sizes of each predictor directly (Schielzeth 2010). Multicollinearity among predictor variables was checked before use in multiple regression analyses, retaining only those variables which were not highly correlated (r = <0.60).

Models were ranked using the information theoretic approach (Burnham & Anderson 2002) to select the best combination of effects from the global model. Models were compared using corrected Akaike Information Criterion (AICc), with all possible combinations of predictors identified using the dredge function in MuMIn (Barton 2016). The best fitting models were evaluated based on their ΔAICc, with values < 4 considered to be equally parsimonious (Burnham & Anderson 2002). Akaike weights were calculated for each explanatory variable, in order to compare the relative importance of each variable in the top set (ΔAICc < 4) of models. Model coefficients were averaged across this top set (full averaging) and the resulting averaged coefficients were used for predictions and 95% confidence intervals. Confidence intervals were calculated as 1.96* the standard error of the model predictions. This method was possible as the most important coefficients in explaining variation in the response variable differed little between those models within the top set. To account for the variation explained solely by the fixed effects, as well as the variation explained by both the fixed and random effects, both the marginal and conditional R^2 values are reported for each model, respectively (Nakagawa & Schielzeth 2013).

Redundancy Analysis (RDA) was used to investigate how invasion and environmental variables influence riparian vegetation composition (McCune & Grace 2002). An indirect gradient approach, Detrended Correspondence Analysis (DCA), was used to select between linear or unimodal approximation. As the length of the first axis was small (spring =2.05, summer =2.09), we selected a method based on linear response. The RDA was performed for spring and summer separately using transformed species cover data (Hellinger transformation). All invasive species were excluded from the analyses. Fixed effects for all models were bank position (plot); soil moisture; channel gradient; coefficient of variation for flow regime; organic matter content; mean site soluble reactive phosphorus and suspended solids concentrations. To account for variation in species composition, predictors were selected by forward selection. The significance of the model was tested using a Monte Carlo permutation test (999 permutations). Eigenvalues were used to assess the effectiveness of each ordination axis in explaining the vegetation-environment relationship (McCune & Grace 2002).

Species characteristic of invaded and uninvaded sites were identified using indicator species analysis (IndVal; Dufrene & Legendre 1997) applied to percentage cover data. *I. glandulifera* was used as the specification for invaded sites as this species was most prolific. Therefore *I. glandulifera* was removed from this analysis. IndVal assesses the specificity and fidelity of species for different groups, with the index ranging from 0%, denoting no presence in a survey group, to 100%, indicating that a species occurs in only one group of samples and is present in all samples within that group. The significance of these values was tested using a Monte Carlo randomisation procedure (Dufrene & Legendre 1997).

All statistical analyses and graphics were produced using R Studio version R 3.2.2 (R Development Core Team 2015), with the additional packages; vegan (Oksanen 2015); labdsv (Roberts 2007), lme4 (Bates *et al.* 2015) and MuMIn (Barton 2016).

3.4 Results

3.4.1 Environmental effects on IAP and dominant native plants

Overall the effect of environmental variables on both IAP and dominant native cover showed contrasting patterns. Seasonally, soil moisture had the greatest effect on the cover of IAPs (Table 1). This negative effect was greatest in summer (Fig. 2a) and was similar at different bank elevations. In contrast, dominant native plant cover was positively associated with soil moisture regardless of season (Fig 2b) or bank position.

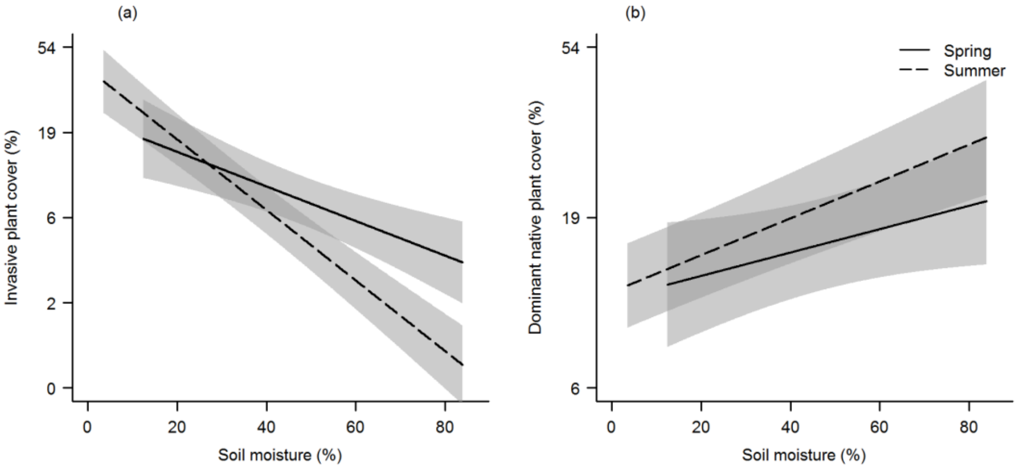

Fig 2. Full model averaged predicted values (lines ± 95% CI) from the LMM analysis of percentage a) invasive alien plant cover and b) native dominant plant species cover as a response to the interaction effect between percentage soil moisture and season (spring and summer).

Table 1. Full model-averaged parameter estimates for LMER response invasive alien plant percentage cover, dominant native plant percentage cover, subordinate native plant percentage cover and subordinate native plant richness analyses ±95% confidence intervals. Confidence intervals were calculated using full model averaged standard errors. The estimates for season are relative to first season period (spring) and estimates for bank position two and three are relative to bank position one. All explanatory variables were standardised to 1SD prior to analyses. Relative variable importance (RVI) is also given.

	Invasive plant cover				Dominant native plant cover				Subordinate native plant cover				Subordinate native sp richness			
Predictor	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI	Estimate	−95% CI	+95% CI	RVI
Intercept	2.34	2.05	2.62		2.80	2.54	3.07		5.91	5.31	6.51		1.80	1.71	1.90	
Soil moisture	-0.37	-0.55	-0.18	1	0.12	0.00	0.25	1								
Channel slope	0.11	-0.22	0.45	1	0.02	-0.30	0.35	1								
Tree density	0.10	-0.09	0.28	1	-0.18	-0.33	-0.03	1								
Flow variability	0.10	-0.21	0.42	0.74	0.12	-0.20	0.44	1								
Soluble reactive P	-0.43	-0.72	-0.14	1	0.12	-0.17	0.41	0.61								
Suspended solids	0.33	0.02	0.63	1	0.17	-0.13	0.47	1								
Dominant native plant cover									-1.30	-1.64	-0.96	1	-0.24	-0.31	-0.17	1
Invasive plant cover									-0.41	-0.79	-0.02	1	-0.08	-0.16	-0.01	1
Season	-0.30	-0.49	-0.12	1	0.21	0.05	0.36	1	1.05	0.74	1.37	1	-0.08	-0.14	-0.02	1
Bank position (Quadrat 2)	0.01	-0.19	0.20	1	-0.15	-0.31	0.02	1	1.04	0.68	1.40	1	-0.10	-0.17	-0.04	1
Bank position (Quadrat 3)	-0.36	-0.55	-0.16	1	-0.11	-0.27	0.06	1	1.58	1.22	1.94	1	-0.09	-0.15	-0.02	1
Soil moisture x season	-0.38	-0.58	-0.18	1	0.02	-0.09	0.13	0.3								
Soil moisture x quadrat 2	0.00	-0.09	0.09	0.22												
Soil moisture x quadrat 3	-0.02	-0.16	0.11	0.22												
Channel slope x quadrat 2	-0.50	-0.76	-0.24	1	0.27	0.07	0.48	1								
Channel slope x quadrat 3	-0.53	-0.78	-0.28	1	0.37	0.17	0.58	1								
Tree density x season	-0.21	-0.37	-0.05	1	-0.01	-0.08	0.06	0.23								
Tree density x quadrat 2	0.14	-0.06	0.34	1	0.12	-0.05	0.29	1								

Tree density x quadrat 3	0.38	0.18	0.57	1	0.36	0.19	0.53	1								
Flow variability x season					0.05	-0.10	0.19	0.45								
Flow variability x quadrat 2	0.11	-0.18	0.41	0.43	-0.32	-0.53	-0.12	1								
Flow variability x quadrat 3	0.09	-0.17	0.34	0.43	-0.41	-0.62	-0.21	1								
Soluble reactive P x season	0.24	0.06	0.42	1	-0.06	-0.23	0.11	0.39								
Suspended solids x season	-0.33	-0.51	-0.15	1	0.19	0.02	0.36	0.98								
Dominant native plant cover x season									-0.12	-0.47	0.22	0.50	-0.10	-0.16	-0.03	1
Dominant native plant cover x quadrat 2									0.07	-0.23	0.38	0.30	0.08	0.00	0.15	1
Dominant native plant cover x quadrat 3									0.08	-0.24	0.40	0.30	0.14	0.07	0.22	1
Invasive plant cover x season									-0.85	-1.20	-0.50	1	-0.15	-0.21	-0.08	1
Invasive plant cover x quadrat 2									-0.85	-1.22	-0.47	1	-0.02	-0.10	0.05	0.46
Invasive plant cover x quadrat 3									-0.87	-1.27	-0.47	1	-0.03	-0.13	0.06	0.46

IAP cover was positively associated with proximity to trees in spring (Fig. 3a), in contrast to dominant native cover, which showed a negative association in both spring and summer (Fig. 3b). Additional site effects included lower IAP cover further from the water's edge (quadrat 3) at sites with a steeper channel gradient. Dominant native plants showed the opposite pattern, increasing in cover from the water's edge at site with a steeper channel gradient (Table 1).

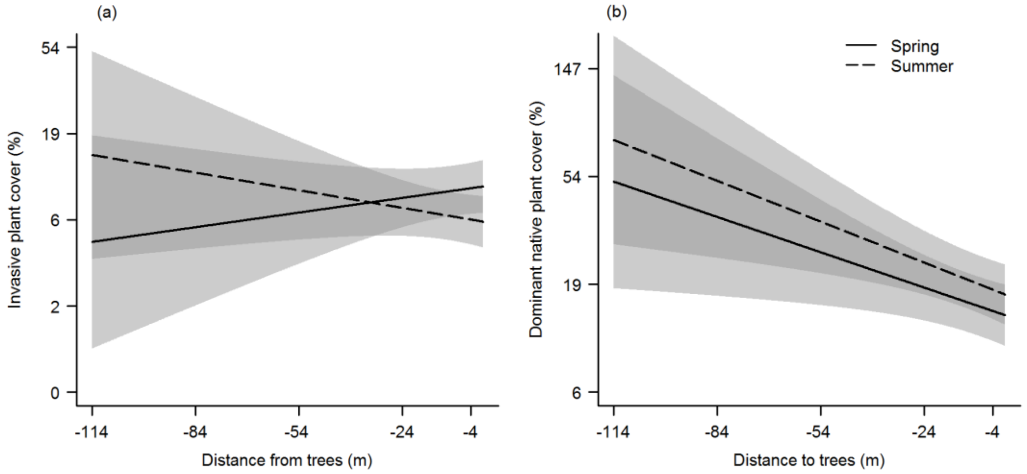

Fig 3. Full model averaged predicted values (lines ± 95% CI) from the LMM analysis of percentage a) invasive alien plant cover and b) native dominant plant species cover as a response to the interaction effect between the proximity of trees along the riparian bank and season (spring and summer).

3.4.2 Water quality effects on IAP and dominant native plants

In contrast to IAP cover (Fig. 4a), native dominant plant cover was positively associated with river water soluble reactive phosphorus concentrations in both spring and summer (Fig. 4b). IAP cover was positively associated with suspended solids in river water in spring (Fig. 4c), whereas there was a positive association between dominant native cover and suspended solids in both spring and summer (Fig. 4d).

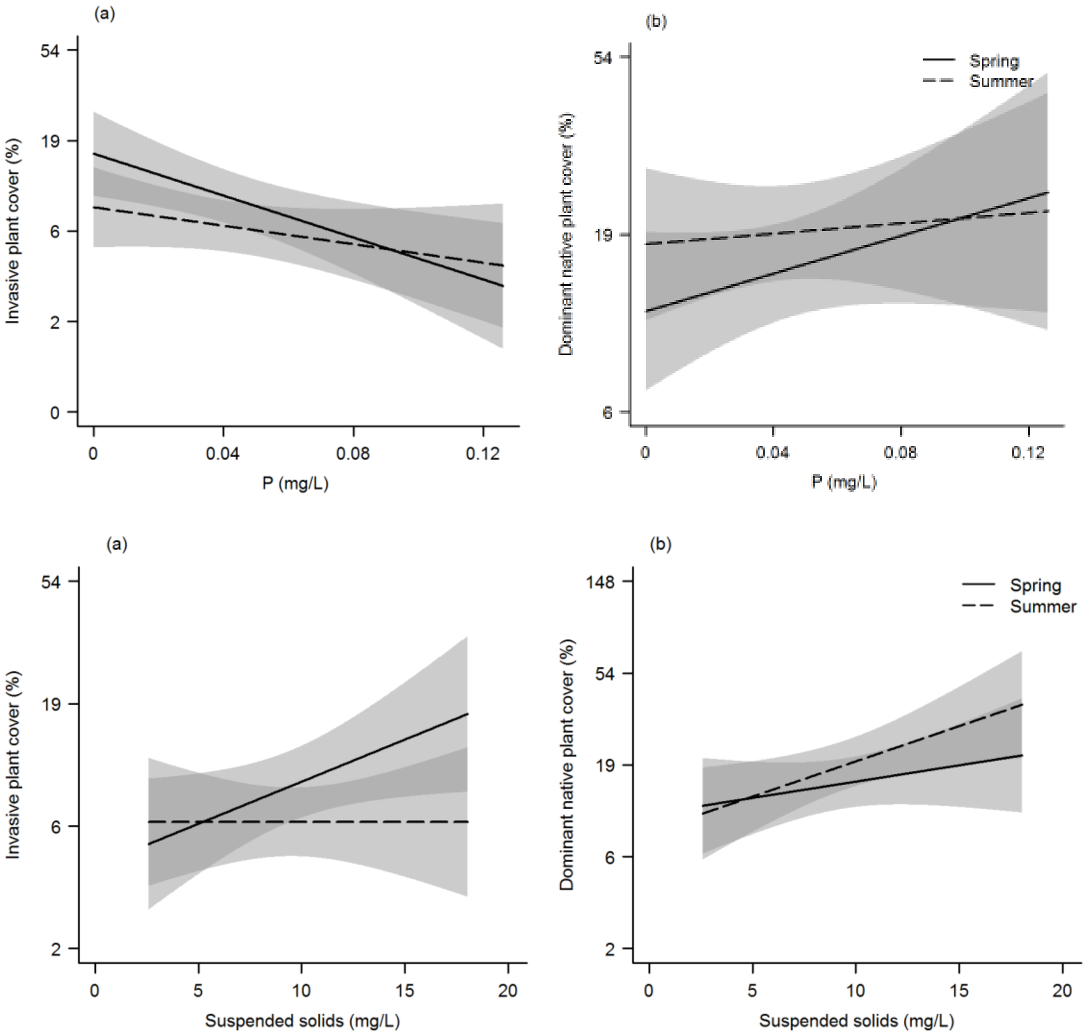

Fig 4. Full model averaged predicted values (lines ± 95% CI) from the LMM analysis of percentage invasive alien plant cover and native dominant plant species cover as a response to the interaction effect between soluble phosphorus concentrations (a,b) and suspended solids (c,d) in spring and summer (season).

3.4.3 Native subordinate species richness and cover

Native subordinate species cover and richness shared similar responses (Table 1) to dominant native and IAP cover, however the effect on subordinate native species richness was weak. Overall subordinate native cover and richness declined with increasing dominant native and IAP cover. There was a seasonal effect of IAP cover affecting subordinate native cover, with a greater negative effect in summer than spring (Fig. 5a). The negative effect of IAP cover also increased further from the water's edge (Table 1), whereas there was no difference in the effect of dominant native species cover across the riparian bank or seasonally (Fig. 5b).

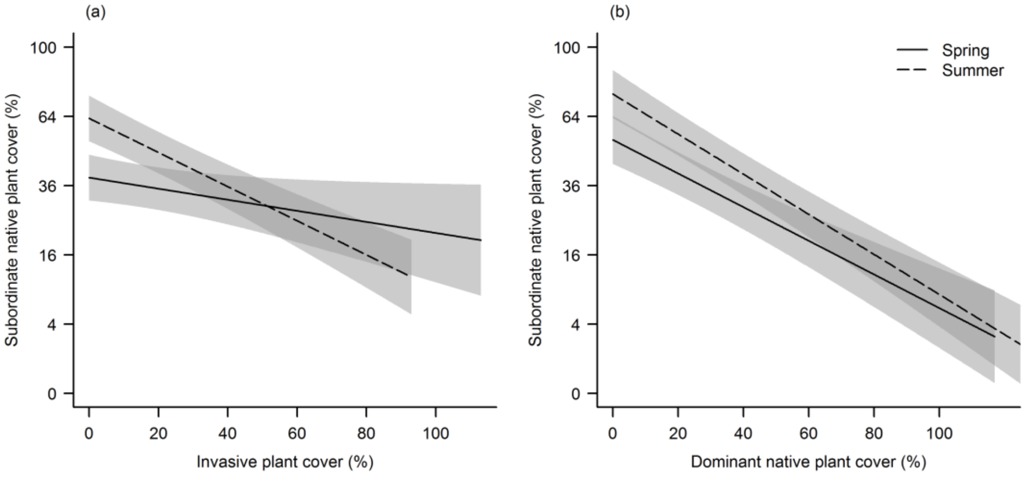

Figure 5. Full model averaged predicted values (lines ± 95% CI) from the LMM analysis of percentage subordinate native plant cover as a response to the interaction between a) invasive alien plant cover and b) native dominant plant species cover in spring and summer (season).

3.4.5 Community composition

Species richness at quadrat and site scale, and in terms of overall species pool at nine paired invaded and uninvaded sites is compared in Table 2. There were minimal differences in richness at all scales between invaded and uninvaded sites

Table 2. Species richness and associated standard errors across all sites, per site and per plot (quadrat) within a site, for both invaded and uninvaded sites. The number of indicator taxa are also presented.

	Mean per plot (n=189)	SE	Mean per site (n=9)	SE	Total species	Indicator taxa
Invaded	5	0.2	35	3	102	10
Uninvaded	6	0.2	36	2.6	110	29

Patterns in species composition were directly related to environmental variables. The RDAs performed on species cover data were significant for both spring (F-ratio = 8.71, P = 0.001) and summer (F-ratio = 10.64, P = 0.001). The variance (constrained inertia) explained by the RDA axes was 14.5% for spring and 12.4% for summer. All predictors were retained in the model with an adjusted R2 of 12.3% and 11.8% for spring and summer respectively. Environmental variables significantly explained variation in species composition in both spring (eigenvalues: axis 1 = 0.05, p = 0.001; axis 2 = 0.03, p = 0.001) and summer (eigenvalues: axis 1 = 0.04, p = 0.001; axis 2 = 0.02, p = 0.001).

The associated RDA biplot separated three groups of species according to bank position (Fig. 6). In spring, species associated with high soil moisture and a more variable flow regime included *P. arundinacea*, *Myosotis scorpioides* and *Rumex obtusifolius* closest to the water’s edge (Q1). Mid-bank (Q2) species included Stellaria media and *Poa trivialis*, whilst *A. podagraria* and was associated with drier areas at the top of the bank (Q3). *Phalaris arundinacea*, *M. scorpioides* and *Persicaria amphibia* were found closest to the water’s edge in summer (Fig. 6a). Species associated with areas of higher soil moisture, channel slope and which experienced greater variation in flow included the grasses *G. maxima*, *Arrhenatherum elatius* and *Holcus mollis*. Species associated with increased river water phosphorus included *P. hybridus* and *Galium aparine*. The most heavily invaded sites occurred, on average, at low soil moisture and closer to trees along the bank. (Fig. 6b).

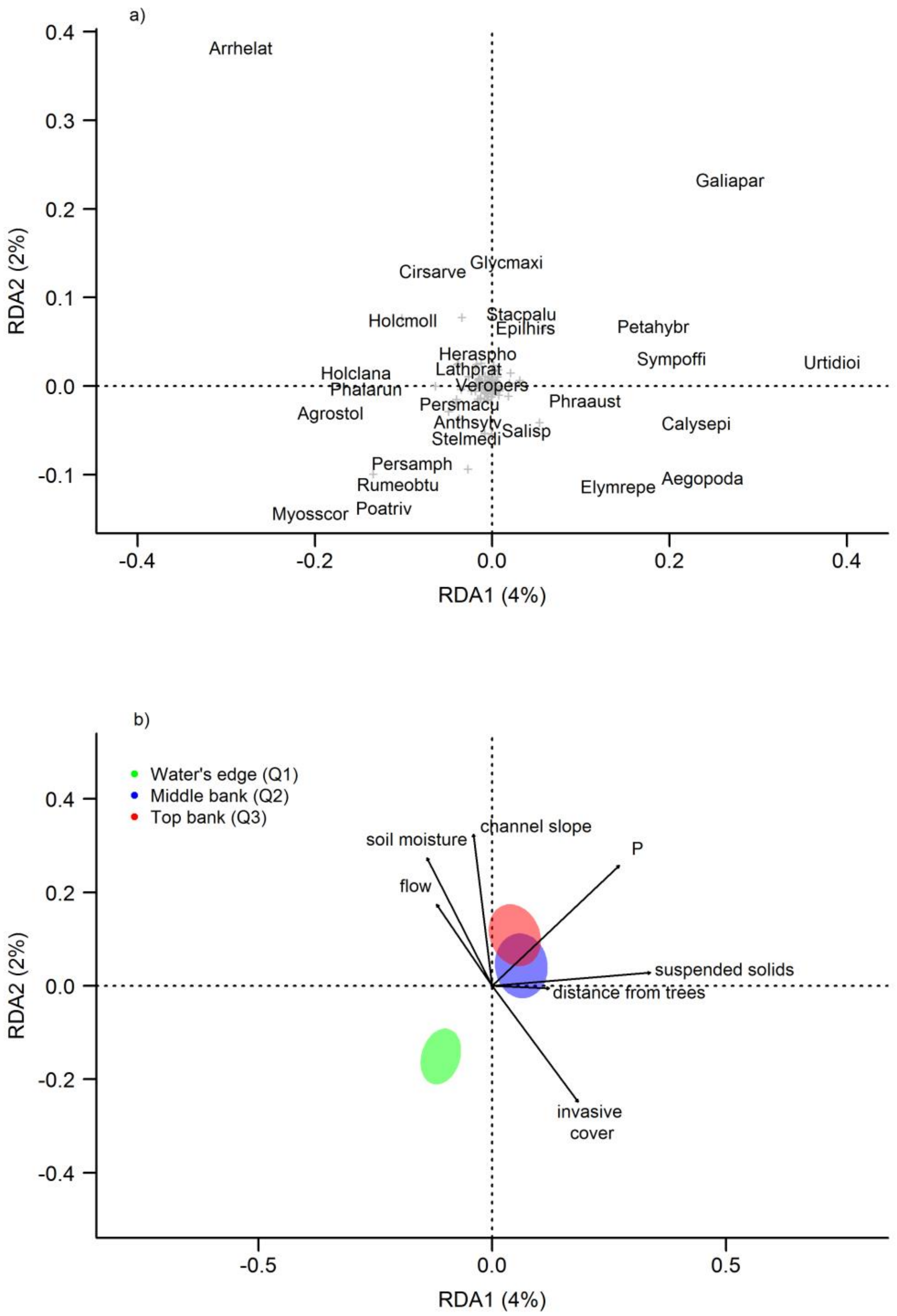

Fig 6. Redundancy analysis (RDA) of summer vegetation on all environmental variables. Constrained axes explain the variability in the data. A) The species' percentage cover estimates were used as importance values and are indicated with +. Abbreviations: Arrhelat= *Arrhenatherum elatius,* Cirsarve= *Cirsium arvense*, Holcmoll = *Holcus mollis*, Holclana= *Holcus lanatus*, Phalarun= *Phalaris arundinacea*, Agrostol= *Agrostis stolonifera*, Persamph=*Persicaria amphibia*, Rumeobt= *Rumex obtusifolius*, Poatriv= *Poa trivalis*, Myosscor= *Myosotis scorpioides*, Glycmaxi= *Glyceria maxima*, Stacpalu= *Stachys palustris*, Epilhirs= *Epilobium*

hirsutum, Heraspho= *Heracleum sphondylium, Lathprat = Lathyrus prantense,* Veropers= *Veronica hederifolia,* Persmacu= *Persicaria maculosa,* Anthsylv= *Anthriscus sylvestris,* Stelmedi= *Stellaria media,* Salisp= *Salix spp.*, Phraaust= *Phragmites australis*, Sympoffi= *Symphytum officinale*, Petahybr= *Petasites hybridus*, Calysepi= *Calystegia sepium*, Aegopoda= *Aegopodium podagraria*, Elymrepe= *Elymus repens*, Galiapar= *Galium aparine*, Urtidio= *Urtica dioica.* B) Environmental variables are indicated with arrows.

The IAPs *Fallopia japonica* and *H. mantegazzianum* were strong indicators of sites invaded by *I. glandulifera*, alongside two other alien species, *C. sibirica* and *M. guttatus* (Table 3). A few native ruderal species (including *Stellaria media* and *Rumex crispus*) were also indicative of invaded sites, plus willows, *Salix* spp. A larger pool of taxa (29 species) were significant indicators of the paired uninvaded sites including native dominant species (e.g. *U. dioica, P. arundinacea* and *P. hybridus)* and other grasses (e.g. *Arrhenatherum elatius*, *Poa trivalis* and *Holcus lanatus*). There was also a greater frequency of species associated with inundation zones (including *Agrostis stolonifera, Myosotis scorpioides* and *Persicaria amphibia),* as well as other taller ruderal, herbs (including *Stachys palustris* and *Chamerion angustifolium*).

Table 3**.** Significant indicator species for the nine invaded and uninvaded rivers sites. Observed indicator values (IV) and their significance are given. An asterisk indicates that species were very highly (***), highly (**) or significantly (*) associated with a particular type of site, based on Monte Carlo permutation tests. Invasive alien and native dominant plant species are shown in bold. Invasive alien plants are denoted by ▲.

Species	Observed IV	Species	Observed IV	Species	Observed IV	Species	Observed IV
Invaded		Uninvaded		Uninvaded		Uninvaded	
Stellaria.media ***	11.6	**Urtica dioica*****	56.7	*Holcus lanatus****	16.9	*Lathyrus pratensis****	10.2
*Rumex crispus****	8.8	*Galium aparine****	54.9	*Calystegia sepium**	17	*Galium cruciata****	9.8
Salix spp. ***	7.4	*Arrhenatherum elatius****	47	*Lolium perenne****	14.7	**Epilobium hirsutum***	9.7
*Alliaria petiolata****	7.1	*Cirsium arvense****	44	*Heracleum sphondylium****	14.4	*Stellaria graminea****	9.5
▲Claytonia sibirica***	6.9	**Phalaris arundinacea*****	35.3	*Stachys palustris****	14.2	*Chamerion angustifolium****	7.9
▲Mimulus guttatus**	6.7	*Symphytum officinale****	24.3	**Fillipendula ulmaria*****	12.2	*Valeriana officinalis****	6.9
*Phragmites Australis**	4.8	*Poa trivialis****	22.9	*Agrostis stolonifera***	11.7	**Rubus fruticosus*****	5.2
▲Heracleum mantegazzianum***	4.8	*Myosotis scorpioides***	22.7	*Persicaria amphibia***	11.4	Viccia cracca**	3.7
▲Fallopia japonica**	3.7	*Rumex obustifolius****	20.7	**Petisites hybridus*****	11	*Veronica chamaedrys**	3.2
Veronica beccabunga	3.2	*Holcus mollis***	18.2	*Rumex acetosa***	10.7		

3.5 Discussion

Our study shows that environmental variables impact the abundance of IAP and native dominant plants differently, both seasonally and with changing bank elevation. Increasing cover of both IAP and native dominant plants negatively affects subordinate species cover to a similar degree, but IAPs have more strongly seasonal effects and at higher bank positions. Invasion therefore has potential to alter the vegetation of riparian zones both spatially and temporally, with the magnitude of effect being moderated by local environmental conditions and effects on composition outweighing those on richness.

Fig 7. Spring vegetation along the Dean Water, May 2014. Foreground species include *Impatiens glandulifera* and *Urtica dioica*.

3.5.1 Abiotic influences on cover of invasive and native dominant species

Soil moisture had the greatest effect on both invasive alien and native dominant plants, but in opposing directions. Invasive alien plant species were negatively affected by increasing soil moisture. This effect was most prominent in spring, and closest to the channel edge. Tickner et al. (2001) found that *I. glandulifera* seedlings were sensitive to early season flooding both during and after germination. Invasive species colonisation, particularly by *I. glandulifera*, tends to be associated with damp conditions (Hejda & Pyšek 2006). However, previous experimental work has shown that *I. glandulifera* grows more vigorously in drier conditions (Tickner *et al*. 2001; Baattrup-Pedersen *et al*. 2013). In contrast to the negative effect on IAP cover, native dominant plant cover was positively associated with soil moisture in spring. Although common native dominant species of riverbanks such as *U. dioica* thrive in drier habitats they are also tolerant of winter inundation, while species such as *P. arundinacea* and *G. maxima* tolerate permanent saturation (Grime, Hodgson & Hunt 1988). This suggests that native dominant species will be less sensitive to the effects of flooding in the early part of the growing season but that drought conditions or artificial influences that promote dewatering of banks, such as channel incision or bank aggradation, will favour IAPs.

Invasive alien plant cover was more sensitive to environmental variables in spring, when plants had recently germinated. Contrary to the view that greater nutrient availability facilitates IAP growth (Lake & Leishman 2004), increased river water phosphorus concentrations reduced IAP cover, perhaps because native dominant species with strong vegetative growth, such as *P. arundinacea* and *U. dioica,* were more responsive to higher fertility and then better able to resist invasion. Higher nutrient concentrations, combined with stronger fluvial disturbance (e.g. scour, sediment deposition) as experienced closest to the water's edge, have previously been shown to increase both native and IAP richness through increased resource and habitat availability (Hobbs 1989). Our results suggest that native dominant species have a competitive advantage in fertile habitats disturbed by spring flooding and where IAP cover is reduced by soil saturation.

Whilst our study highlights environmental conditions that may restrict IAP growth once established, some physical characteristics of the riparian zone can also promote the abundance of IAPs. Rivers with a shallower channel gradient (low energy rivers), and higher tree densities were positively associated with IAP cover. Steeper channel gradients may reduce the deposition of seeds or their germination success at higher bank elevations due to scouring, rapid recession of water and reduced fine sediment deposition. The additional benefit to IAPs of greater tree density may be linked to increased trapping of fine sediments which provide an ideal seed bed, as well as reduced competition from native dominant herbaceous species (Baattrup-Pedersen *et al*. 2013). Soil moisture beneath large trees is also likely to be reduced by evapotranspiration and superior drainage, with deposited sediment enhancing this effect. Some IAPs also appear to be more shade tolerant than the native species that commonly dominate river banks, with *I. glandulifera* regularly growing in non-riverine habitats in moderate shade (Čuda *et al*. 2013).

The differentiation in growing conditions of native dominant and IAPs within a small geographical area suggests that some habitats and the flora they support are invasion resistant. This undermines the widely practiced use of uninvaded plots as a proxy for the pre-invasion state (Sax, Kinlan & Smith 2005; Thomaz *et al*. 2012) since uninvaded plots located in a region where invasion is widespread may in fact be uninvadable due to differences in local conditions, rather than simply awaiting invasion.

Fig 8. Inundated bank on the River Almond, March 2014.

3.5.2 Impact on native subordinate species

Through spring to summer IAPs and native dominant plants had a negative effect on subordinate plant richness and cover. Cover of native dominant plants, including species such as *P. arundinacea* and *U. dioica*, had a greater negative effect on subordinate species richness and cover closest to the water’s edge. These species exhibit rapid vegetative regrowth in spring, potentially boosted by fertile river water and sediments which appear to moderate the influence of IAPs, either directly or via enhanced growth of native dominant species (Tickner 2000). Although native dominant species may have a competitive advantage over IAPs closer to the water's edge, where soil moisture is higher, IAPs had an increasingly negative effect on subordinate species cover in summer, as well as at the top of the river bank, when the focal IAPs often attain their greatest height and coverage (Beerling, Bailey & Conolly 1994; Beerling & Perrins 2012).

Dominant plant species, whether native or invasive alien, strongly modulate species interactions (Bottollier-Curtet *et al.* 2013). The native dominant *U. dioica*, for example, commonly forms monodominant stands along river corridors, implying that even if an IAP displaces *U. dioica* it might exert only a limited effect on an already depressed plant species diversity (Hejda & Pyšek 2006; Hejda *et al.* 2009). It is often assumed that the superior competitive abilities of invasive plants that enable them to displace native dominant species, will lead to the inevitable reduction of native subordinate species (Bottollier-Curtet *et al.* 2013). Our study shows that the effect of IAP cover on native subordinate species richness was very similar to that of native dominant species, suggesting that IAPs do not in fact affect subordinate species richness any more so than do native dominant plants. Other studies have also found that the effect of IAPs on native species richness is either negligible (Daehler 2003) or that strong effects are typically seen only at the very highest invasive cover (Hulme & Bremner 2005), particularly in studies focused on *I. glandulifera*. In our study IAPs had a weaker or similar negative effect on native subordinate plants overall, compared to native dominant plants. Comparison of paired invaded and uninvaded sites at plot, site and species pool scale also confirmed that richness is a poor metric with which to assess invasion status of riparian zones. Under favourable growing conditions for IAPs it is possible that increasing cover may lead to the full exclusion of some native subordinate species such that negative effects accumulate with time. In our study all sites had been invaded for at least 10 years, making it unlikely that additional effects of IAPs on native subordinate species have yet to be realised (Iacarella & Ankiewicz 2015).

3.5.3 Community composition

Ordination showed that environmental conditions played a significant role in determining community composition, with bank elevation foremost, consistent with Goodson *et al. (2003).* Uninvaded sites generally had higher soil moisture and a steeper channel gradient, consistent with the mixed effects modelling. While richness at various scales could not discriminate between paired invaded and uninvaded sites there were strong compositional differences between them. *Fallopia japonica* and *H. mantegazzianum* were significant indicators of *I. glandulifera* dominated sites, having high fidelity and specificity for sites invaded by this species. The aliens *C. sibirica* and *M. guttatus* were also indicative of these sites, as well as woody *Salix* species. IAP abundance is likely promoted by *Salix* spp., whether directly due to the superior shade tolerance of IAPs compared to native dominant riparian plants or, indirectly, by maintaining gaps through shading, reducing soil moisture or acting as a focus for fine sediment deposition (Gurnell *et al*. 2012). Interspecific competition between co-occurring alien plants is still poorly understood (Kuebbing & Nuñez 2014), but, if these interactions are weaker than those between native and alien species, the presence of one IAP, may prove conducive to the success of another (Kuebbing & Nuñez 2014).

Native dominant species, such as *P. arundinacea*, *U. dioica* and *A. podagraria*, were strongly indicative of uninvaded sites, alongside common grasses such as *Agrostis stolonifera* and *Holcus lanatus*. There was also a larger core of native subordinate species indicative of uninvaded sites. This suggests that only a small pool of species regularly co-exist alongside IAPs, potentially leading to a flora that is prone to further invasion and, potentially, more resistant to restoration (Smart *et al.* 2006) and less resilient to fluvial disturbance. In contrast, since uninvaded sites occur in close proximity to invaded sites, it would appear their vegetation is either resistant to invasion (e.g. high stem densities of grasses might limit recruitment opportunities) or associated with growing conditions that are less conducive to the growth of IAPs. However, most of the species encountered in uninvaded plots in the riparian zone were common and widespread in the UK, as with studies of other habitats (Maskell *et al*. 2006), suggesting that any specific threat to their status from our focal IAPs will be small (Hulme & Bremner 2005).

The replacement of a native dominant species within the riparian vegetation by an IAP not only has direct implications for species composition but also indirect environmental impacts. The roots and rhizomes of perennial native dominant plants help to minimise soil erosion along river banks during high winter flows. Year-round vegetation cover contributes to the structural integrity of the riparian zone by protecting soil against erosion, as well as trapping and retaining flood-borne sediment (Gurnell *et al.* 2012). Seasonal dieback of the large annual I. glandulifera, which also has a shallow root system, leads to rapid collapse of large monocultures, leaving river banks potentially exposed to erosion (Greenwood & Kuhn 2014) by winter *floods that* have themselves increased in frequency in recent decades (Werritty 2002). Regardless of the weak effect of IAPs on native plant species richness, their negative influence on cover of subordinate vegetation may therefore still impact native communities over time via other processes.

3.5.4 Conclusion

We show for the first time how invasive alien and native dominant species respond differently to local environmental conditions both temporally (through the growing season) and spatially (across river banks). Our findings reiterate the importance of competition as a factor in structuring riparian vegetation, specifically at fluvially less disturbed higher bank elevations. IAPs pose an additional pressure on an already dynamic habitat and their sensitivity to soil moisture and channel gradient is therefore particularly instructive for land management and river restoration. Eradicating IAPs from interconnected watercourses is an unachievable goal (Hulme 2012) but knowing the risks of invasion, and maintaining IAPs at a low cover by promoting environmental conditions at a local scale that favour native dominant species, will reduce impacts on native species and alleviate potential problems such as erosion of river banks.

Chapter 4. Interannual variation in riparian plant communities: invasion legacy effects and the role of sediment deposition.

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Intention to submit: *Biological Invasions*

Author comments: ZP and NW jointly developed the project concept. Field data collection was carried out by ZP. The manuscript was prepared by ZP with comments from NW. The results were presented at the 13th International Conference on Ecology and Management of Alien Plant Invasions, Hawai'i (September 2015).

4.1 Abstract

Riparian zones are the product of interactions occurring at the land-water interface between fluvio-geomorphological processes, such as sediment deposition, and biota, such as vegetation. Establishment of invasive alien plant (IAP) species along river banks may influence the stability of above-ground vegetation through competition as well as having effects on soil propagule banks. Riparian zones heavily invaded by large herbaceous plant species are often associated with a diminished propagule bank. This may contribute to instability in the above-ground native community, expressed as higher turnover or fluctuations in native plant abundance at high IAP cover. However, propagules associated with fine sediment deposited in riparian zones may also replenish propagule banks thus supporting recruitment of native species. Vegetation surveys across rivers varying in flow regime, were carried out over two years to assess changes in community composition and diversity. Artificial turf mats were used to quantify over-winter sediment deposition and germination trials were used to determine the viable propagule bank in soil and freshly deposited sediment. Sediment deposition was positively associated with both the diversity and number of propagules deposited at a site. However, viable propagule number was lower at sites which had previously been heavily invaded. Seasonal turnover in the above-ground vegetation was accentuated at previously invaded sites. Heavily invaded sites

were also negatively associated with native diversity, suggesting that a legacy effect (previous history of invasion) of competition not sediment deposition drives above-ground vegetation structure at invaded sites. The interaction between fluvial disturbance via sediment deposition and invasion pressure, has both scientific and applied relevance when prioritising riparian habitats for management and restoration.

4.2 Introduction

The major threats to biodiversity in riparian habitats include land use change, climate change, and biological invasions (Flanagan, Richardson & Ho 2015). Riparian habitats are complex, non-equilibrium systems, the characteristics of which exert strong influence on riparian biota (Naiman & Decamps 1997). Riparian habitats exhibit high biodiversity due to their dynamic nature, high spatial and temporal heterogeneity, and potential for waterborne dispersal (hydrochory). Invasive alien plant species (IAPs) commonly use riparian zones as corridors for dispersal (Naiman & Decamps 1997). Climate change scenarios and empirical evidence suggests a recent and ongoing increase in precipitation, resulting in a greater frequency of high-flow events in autumn and winter across the UK (Werritty 2002). A single extreme hydrological event can change invasion dynamics (Richardson *et al.* 2007) by increasing opportunities for dispersal. Changes to riparian zones mediated by natural disturbances, such as flooding and sediment deposition, can promote the colonisation and establishment of IAPs, thus potentially impacting the structure of native vegetation and the overall functioning of riparian ecosystems (Richardson *et al.* 2007).

Extreme flood events can influence the early stages of growth and colonisation of riparian vegetation (Truscott *et al.* 2006), providing opportunities for dispersal and supply of viable propagules which governs the distribution of riparian species (Moggridge & Gurnell, 2009). Seasonal variation in flow regime and inundation of riparian habitat creates environmental conditions that challenge many terrestrial species (Naiman & Decamps 1997). However, coupled with sediment accumulation, new habitats can be created potentially supporting colonisation and establishment of IAPs due to high levels of resources and a lack of competition from other plants (Richardson *et al.* 2007). IAPs have been implicated in the decline of both above-ground native vegetation (Maskell *et* *al.* 2006; Hejda *et al.* 2009) and the abundance of native species within the propagule bank (Gioria & Osborne 2010). Large stands of IAPs, particularly *Heracleum mantegazzianum*, can produce prolific seed banks (Gioria, Dieterich & Osborne 2011). Propagule pressure itself is an invasion mechanism (Lockwood *et al.* 2005), as an abundant propagule supply contributes to population-level resilience, facilitating proliferation and spread (Gioria & Pyšek 2015). Gioria and Osborne (2010) showed that the seed banks of invaded sites are dominated by genera or species which form persistent seed banks, resulting in potential homogenisation of flora associated with highly invaded sites. Many factors such as climate, flow of water and sediment deposition interact to mediate plant invasions and their long term effects along river corridors (Capon & Brock 2006; Truscott *et al.* 2006). Despite this, these factors are rarely examined together when trying to explain spatial patterns of native and non-native plants (McShane *et al.* 2015).

One of the most important physical functions of riparian areas is the ability to trap and buffer the transfer of sediment (Steiger & Gurnell 2003). Riparian vegetation modifies sediment transport either by altering channel hydraulics or by physically entrapping materials, most significantly in lowland environments (Moggridge *et al.* 2009). There has been increasing interest in sedimentation processes and the association between flood events and increased sedimentation along natural rivers (Steiger & Gurnell 2003), partly driven by climate-related changes in flow regime and increased awareness of the link between land management and sediment entry to rivers. Sediment redistribution in a river is an exchange between erosion and deposition, causing disturbance along riparian corridors (Nilsson & Svedmark 2002). Large amounts of deposited sediment may disturb established vegetation but favour young and productive stages of succession by creating invadible patches (Nilsson & Svedmark 2002). High sediment loads can also bury pre-existing vegetation and the legacy seedbank (Nilsson *et al.* 1993). Dittmar and Neely (1999), for example, showed a decline in seedling density with increasing sediment depth, and thus a potential impact of recent sediment deposition on developing or existing vegetation. However, evidence from Goodson et al. (2003) indicates that large numbers of propagules can also be deposited at sites experiencing greater sediment deposition. Soil seed banks are a reserve of viable propagules which play a central role in species' recruitment, facilitating the storage and establishment of both IAPs and native species (Gioria & Pyšek 2015) .

Riparian habitats are an integral component of river ecosystem function and riverbanks are the location of the most marked hydraulic, geomorphological and ecological changes within the riparian zone (Goodson *et al.* 2003). Long-term deposition rates (decades) are important in the geomorphological development of riparian zones. However, assessing annual (short-term) rates is important in understanding relationships between sedimentation and the biodiversity of riparian zones (Steiger & Gurnell 2003). The cumulative contribution of short- and long-term deposition rates may produce a legacy effect (the impacts that a site's antecedent condition, i.e. history of invasion or sedimentation, have on current processes; Cavender-Bares *et al*. 2016) with immediate short-term implications for riparian vegetation and eventual long-term impacts on both vegetation and propagule banks. Although riparian zones are inherently dynamic, the addition of multiple stressors, such as invasion by IAPs and increased sediment deposition, associated with land-use change and climate-related changes in flow, may lower community stability or affect resilience to re-establish in the long-term.

The aim of this study was to assess the contribution of IAPs and over-winter sediment deposition to short-term (interannual) changes in native riparian vegetation composition and diversity. We focused on the IAPs *Impatiens glandulifera, H. mantegazzianum* and *Fallopia japonica* as previous studies have associated these species with negative impacts on native riparian vegetation (Hejda *et al.* 2009; Pyšek *et al.* 2012) and they are listed by DAISIE as being among the 100 most invasive plant species in Europe. We hypothesized that high cover of these IAPs would increase turnover and reduce above-ground diversity, thus destabilising native vegetation, but that greater sediment deposition over-winter may increase diversity by creating canopy gaps and acting as a propagule reservoir. This may reduce negative impacts of IAP cover on native diversity and composition, with changes in the propagule bank associated with over-winter deposition being the primary driver of change in composition of above-ground vegetation. Alternatively, in invaded catchments some IAPs may benefit disproportionately from increased sediment loading to the riparian zone. Firstly we addressed which variables, such as flow regime changes and IAP cover, influence sediment deposition along river banks and how sediment loading is related to the number and diversity of propagules deposited. Thereafter we asked i) does seasonal and interannual turnover in native vegetation differ between sites?; ii) is IAP cover, over-winter sediment deposition or change in composition of the propagule bank related to interannual or seasonal turnover and diversity of native vegetation, iii) are these relationships dependent on current levels of IAP cover or a legacy effect from the previous year's invasion?

4.3 Methods

4.3.1 Field surveys

Surveys were conducted along 20 lowland rivers in Central Scotland, UK (Fig. 1). Rivers ranged between 10-75 m in channel width and 5-40 m in elevation above sea-level. These rivers also showed a gradient of change in mean annual flow over the last 22 years, ranging from a 4-28% average increase (Appendix Table 3). Based on initial site searches that revealed the widespread extent of *I. glandulifera* relative to the other IAPs, sites were selected that contained at least this species and were concentrated on the most downstream accessible point on each river. This species is the most frequently occurring IAP across rivers in Scotland and forms continuous monocultures along lowland rivers (Seager *et al.* 2012; Pattison, Minderman & Willby 2016 (Ch2)). All study sites were adjacent to agricultural land or in urban/suburban areas. Sites varied in their level of invasion (quantified by % cover of IAPs), thus affording a gradient of potential invasion impact. Vegetation surveys were conducted during August 2013 (year 1), May 2014 (year 2 spring) and August 2014 (year 2 summer), in order to quantify turnover between seasons and years. Surveys began at a randomly selected point along a 100 m reach. At the start of each surveyed reach, a transect was established perpendicular to the water's edge and three plots of 1 m^2 plots were positioned equidistantly between the water's edge (Q1), mid-bank height (Q2) and the bank top (Q3). 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 420 plots sampled across all rivers in each field season (Fig 2). In each plot, all species were identified and abundance was quantified using the five point DAFOR 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, allowing for different canopy layers. Abundance scores were then converted to percentage cover for analyses (1= 1%, 2=6%, 3=18%, 4=38%, 5= 75%).

Alien species were defined according to Preston et al. (2002) as those which colonised Britain with the aid of humans. In addition to *I. glandulifera*, *H. mantegazzianum* and *F. japonica* other IAPs recorded included *Claytonia sibirica*, *F. sachalinensis*, *F. x bohemica* and *Mimulus guttatus* and, within the propagule bank, *Epilobium brunnescens*. Percentage cover of all invasive alien species were combined and used to assess the effect of IAP cover on aspects of the native community. *I. glandulifera* accounted for 90% of the total cover of recorded IAPs. Species other than *I. glandulifera* were too infrequent to assess effects of specific IAPs.

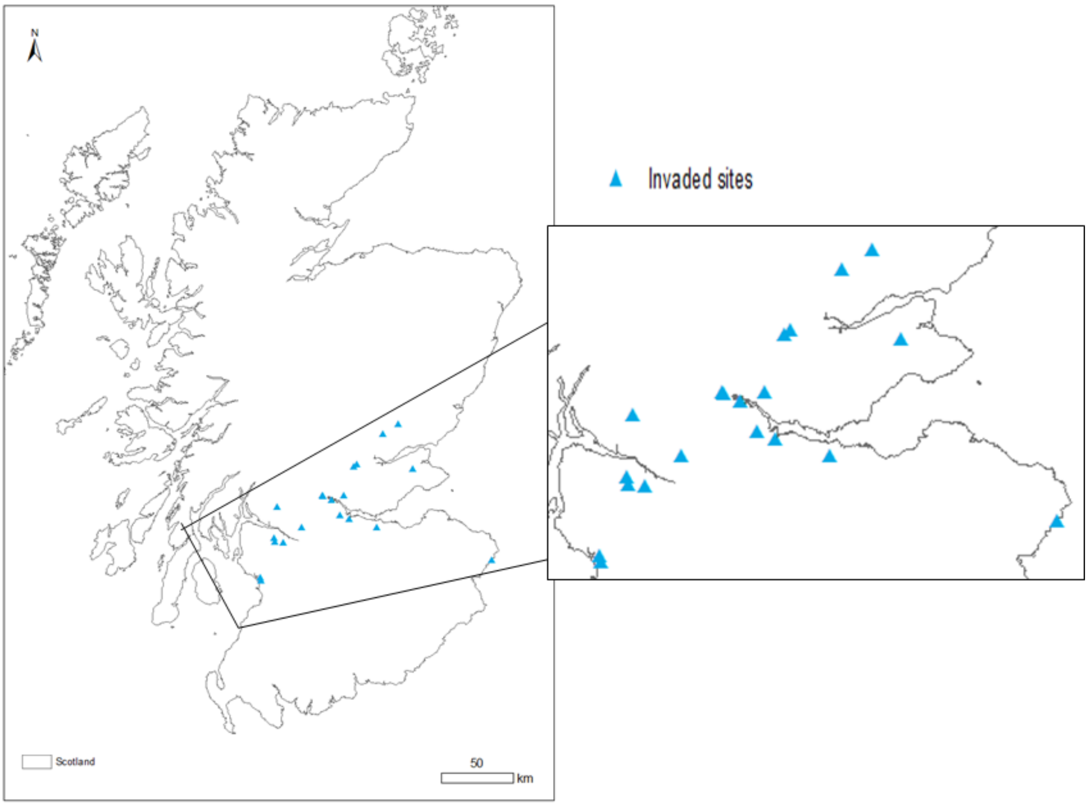

Fig 1. Location of survey sites across the central belt of Scotland included in this study (scale and locations approximate).

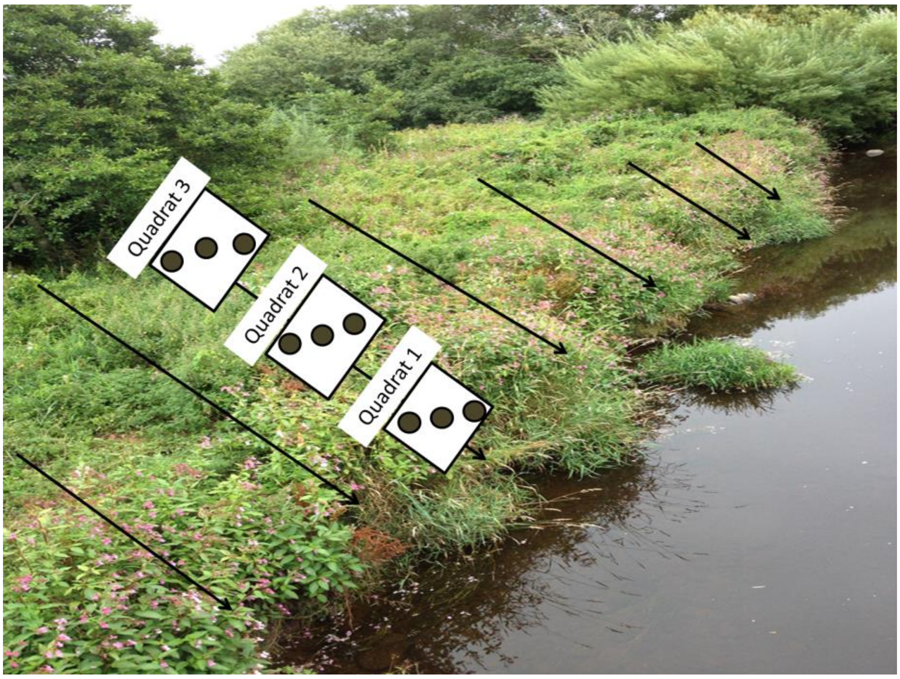

Fig 2. Reach scale (100m) sampling design. Arrows represent transects. Squares represent quadrats at positions 1 (closets to the water's edge), 2 (middle of riparian bank) and 3 (top of the riparian bank denoted by the trash line).which were placed at each transect. Circles represent soil cores taken in every quadrat. Astroturf mats were placed at the first, middle and last transect.

4.3.2 Propagule bank collection

Samples of the riparian soil propagule bank (encompassing both seed and vegetative propagules) were collected during September 2013 (year 1) to assess propagule bank composition after summer germination had already taken place. Soil cores were obtained from the three zones of the river bank (Q1, Q2 and Q3) at each site using a five cm deep, seven cm diameter corer, with three replicate cores taken in each plot, aggregated and sealed in plastic bags. Cores were kept in storage at $5^{o}C$ until early April 2014 when they were processed. In total, 21 bulked soil samples were obtained from each site, each representing the unique bank zone x transect positions.

Overwinter deposition of propagules was measured using artificial turf (AstroTurf ®) mats (Fig 3). Each mat was 30 x 30 cm, with 1.5 cm length bristles. Eighteen mats were placed at each site across the three bank zones by the end of September 2013. The mats were distributed widely (within the site and up to 200 m upstream) to provide good coverage of the range of conditions for deposition of material. Mats were retrieved in March 2014 (year 2) and placed in sealed plastic bags for storage (a maximum of 2 weeks at 4-8°C) until they were processed. All mats were weighed in order to determine spatial (between site and across the river bank) patterns of overwinter deposition of sediment. This method provides a direct measure of sedimentation at discrete sites, over specific time periods and is indicative of the potential role of hydrochory in contributing propagules to the riparian propagule bank (Steiger & Gurnell 2003).

Fig 3. From left to right an AstroTurf mat when first placed at the River Endrick in September 2013 on collection in March 2014.

4.3.3 Germination trial

Soil cores were aggregated and hand mixed for each bank zone, thereafter separated into three subsamples per bank zone for each site, to allow for available space in polytunnels. Each subsample was spread to an even depth (always less than 2 cm) in a tray previously filled with 3–4 cm sterile soil (John Innes #2), in a 25 x 30 cm seed tray. Astroturf mats were punctured to allow moisture exchange after watering and were then placed in trays previously filled with 3–4 cm sterile soil (Gurnell *et al.* 2007). Mats with little deposited sediment were augmented with additional sterile soil to prevent desiccation and to provide adequate rooting depth for seedlings. Mat trays measured 1.5 m^2 and held four mats. Wooden barriers were constructed to maintain separation of mats (Fig 4). Soil cores and mat samples were then arranged randomly in polytunnels. Polytunnels were left unheated to allow exposure of seeds to a wide range of temperatures, broadly resembling those encountered in the field and were watered twice daily (10 minutes per watering) using an automated pipe-feed system. Such conditions have been found to be highly conducive to germination of a wide range of species (Abernethy & Willby 1999).

The seedling emergence method was used to quantify the propagule bank, in which species and their abundance are estimated from the identification of seedlings, following greenhouse germination of soil samples (Gurnell *et al.* 2007). As seeds germinated, they were identified to species level and then removed or, where further growth was needed for identification purposes, grown on in separate pots to prevent overcrowding. Once plants had flowered and could be identified they were removed to prevent reseeding. Wherever possible, seedlings were identified to species level although in a small number of cases (<5% of individuals) it was only possible to identify to genus. The number of seedlings germinating was counted weekly to ensure that seedlings did not emerge and die between counts. Although the seedling emergence method may underestimate absolute seed density it is a good comparative measure of the viable portion of the seed bank (Abernethy & Willby 1999). The germination trial extended over five months from April 2014 until September 2014. Over the final month of the trial there was negligible emergence of seedlings of species not already recorded.

Fig 4. From left to right: AstroTurf mats in the initial stages and after 3 months of growth.

4.3.4 Flow regime indicators

To assess the effect of hydrology on sediment deposition, daily mean flow data were obtained from the Centre for Ecology and Hydrology's National River Flow Archive, based on data from the most downstream gauging station on each surveyed river. Using data from 1990 to 2014, the percentage increase in mean flow over the last 24 years was calculated, to characterise the general long term trend in flow across each of the 20 rivers. The rivers studied showed a gradient of increase in mean annual flow over the last 24 years, ranging from a 4-28% (Appendix Table 3). The coefficient of variation was used to express variability in flow in each river using daily mean flow data. Flood frequency, expressed as the mean number of days per year on which flows exceeded a threshold of five times the median flow (FRE5), was used as an indicator of fluvial disturbance to assess the effect of flooding on the amount of sediment deposited after winter.

4.3.5 Statistical analysis and model selection

To quantify seasonal turnover of native species in above-ground vegetation or the seed bank, Bray–Curtis dissimilarity (BCI) was calculated using species cover data (%, square-root transformed) and total no. of seedlings from the propagule bank (log transformed), respectively. Native species richness was calculated using Shannon's diversity index of above-ground vegetation (% cover) for year 2 spring and summer and propagule bank vegetation on the mats (no. of seedlings).

Linear mixed effects models (LMMs) were used to model sources of variation in sediment deposition and diversity of year 2 propagules, whilst generalized linear mixed effects model was used to model the number of propagules deposited in year 2 on the mats. Fixed effects were bank position, IAP cover, flood frequency (FFE*5) and variation in flow regime (coefficient of variation). LMMs were used to model seasonal and interannual changes in standing vegetation. The response variables were BCI and Shannon's Diversity indices. Fixed effects were BCI index of turnover of propagules between year 1 and 2, IAP cover and sediment (kg per mat).River was included as a random intercept in models to account for pseudoreplication. All predictors were standardised to one standard deviation prior to statistical analyses, in order to assess effect sizes of each predictor. We checked for multicollinearity among the predictor variables none of which were highly correlated ($r = < 0.60$).

Models were ranked using the information theoretic approach (Burnham & Anderson 2002) to select the best combination of interaction effects from the global model. Models were compared using AICc (correcting for small sample sizes), with all possible combinations of predictors identified using the dredge function in MuMIn. The best fitting models were evaluated based on their ΔAICc, with values < 4 considered to be equally parsimonious (Burnham & Anderson 2002). Akaike weights were calculated for each explanatory variable, in order to compare the relative importance of each variable in the top set of models (ΔAICc < 4). The top model with the highest model weight and lowest AIC value was chosen for interpretation of coefficients. Bootstrapping was used to calculate 95% confidence intervals. To account for the variation explained solely by the fixed effects, as well as the variation explained by both the fixed and random effects, both the marginal and conditional R^2 values are reported for each model, respectively (Nakagawa & Schielzeth 2013).

All statistical analyses were conducted using R 3.2.2 (R Development Core Team 2015), with the additional R packages vegan (Oksanen 2015), MuMIn (Barton 2016), lme4 (Bates *et al.* 2015) and boot (Canty 2016).

4.4 Results

Of the 360 mat pairs installed in the field in September 2013, 279 were still in place or recoverable in April 2014. The 23% loss represents erosion, burial or animal/human intervention. All 279 mats had trapped some viable seeds, and in all cases there was sufficient sediment to determine total wet weight.

4.4.1 Sediment deposition

The amount of sediment deposited over winter (Year 1 to 2) was positively associated with cover of IAPs in year 1 (Fig. 5a). Bank elevation (quadrat position) was associated with a decline in amount of sediment deposited (Fig. 5b). The greatest amount of sediment was deposited closest to the water's edge. The best approximating model within the delta <4 topset had a model *Wi* 0.55 (Table 1), with a marginal R^2 of 0.31 and a conditional R^2 of 0.74 (Table 2).

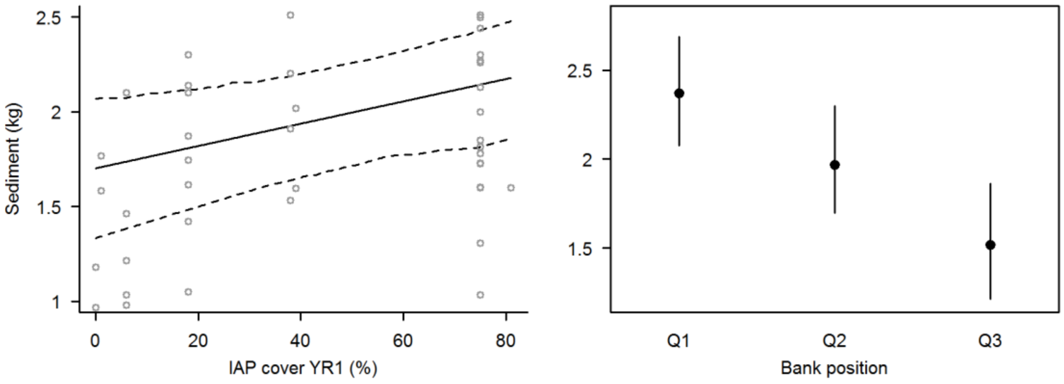

Figure 5. Predicted values (dashed lines ± 95% CI) from the LMM analysis of sediment (log) deposited on the bank over winter. Modelled effects of a) mean % IAP cover in year 1 and b) bank position on sediment deposition. Q1 refers to water's edge and Q3 to top of bank.

Table 1**.** Model selection summary for models that had ΔAICc values of < 4 for each response variable. Models are ranked by AICc weight (W_i), where higher weighted models have more support. Log-likelihood ratio values are given. The variable quad is a proxy for bank elevation.

Response	Model parameters	logLik	AIC$_c$	Δ_i	W_i
Sediment	Quad + Invasive cover Yr1	-46.73	107.10	0.00	0.55
	Quad + Invasive cover Yr1 + Flood freq	-46.50	109.20	2.10	0.19
	Quad + Invasive cover Yr1 + Flow variability	-46.63	109.40	2.37	0.17
	Quad	-49.83	110.80	3.71	0.09
No. seedling Yr2	Quad + Sediment + Invasive cover Yr1	-981.17	1975.90	0.00	0.51
	Quad + Sediment + Invasive cover Yr1 + Flow variability	-980.77	1977.70	1.77	0.21
	Quad + Sediment + Invasive cover Yr1 + Flood freq	-981.09	1978.30	2.40	0.15
	Quad + Sediment + Invasive cover Yr1 + Flow variability + Flood freq	-980.16	1979.20	3.22	0.10
Seedling diversity Yr2	Sediment + Flood freq	-24.34	59.80	0.00	0.27
	Sediment + Flow variability	-24.89	60.90	1.09	0.16
	Sediment	-26.27	61.30	1.47	0.13
	Sediment + Flood freq + Flow variability	-24.04	61.70	1.88	0.10
	Sediment + Flood freq + Invasive cover Yr1	-24.16	61.90	2.12	0.09
	Sediment + Flood freq + Quad	-23.21	62.60	2.79	0.07
	Sediment + Flow variability + Invasive cover Yr1	-24.63	62.80	3.06	0.06
	Sediment + Invasive cover Yr1	-26.02	63.10	3.36	0.05
	Sediment + Flow variability	-23.70	63.50	3.75	0.04
	Sediment + Quad	-25.05	63.70	3.89	0.04
Turnover Yr1 to Yr2 summer	NULL	56.15	-105.90	0.00	0.27
	Sediment	57.18	-105.60	0.26	0.24
	Invasive cover Yr2 summer	56.26	-103.80	2.09	0.09
	Invasive cover Yr1	56.23	-103.70	2.14	0.09
	Propagule turnover	56.20	-103.70	2.21	0.09
	Sediment + Invasive cover Yr2	57.31	-103.50	2.38	0.08
	Sediment + Propagule turnover	57.19	-103.30	2.61	0.07
	Sediment + Invasive cover Yr1	57.18	-103.20	2.63	0.07
Turnover Yr1to Yr2 spring	Propagule turnover	73.62	-138.50	0.00	0.21
	Propagule turnover + Sediment	74.57	-138.00	0.48	0.17
	NULL	71.81	-137.20	1.32	0.11
	Sediment	72.92	-137.10	1.39	0.11
	Propagule turnover + Invasive cover Yr1	73.97	-136.80	1.68	0.09
	Propagule turnover + Invasive cover Yr2 spring	73.62	-136.10	2.37	0.07
	Propagule turnover + Sediment + Invasive cover Yr1	74.63	-135.70	2.83	0.05
	Propagule turnover + Sediment + Invasive cover Yr2 spring	74.60	-135.60	2.89	0.05
	Invasive cover Yr1	72.07	-135.40	3.10	0.05
	Invasive cover Yr2 spring	71.89	-135.10	3.45	0.04
	Sediment + Invasive cover Yr1	72.94	-134.80	3.74	0.03
	Sediment + Invasive cover Yr2 spring	72.92	-134.70	3.77	0.03

Turnover Yr2 spring to Yr2 summer	Invasive cover Yr1	68.13	-127.50	0.00	0.36
	Invasive cover Yr1 + Invasive cover Yr2 summer	68.62	-126.10	1.40	0.18
	Invasive cover Yr1 + Propagule turnover	68.45	-125.80	1.74	0.15
	Invasive cover Yr1 + Sediment	68.15	-125.20	2.34	0.11
	Invasive cover Yr1 + Invasive cover Yr2 summer + Propagule turnover	68.99	-124.40	3.13	0.08
	NULL	65.39	-124.30	3.18	0.07
	Invasive cover Yr1 + Invasive cover Yr2 summer + Sediment	68.62	-123.70	3.87	0.05
Diversity Yr2 spring	Invasive cover Yr1	-14.25	37.20	0.00	0.23
	NULL	-15.64	37.70	0.47	0.18
	Invasive cover Yr1 + Invasive cover Yr2 spring	-13.72	38.60	1.32	0.12
	Sediment	-15.22	39.20	1.94	0.09
	Invasive cover Yr1 + Propagule turnover	-14.13	39.40	2.14	0.08
	Invasive cover Yr1 + Sediment	-14.16	39.40	2.19	0.08
	Propagule turnover	-15.50	39.70	2.50	0.07
	Invasive cover Yr2 spring	-15.59	39.90	2.68	0.06
	Invasive cover Yr1 + Invasive cover Yr2 spring + Sediment	-13.53	40.60	3.40	0.04
	Invasive cover Yr1 + Invasive cover Yr2 spring + Propagule turnover	-13.55	40.70	3.45	0.04
	Invasive cover Yr2 spring + Sediment	-15.05	41.20	3.98	0.03
Diversity Yr2 summer	Invasive cover Yr1	-6.98	22.70	0.00	0.29
	Invasive cover Yr1 + Propagule turnover	-6.22	23.50	0.86	0.19
	Invasive cover Yr1 + Invasive cover Yr2 summer	-6.60	24.30	1.61	0.13
	Invasive cover Yr1 + Sediment	-6.91	24.90	2.24	0.09
	Invasive cover Yr1 + Invasive cover Yr2 summer + Propagule turnover	-5.77	25.10	2.44	0.09
	Invasive cover Yr2 summer	-8.48	25.70	3.01	0.06
	Invasive cover Yr1 + Sediment + Propagule turnover	-6.16	25.90	3.21	0.06
	Propagule turnover	-7.54	26.20	3.50	0.05
	Invasive cover Yr1 + Invasive cover Yr2 summer + Sediment	-6.51	26.60	3.91	0.04

Table 2. The best approximating model, for each response variable, from the model selection summary for models that had ΔAICc values of < 4. Relative variable importance (RVI) for each model parameter is given in brackets. Marginal (R^2m) and conditional (R^2c) R^2 are given.

Response	Model parameters	R^2m	R^2c
Sediment	Quad (1) + Invasive cover Yr1 (0.91)	0.31	0.74
No. of propagules Yr2	Quad (1) + Sediment (1) + Invasive cover Yr1 (1)	0.11	0.11
Propagule diversity Yr2	Sediment (1) + Flood frequency (0.53)	0.05	0.25
Turnover Yr1 to Yr2 summer	NULL	-	-
Turnover Yr1 to Yr2 spring	Propagule turnover Yr1 - Yr2 (0.64)	0.03	0.67
Turnover Yr2 spring to Yr2 summer	Invasive cover Yr1 (0.93)	0.08	0.40

Diversity Yr2 spring	Invasive cover Yr1 (0.58)	0.05	0.10
Diversity Yr2 summer	Invasive cover Yr1 (0.89)	0.12	0.12

4.4.2 No. of propagules deposited over winter

The best approximating model in the delta < 4 topset had a model *Wi* 0.51 (Table 1), with a marginal R^2 of 0.11 and a conditional R^2 of 0.11 (Table 2). The amount of sediment deposited over winter was positively associated with the number of propagules deposited within the sediment (Fig. 6a). However, despite being positively associated with sediment deposition, the cover of IAPs in year 1 was negatively associated with the number of propagules deposited (Fig. 6b). The number of viable propagules deposited reduced with increasing elevation from the water's edge. At the top of the bank (Q3) there were less propagules deposited, consistent with the reduced sediment load (Fig. 6c).

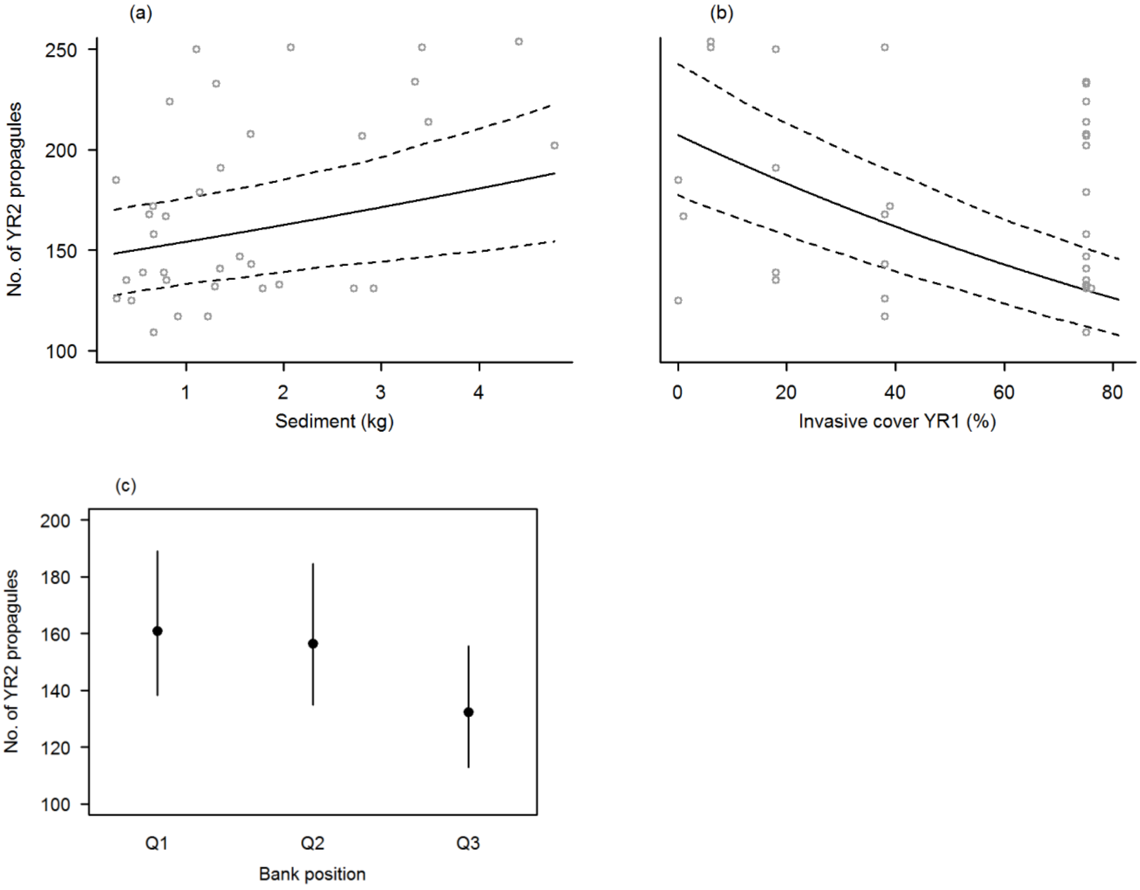

Figure 6. Predicted values (dashed lines ± 95% CI) from the GLMM analysis of number of viable propagules deposited on the bank over winter. Figure a) shows the modelled effect of mass of sediment deposited, b) mean % IAP cover in year 1 and c) the effect of bank position on the number of viable propagules deposited.

4.4.3 Over winter propagule diversity

The diversity of viable propagules deposited over winter (between years 1-2) was positively associated with both the weight of sediment deposited (Fig. 7a) and the mean annual flood frequency (FFE*5) (Fig. 7b). The best approximating model in the topset had a *Wi* 0.27 (Table 1), with a marginal R^2 of 0.05 and conditional R^2 of 0.25 (Table 2). The cover of IAPs present in year 1 was unrelated to the diversity of over-winter deposited propagules.

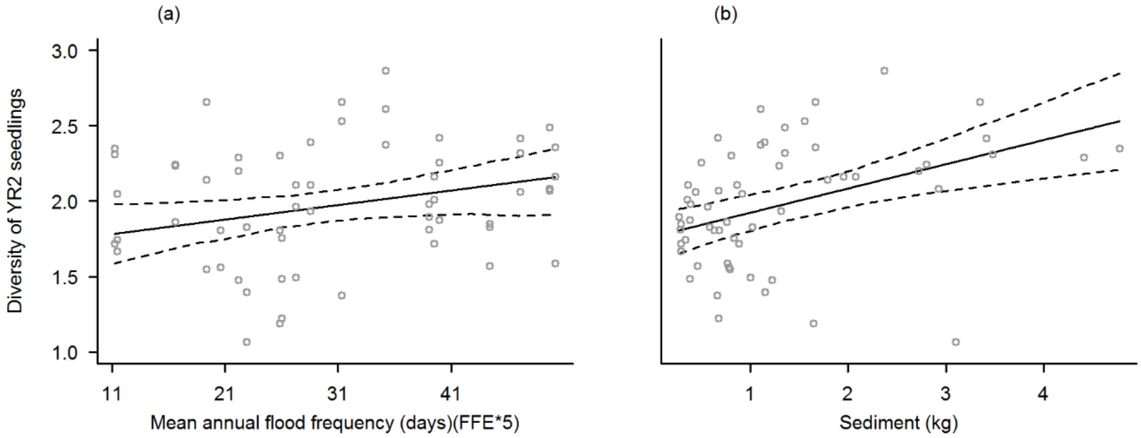

Figure 7. Predicted values (dashed lines ± 95% CI) from the LMM analysis of Shannon diversity for native propagules, germinated from over-winter deposition on the mats in year 2. Figure a) shows the effect of mean annual flood frequency and b) mass of sediment deposited over winter.

4.4.4 Turnover of vegetation

Turnover in the above-ground native vegetation between summer year 1 and 2 was not explained by model predictors, as the best approximating model within the top set was the null (Table 1). Seedling turnover was retained in the best approximating model for predicting turnover in above-ground vegetation between summer year 1 and spring year 2. The model weight was W_i 0.21 (Table 1) with a marginal R^2 of 0.03 and a conditional R^2 of 0.67 (Table 2). Greater turnover between the propagule bank in year 1 and 2 was associated with increased similarity of the above-ground vegetation between year 1 and spring year 2 (Fig 8a). However, the null model was also present within the delta < 4 topset. Within the topset of delta < 4 all models are equally plausible, therefore these results should be interpreted cautiously. The best approximating model for predicting turnover in the above-ground vegetation between spring and summer year 2 had a weight of W_i 0.36 (Table 1) and a marginal R^2 of 0.08 and conditional R^2 of 0.40 (Table 2). Greater invasive cover in year 1 was associated with increased dissimilarity in the above-ground vegetation between seasons in year 2 (Fig 8b). However, within the top set the null model was present with a W_i 0.06.

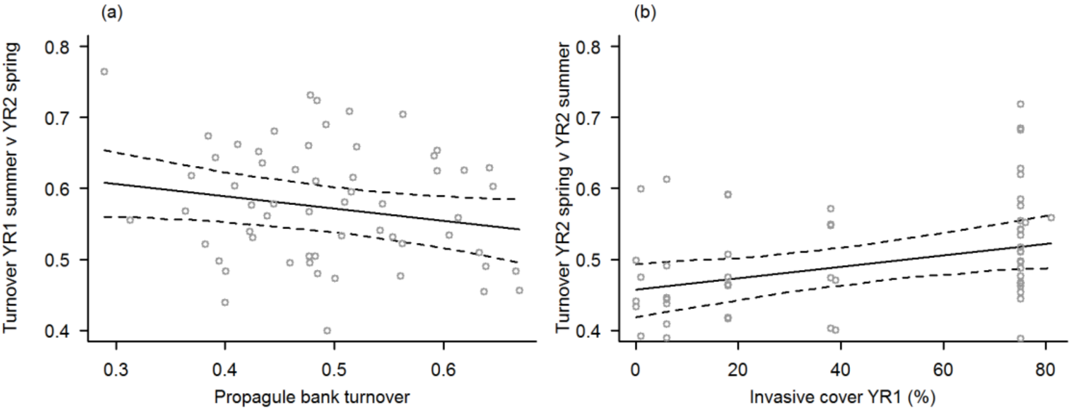

Figure 8. Predicted values (dashed lines ± 95% CI) from the LMM analysis of BCI dissimilarity between native, above-ground vegetation in a) summer year 1 to spring year 2 and b) spring to summer year 2. Figure (a) shows the effect of turnover in propagule bank composition between year 1 and year 2, as measured by the BCI and (b) shows the effect of invasive cover in year 1.

4.4.5 Diversity of above-ground vegetation

Diversity of native, above-ground vegetation in spring was negatively associated with invasive cover in year 1 (Fig. 9a). The best approximating model in the topset had a *Wi*

0.23 (Table 1), with a marginal R^2 of 0.05 and conditional R^2 of 0.10 (Table 2). Diversity in summer year 2 was also negatively associated with invasive cover in year 1 (Fig. 9b). The best approximating model in the top set had a *Wi* 0.29 (Table 1), with a marginal R^2 of 0.12 and conditional R^2 of. 0.12 (Table 2). For both spring and summer diversity in year 2, the negative effect of IAP cover in summer of the *previous* year (year 1) was therefore greater than that of IAP cover in both spring and summer in year 2 (Fig. 10).

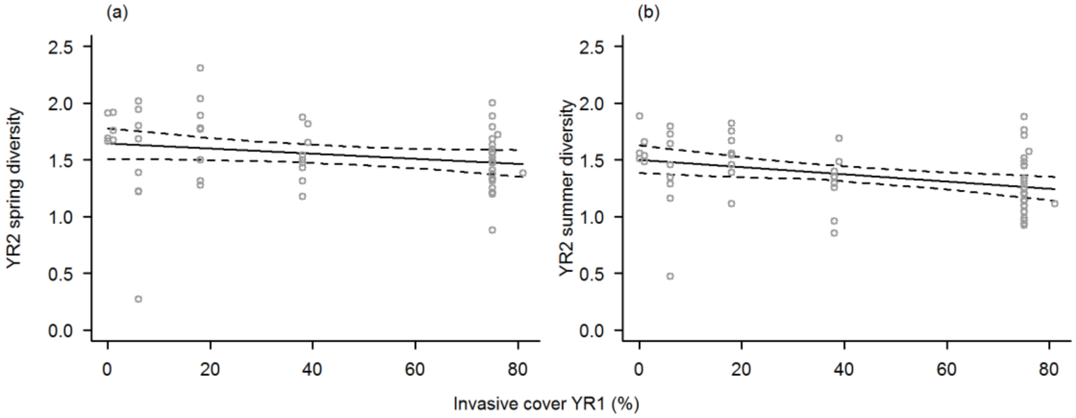

Figure 9. Predicted values (dashed lines ± 95% CI) from the LMM analysis of Shannon diversity of native, above-ground vegetation in a) spring year 2 and b) summer year 2 as a response to invasive alien plant cover in summer year 1.

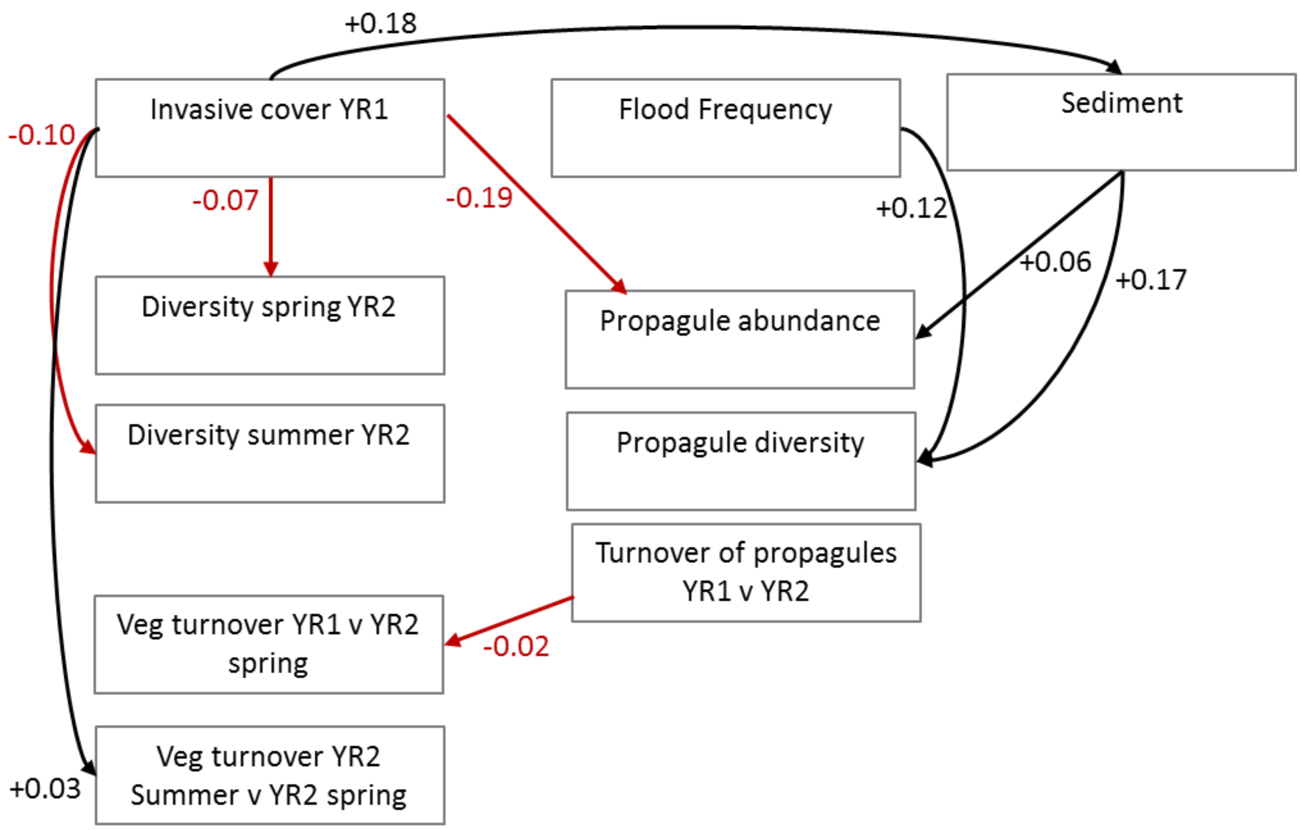

Figure 10. Summary diagram displaying correlations between predictor and response variables, with comparable model coefficients. Boxes represent measured variables. Arrows represent unidirectional relationships among variables. Black arrows denote positive relationships, and red arrows negatives ones. Standardized regression coefficient are displayed alongside arrows. The variable bank position is not displayed within this graph (see table 1).

4.5 Discussion

Over-winter sediment deposition following floods is widely regarded as an important mechanism for the dispersal of plant propagules in riparian areas (Andersson & Nilsson 2002; Gurnell *et al.* 2008). Large quantities of plant propagules have been recorded in freshly deposited sediment yet linkages between the presence of IAPs and sediment deposition have received limited attention (Baattrup-Pedersen *et al.* 2013a). This is surprising given the growing interest and awareness of the ecological impacts of fine sediment in rivers (Jones *et al.* 2012). Our study showed that sediment deposition was positively associated with both the diversity and amount of propagules deposited at a site. However, viable propagule number (but not diversity) was lower at sites which had previously been heavily invaded. Seasonal turnover in the above-ground vegetation was also accentuated at previously invaded sites. Heavily invaded sites were associated with lower native diversity, suggesting that a legacy effect of competition, not disturbance via sediment deposition, is a more important determinant of above-ground native vegetation structure at invaded sites.

4.5.1 Sediment and invasion

Changes in fluvial disturbance, expressed via flood frequency and sediment deposition, can potentially influence riparian vegetation structure on both a short temporal and fine spatial scale (Steiger *et al.* 2003). Competition with IAPs and their subsequent impact on native communities is often regulated by local environmental conditions (Pattison, Vallejo-Marin & Willby (Ch3)). Therefore, inter-annual changes in environmental conditions may either constrain the growth and impact of IAPs locally, aid their establishment via enhanced propagule dispersal to newly created patches, or, once dense monocultures are established, have no further measurable effect (Bellard *et al.* 2013). Dominance by IAPs may subsequently lead to less resilient and diverse plant communities over a short-time scale, if certain species are filtered out due through competition or other changes in the environment that accompany invasion (Gaertner *et al.* 2014). This may, however, be reversed if sediment deposition during floods reduces the competitive ability of IAPs and favours recruitment and colonisation of sediment-borne propagules of native species (Steiger *et al.* 2003).

Our study showed that invasion by IAPs has a legacy effect, indirectly influencing sediment deposition along highly invaded river banks. Pattison, Vallejo-Marin and Willby (Ch3) found that invasion cover increased with proximity to trees in the riparian zone, whilst Gurnell, Bertoldi & Corenblit (2012) found that stands of emergent aquatic macrophytes and riparian trees rooted into the bank toe formed hotspots for the retention of sediments. However, *I. glandulifera* which dominated along the bank may be less efficient at trapping sediment compared to some native plant and tree species, due to its small rooting depth (Gurnell 2015) and die back over winter. We suggest that the proximity of invaded stands to trees reflects an indirect association with high sediment deposition rather than trapping (e.g. shaded conditions, lower soil moisture; refer to Ch3) or, alternatively, that heavily invaded sites are indicative of conditions upstream. Greenwood and Kuhn (2014) found evidence of increased sediment erosion along river banks invaded by *I. glandulifera*, which implies that sediment loading downstream may be increased within invaded river systems. Alternatively, the probability of invasion may increase in lowland rivers where sediment loading is already high due to adjacent land use types (Bruno *et al.* 2014; Pattison, Minderman & Willby (Ch2)). Since dense native vegetation helps to minimize soil erosion by stabilising the bank (Nilsson & Svedmark 2002), it is likely that any replacement by invasive species will accentuate sediment loading downstream.

River flows have increased over the last 20 years across Scotland (Werritty 2002; Critchlow-Watton *et al.* 2014), increasing the potential for fluvial disturbance. The rivers surveyed in this study spanned a range of flow variability and flood frequencies that have altered in response to changes in climate and anthropogenic pressure. However, neither the variability in long term flow or annual flood frequency were present within the top model for sediment deposition. It may be that different aspects of flow regime such as the duration of flood events, are more important in determining depositional processes. Goodson et al. (2002), for example, found that the duration of inundation was strongly related with river bank sediment deposition along the River Dove, UK. The amount of sediment deposited also decreased away from the water's edge, supporting our results that higher bank elevations are more rarely inundated by flood water, particularly for an extended duration, and thus receive a reduced sediment load (Goodson *et al.* 2002). Bank face sediment deposition can be typical of low energy streams with greater vegetation coverage, which is often enhanced along river with intensive agriculture across the floodplain (Gurnell *et al.* 2008). Catchment topography and land use may also override the effects of flow regime in terms of sediment inputs (Jones *et al.* 2012).

4.5.2 Propagules deposition

Increased sediment deposition was associated with a more abundant and diverse, viable propagule bank. Our study, like Goodson et al. (2002), also found that the abundance of viable propagules decreased at higher bank elevation. The abundance of viable seed within over-winter sediment deposition demonstrates the potential importance of hydrochory and deposition in structuring vegetation within the riparian zone (Baattrup-Pedersen *et al.* 2013a) However, viable propagules were less abundant at sites heavily invaded in year 1, despite sediment deposition being higher in these sites. This suggests that competition from IAPs reduces local seed rain from native species or that IAPs themselves have lower seed rain than native dominant species which reduces local or upstream propagule inputs in widely invaded rivers. Thus IAPs have more influence on the above-ground vegetation than over-winter deposition of propagules.

Sediment transport has the potential to increase the available propagule bank store within riparian zones since propagules are also transported at times of flood (Nilsson *et al.* 2010) and deposited alongside sediment. Both the amount of sediment and incidence of flooding was positively associated with diversity of the over-winter propagule bank. Propagule diversity decreased further from the water's edge, reflecting sediment deposition patterns along the riparian bank. Although the abundance of viable propagules declined at previously invaded sites, the same effect was not seen with propagule diversity. Pattison, Vallejo-Marin and Willby (Ch3) showed a similar pattern in the above-ground vegetation. Locally the abundance of native species was reduced to a greater extent than diversity at highly invaded sites. Patches of freshly deposited sediment can act as newly created habitat, being associated with nutrients, organic matter and viable propagules (Nilsson & Svedmark 2002). Although large numbers of viable, diverse propagules may be present in deposited sediments, these may not necessarily be able to germinate, grow and become established (Goodson *et al.* 2003). In fact the similarity between the above-ground vegetation and the propagule bank in riparian habitats is often low (Tabacchi *et al.* 2005), with propagule banks often having high abundance of persistent, ruderal species such as *Juncus effusus* and *Epilobium* spp. that are poorly represented in the standing vegetation.

4.5.3 Turnover of vegetation

Invaded sites are often associated with highly disturbed habitats (Diez *et al.* 2012). However, initial colonisation often coincides with a disturbance event, creating habitat which can be colonised (Richardson *et al.* 2007), with the potential to create dominant monospecific stands. Therefore, we were interested in whether high levels of invasion was associated with reduced short term stability of above-ground vegetation. Turnover in above-ground vegetation was greatest between summer year one and two, however neither sediment deposition, flow regime nor IAP cover could explain these interannual changes. We suggest that community turnover was influenced by environmental conditions that were out-with our study, such as variation in mean summer temperature. Turnover in the propagule bank after over-winter deposition of propagules was, perhaps surprisingly, associated with a more similar above-ground plant community between summer year one and spring year two, although this effect was very weak and is difficult to explain. Dynamic propagule bank composition is probably an intrinsic feature of natural riparian zones. Perennial dominant native species will often limit recruitment from this bank but are evidently also associated with greater vegetation stability than IAPs.

Greater turnover in standing vegetation between spring and summer in year two was associated with high cover of IAPs in year one. We would expect some variation in above-ground plant communities simply due to seasonality, however our results suggest that this variation is accentuated at highly invaded sites. There has been a lack of consistent results regarding the similarity between the propagule bank and above-ground vegetation (Boedeltje *et al.* 2004; Tabacchi *et al.* 2005). Pattison, Vallejo-Marin and Willby (Ch3) showed that in summer, riparian vegetation is influenced more by competitive effects of invasion but in spring is driven mainly by abiotic conditions. Where spring native vegetation is similar across sites, those sites with the greatest initial coverage of IAPs are therefore expected to change the most between spring and summer compared to those that have little or no invasion. Invasion by IAPs is hence an additional influence on vegetation community structure.

4.5.4 Above-ground diversity

We were also interested in whether cover of IAPs and disturbance via sediment deposition would differentially impact above-ground native plant diversity. Greater cover of IAPs in year one, rather than year two, was associated with reduced diversity in both spring and summer year two. However, sediment loading could not explain variation in diversity, despite greater deposition being associated with higher propagule diversity and abundance. Floods or other disturbances frequently create gaps for colonisation, which, in conjunction with propagule deposition, could provide an effective mechanism for increased diversity (Jansson *et al.* 2005). However, it seems that diversity of above-ground vegetation is mainly determined by competition with IAPs (or other local abiotic factors that moderate this competition – see Ch3), rather than propagule supply. Sites which are highly invaded may reflect a degraded catchment, reducing seed rain downstream due either to the diminished propagule supply associated with competition of IAPs with native species, or other pressures. Any expression of a positive effect of sediment introducing greater diversity of propagules is supressed by IAPs, suggesting that uninvaded sites subject to high sediment deposition may respond differently to the increased opportunities for recruitment.

4.5.5 Conclusion

Plant dispersal in riverine environments has become an increasingly active research field, in part because it has implications for flow regulation, restoration, climate change, and the spread of alien species (Nilsson *et al.* 2010). Although the over-winter propagule bank is a potential pool of recruits to the vegetation, IAPs can disrupt this relationship by having a greater effect on community composition through competition than do abiotic variables. Our results suggest that above-ground vegetation is not driven by recruitment from over-winter propagules at invaded sites, rather there is a legacy effect of IAPs which have a greater impact on both diversity and turnover within the above-ground vegetation at heavily invaded sites. Observational studies such as this are important to better understand the community responses to invasion against a backdrop of climate- and land use-related changes in flow regime and sediment loading. They provide insights into the relative importance of environmental variables in determining outcomes of competitive interactions between established native riparian and alien plant species (Flanagan *et al.* 2015), thereby informing restoration and management actions.

Chapter 5. Propagule bank and established vegetation linkages in invaded riparian zones

Author names: **Zarah Pattison & Nigel Willby**

Author comments: ZP and NW jointly developed the project concept. Field data collection was carried out by ZP. The manuscript was prepared by ZP with comments from NW.

5.1 Abstract

The seasonal propagule bank and above-ground vegetation of riverbanks were sampled in order to compare the similarity of their composition across a gradient of invasive alien plant (IAP) cover (namely *Impatiens glandulifera, Fallopia japonica* and *Heracleum mantegazzianum*) and local environment conditions. Density and richness of the riparian propagule bank were also compared to the above-ground vegetation to determine the contribution of viable propagules to above-ground vegetation and to identify any features of the propagule bank that may promote or resist invasion by IAPs. Our study showed a general trend of high dissimilarity between above-ground and propagule bank vegetation, consistent with other studies in riparian zones. However, in areas with greater coverage of invasive alien and native dominant plants, communities were less similar, suggesting competitive interactions play a greater role in structuring established communities in relation to local environmental variables. The density and richness of propagule banks did not consistently translate into a more abundant and speciose above-ground vegetation, resistant to invasion by IAPs. This suggests that IAP colonisation is not limited by greater native richness and abundance of viable propagules. Long-term monitoring is needed to improve our understanding of the role of recruitment from the propagule bank following both invasion and removal of IAPs, in order to better advise management of propagule banks for restoration.

5.2 Introduction

Riparian habitats are naturally disturbed environments, resulting in high habitat heterogeneity that supports high levels of biodiversity, often reflected as high plant species richness (Tabacchi *et al.* 2005). Riparian zones act as corridors for water-borne dispersal of plants, with flood events and sediment deposition providing opportunities for recruitment and establishment of vegetation (GUrnell *et al*. 2008). Increasing pressure from invasive species, agricultural land use and climate-related changes in flow regime are altering disturbance patterns in riparian zones (Capon *et al.* 2013). Climate change scenarios suggest that summer droughts and wetter winters will become more frequent across north-west Europe, with potentially major ecological consequences for riparian habitats and plant communities (Morecroft *et al.* 2002). Therefore there is a need to assess how riparian vegetation will respond under different invasion and climate scenarios.

The composition of vegetation along river banks is a product of many fluvio-geomorphological processes, emphasizing the linkages between plant distribution, river flow, water levels and sediment transport (Naiman & Decamps 1997). Riparian vegetation is strongly influenced by water available for transport of propagules and the frequency of disturbance associated with flooding (Naiman & Decamps 1997), particularly in dispersing seed during winter flood events (Goodson *et al.* 2003). Riparian propagule bank composition can also be influenced by physical processes such as erosion and deposition of mineral and organic sediment (Abernethy & Willby 1999). Sediment and plant litter loads are directly related to seed transport (Nilsson & Svedmark 2002), with more sediment deposition being associated with a greater abundance of seeds along riverbanks (Cockel & Gurnell 2011; Pattison & Willby (Ch4)). Changes in disturbance regimes, such as increased flood frequency and associated nutrient and fine sediment inputs, can also facilitate invasion by invasive alien plant (IAP) species (Tererai *et al.* 2014).

The similarity between species composition of the propagule bank and above-ground vegetation is still used to interpret contributions of the propagule bank to vegetation maintenance and vice versa (Hopfensperger 2016). However, the degree to which riparian vegetation is maintained by recruitment from the germinable seed bank is still disputed (Tabacchi *et al.* 2005; Nilsson *et al.* 2010). Specifically, the degree to which environmental conditions (e.g. flood frequency, fertility) and competition with invasive alien and native dominant plants (those with the potential to form monospecific stands) impact the similarity between the propagule bank and established vegetation is poorly understood, particularly at a local scale. Invasion by IAPs exerts additional stress on riparian vegetation. Highly invaded sites, support reduced diversity of above-ground vegetation at both coarse (Pattison, Minderman & Willby 2016 (Ch2)) and fine scales (Hulme & Bremner 2005; Pattison, Vallejo-Marin & Willby (Ch3)). However, the degree to which IAPs drive these changes is often questioned (MacDougall & Turkington 2005; Thomas & Palmer 2015). Reduced richness and abundance of native species along invaded river banks can lead to lower richness and density of native propagules, especially under stands of large invasive species such as *Gunnera tinctoria* and *Heracleum mantegazzianum* (Gioria & Pyšek 2015).

Studies comparing the above-ground vegetation and propagule bank composition in invaded and uninvaded sites have shown reduced similarity at invaded sites within various habitats (Larson *et al.* 2013; Kundel, van Kleunen & Dawson 2014), but not specifically within riparian habitats (Gioria & Pyšek 2015). There may be properties of the propagule bank itself which influence invasion success along river banks. For example, species poor, low density propagule banks may increase invasibility, creating conditions which facilitate IAP establishment within the above-ground vegetation (Gioria & Pyšek 2015). Conversely, speciose sediment propagule banks may increase resilience to invasion (Gioria & Pyšek 2015) and environmental disturbance within the riparian zone (Gurnell *et al.* 2006). However, since ecosystem degradation can occur through multiple causes, teasing out the effects of a single factor such as invasion is difficult, and can confound restoration efforts targeted at single stressors (Tererai *et al.* 2015).

The composition of above-ground and propagule bank vegetation is generally related to disturbance intensity (Nilsson *et al.* 2010). Highly disturbed areas commonly show more similarity between these components, as vegetation is replenished through recruitment from a dormant propagule bank (Abernethy & Willby, 1999) or via propagules remobilised and deposited over winter along river margins (Goodson *et al.* 2002, 2003). Alternatively, in more stable sites vegetation is likely to be maintained by vegetative growth from overwintering rhizomes or other below-ground organs, with fewer opportunities for recruitment of long-lived or externally-derived propagules

(Goodson *et al.* 2001). Although soil propagule banks potentially influence vegetation composition after disturbance (Naiman & Decamps 1997), the species richness and abundance of germinable seeds can vary widely in riparian environments (Gurnell *et al.* 2006). However, greater abundance and richness of propagules within the seed bank may not necessarily translate to greater richness and abundance of above-ground vegetation.

Previous studies comparing community composition between the propagule bank and standing vegetation in riparian zones have shown low levels of similarity (Cockel & Gurnell 2011). However, few if any, have studied a gradient of similarity across a variety of rivers and asked how this is related to environmental conditions and competitive dynamics, including invasion. Assessing the extent to which above-ground vegetation is reliant upon local or external propagule inputs is challenging (Saatkamp, Poschlod & Venable 2014). Alongside environmental determinants of the propagule bank, competitive interactions between IAPs and native species should also be considered (Gioria & Pyšek 2015). Although IAPs are generally considered better competitors than natives (Daehler 2003), there is evidence that dominant native species can have a similarly strong influence on above-ground native vegetation (Bottollier-Curtet *et al.* 2011). The degree to which IAPs and dominant native species differ in their effect on subordinate native species is known to vary spatially (Pattison, Vallejo-Marin & Willby (Ch3)) and is likely to influence relatedness between propagule bank and above-ground vegetation both within and between sites.

This study assessed the similarity in species composition between the above-ground riparian vegetation and the propagule bank, along 20 rivers in central Scotland. Sites along these rivers covered a gradient of invasion (by the three major riparian IAPs *I. glandulifera*, *F. japonica* and *H. mantegazzianum*) and environmental conditions. Our aim was to determine how the similarity between above-ground vegetation and the propagule bank composition varied with IAP and native dominant species cover in relation to environment variables (e.g. bank elevation, flow variability). We also asked if the abundance and richness of the native seed bank affected (i) invasibility (the abundance of IAPs within the above-ground vegetation) and (ii) composition of the above-ground native vegetation at a site.

5.3 Methods

5.3.1 Vegetation data

Vegetation surveys were conducted along 20 lowland rivers in central Scotland, UK (see Ch4 Fig. 1). Rivers ranged between 10-75 m in channel width and 5-40 m in elevation. *I. glandulifera* is the most frequently occurring IAP across rivers in Scotland and commonly forms continuous monocultures along lowland rivers (Seager *et al.* 2012; Pattison, Minderman & Willby (Ch2)). Initial site searches revealed the widespread extent of *I. glandulifera* relative to the other IAPs, thus sites were selected that contained at least this species and were concentrated near the most downstream accessible point on each river. This meant that all study sites were adjacent to agricultural land or in urban/suburban areas. Sites varied in their level of invasion (quantified by % cover of IAPs) thus affording a gradient of potential invasion impact. Vegetation surveys were conducted during August 2013 (summer Yr 1), May 2014 (spring Yr 2) and August 2014 (summer Yr 2). Surveys began at a randomly selected point along a 100 m reach. A transect was established perpendicular to the channel and three 1 m^2 plots were positioned equidistantly between the water's edge (Q1), mid-bank height (Q2) and the bank top (Q3). A new transect was established every 10 m, with seven transects per site. A total of 21 plots were sampled within each site, with a combined total of 420 plots sampled across all rivers in each field season. In each plot all plants were identified to species level where possible and species abundance was quantified using the five point DAFOR 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 then converted to percentage cover for analyses (1= 1%, 2=6%, 3=18%, 4=38%, 5= 75%).

Alien species were defined in line with Preston et al. (2002) as those that colonised Britain with the aid of humans. We focused on the IAP species *I. glandulifera, H. mantegazzianum* and *F. japonica,* of which *I. glandulifera* accounted for 90% of the alien plant cover across sites. Other alien plants recorded included *Claytonia sibirica, Fallopia sachalinensis, Fallopia x bohemica* and *Mimulus guttatus.* Percentage cover of all alien species were combined and used to assess the effect of IAP cover on the relationship between the established vegetation and propagule bank. Dominant native species may have a comparable competitive ability to IAPs (Bottollier-Curtet *et al.* 2013). Therefore, to compare the effect of native dominant and IAP species on the association between established vegetation and propagule bank composition, natives were split into dominant and subordinate categories. Native dominant 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 mono-dominant stands alongside rivers in Britain. These species comprised *Aegopodium podagraria, Epilobium hirsutum, Fillipendula ulmaria, Glyceria maxima, Petasites hybridus, Phalaris arundinacea, Phragmites australis, Rubus fruticosus, Symphytum officinale* and *Urtica dioca.* The percentage cover of native dominant and subordinate species was determined by summing the individual % cover of the species belonging to these groups (Appendix Table 5).

5.3.2 Propagule bank collection

Soil samples (encompassing both seed and vegetative propagules) were collected during September 2013 to assess propagule bank characteristics after summer germination and replenishment by *in situ* reproduction. Soil samples were also collected in March 2014 to quantify over-winter deposition plus remnant propagules from the previous year. Soil cores (each 5 cm deep) were obtained from the three zones of the river bank (Q1, Q2, Q3) using a 7 cm diameter corer, with three replicate cores taken per plot, aggregated and sealed in plastic bags. In total 63 cores were taken across each site. Cores were kept in storage at 4°C until early April 2014 when they were processed.

Propagules introduced purely by overwinter deposition were quantified using artificial turf (AstroTurf ®) mats. Each mat was 30 x 30 cm, and covered with 1.5 cm length bristles. Eighteen mats were positioned at each site across the three bank zones in late September 2013. Mats were retrieved in March 2014 and stored in sealed plastic bags for a maximum of 2 weeks at 4-8°C (Fig. 2). All mats were weighed in order to assess differences in overwinter deposition between sites and bank elevations. This method provides a direct measure of sedimentation at discrete sites, over specific time periods and is indicative of the potential for hydrochory to contribute propagules to the riparian propagule bank (Steiger & Gurnell 2003).

Fig 2. Soil core and mat samples stored post collection, prior to germination trials.

5.3.3 Germination trial

Soil cores were aggregated and hand mixed for each bank zone then separated into three subsamples per bank zone, site and sampling date to account for available space in polytunnels (Fig. 3). Each subsample was then spread to an even depth (max. 2 cm) over a 25 x 30 cm seed tray previously filled with 3–4 cm sterile soil (John Innes #2). Mats were placed directly into trays filled with 3–4 cm sterile soil, having first being punctured to ensure that moisture could exchange with the underlying soil (Gurnell *et al.* 2007). Mats with little deposited sediment were augmented with additional sterile soil to prevent desiccation and maintain water percolation across the entire mat. All trays were then arranged randomly on the floor of an unheated polytunnel and watered twice daily (10 minutes per watering) using an automated pipe-feed system. Such conditions have been found to be highly conducive to germination of a wide range of riparian plant species (Abernethy & Willby 1999).

The seedling emergence method was used in which species and their abundance are estimated from the identification of seedlings, following greenhouse germination of soil samples (Gurnell *et al.* 2007). As seeds germinated, they were identified to species level and then removed or, where further growth was needed for identification purposes, grown in separate pots to prevent overcrowding. Once plants had flowered and could be identified they were removed to prevent reseeding. Wherever possible, seedlings were identified to species level although in a small number of cases it was only possible to identify to genus. The number of seedlings germinating was counted weekly to ensure that seedlings did not emerge and die between counts. Although this approach may underestimate absolute seed density it is a good comparative measure of the viable portion of the seed bank (Abernethy & Willby 1999). The germination trial extended over five months from mid-April 2014 until late September 2014.

Fig 3. From left to right: soil cores in the initial stages and after 3 months of growth.

5.3.4 Environmental predictors

Soil moisture was measured using a hand held soil moisture meter (SM150, Delta-T Devices Ltd, Cambridge, UK) at three points within each plot and averaged to obtain a mean percentage soil moisture per plot. Seven soil cores (each 5 cm deep) were taken across each site, combined and used to determine bulk density and organic matter content by loss on ignition following the methods of Wang *et al.* (2011). Tree density was inferred from the inverse of the proximity of a plot to the nearest mature tree and average upstream slope of the channel was calculated from the distance of the site from the river source and the difference in elevation over this distance.

Daily mean flow data were obtained from the Centre for Ecology and Hydrology's National River Flow Archive, based on data from the most downstream gauging station on each surveyed river, to assess the effect of hydrology on riparian vegetation. The Coefficient of Variation was used to express long term variability in flow (Riis *et al.* 2008) for each river using daily mean flow data from 1990 to 2014, as well as a short term two year period from 2012 to 2014 which overlapped with sampling. The percentage change in mean flow over the last 24 years was also calculated to characterise the general long term trend across each of the 20 rivers. The rivers studied showed a gradient of increase in mean annual flow ranging from 4-28% (Appendix Table 3).

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 data. Mean values of Total Oxidised Nitrogen, suspended solids, soluble reactive phosphorus and Alkalinity from this period were calculated from monthly or bimonthly sample data.

5.3.5 Statistical analyses

Native species composition at each site in different sampling seasons was compared using non-metric multidimensional scaling (NMDS), based on a Bray–Curtis dissimilarity (BCI) matrix.The relationship between the composition of subordinate native species (presence/absence) that germinated from the seed bank and those that occurred in field surveys was investigated using the Sorenson's Dissimilarity Index (SDI). SDI enabled comparability between propagule bank (count) and vegetation (abundance) data. SDI was calculated for a variety of propagule bank versus standing vegetation combinations (Fig. 4) at each bank zone (Q1, Q2, Q3) in both spring and summer. SDI ranges from 0 to 1, with 1 indicating no shared species, and has been widely used to assess the dissimilarity between propagule bank and above-ground vegetation (for example Gurnell *et al.* 2008; Casanova 2015). Species richness for both propagule bank seedlings and above-ground vegetation was considered to be the total number of species recorded within each bank zone per site. Total abundance was calculated by summing all species abundances (individual propagules or % cover) from each bank zone.

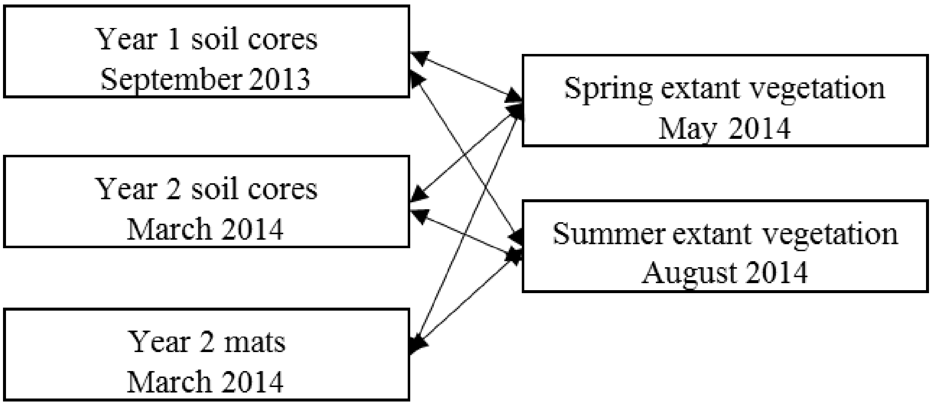

Fig 4. Permutations of Sorenson's Dissimilarity indices, calculated to assess the similarity between the propagule bank from 2013 and 2014 and extant vegetation in 2014. Arrows denote the variables compared to calculate Sorenson's Dissimilarity indices.

To avoid over-fitting the data, predictor variables were reduced to those with the largest effect size within each family of related predictor variables. For example, there were five candidate flow variables describing flow regime. These five variables were modelled as fixed effects against the response and the predictor with the largest effect size was retained for use in further analyses.

To assess which model best explained the relationship between SDI and the most important environmental variables, a set of candidate models were chosen prior to further data analyses (Burnham & Anderson 2002). We used corrected Akaike Information Criterion (AICc) (to correct for small sample sizes) and the information-theoretic approach (Burnham & Anderson 2002) to evaluate multiple regression models and select the ''best'' model from the set of candidate models. Models were compared using AICc, alongside model weights, therefore the model with the lowest AICc was considered the 'best' model given the data (Burnham & Anderson 2002). Thereafter, general linear regression was used to derive parameter estimates for the models with greatest support. Response variables were SDI between cores Yr1 vs vegetation Yr2; cores Yr2 vs vegetation Yr2; and mats vs vegetation Yr2, for both spring and summer data. Fixed effects were dominant native species cover, IAP cover, soil moisture, tree density, channel gradient, short term coefficient of variation of flow, sediment weight, and water column soluble reactive phosphorus and suspended solids concentrations.

In order to assess the contribution of propagule bank species to the abundance of IAPs, dominant and subordinate native species, a set of candidate models were also chosen and treated in the same way. Model response variables used in general linear models were 1) IAP % cover (sqrt transformed); 2), native dominant species % cover (log transformed); 3) native subordinate species % cover (sqrt transformed) and 4) subordinate native species richness (negative binomial). Inspection of the fitted model for subordinate native species richness indicated that the data were overdispersed. A negative binomial likelihood was used as a robust alternative to the poisson distribution for overdispersed data (Gelman *et al.* 1997). Fixed effects were seedling abundance from cores Yr1; mats and cores Yr2; and seedling species richness from cores Yr1, mats and cores Yr2. Abundance and richness of subordinate native species in the propagule bank were used as predictors to model dominant and subordinate native cover and richness in the established vegetation, whilst native species abundance and richness was used to model IAP cover.

Data for each bank position (Q1, Q2, Q3) per season (spring, summer) were modelled separately, as modelling all the data in one global model would result in multiple interactions and this risked overfitting the data. This approach also enabled clear visualisation of the data. All predictors were standardised to one standard deviation prior to statistical analyses, in order to assess relative effect sizes of each predictor directly (Schielzeth 2010). Multicollinearity among predictor variables was checked before use in multiple regression analyses, retaining only those variables which were not highly correlated ($r = <0.60$). The “best” model within the candidate set was used to derive parameter estimates and 95% confidence intervals. R^2 and adjusted R^2 values are reported for each model.

All statistical analyses and graphics were produced using R Studio version R 3.2.2 (R Development Core Team 2015), with the additional packages vegan (Oksanen 2015) and MuMIn (Barton 2016).

5.4 Results

5.4.1 Dissimilarity between seedbank and standing vegetation

Species composition of the above-ground vegetation changed between year and season (Fig. 5). Plots between years diverged, shown by the change in position of the centroid. The greatest difference in the above-ground vegetation community composition occurred between summer year 1 and 2. By comparison the seedbank composition showed little variation between year and season.

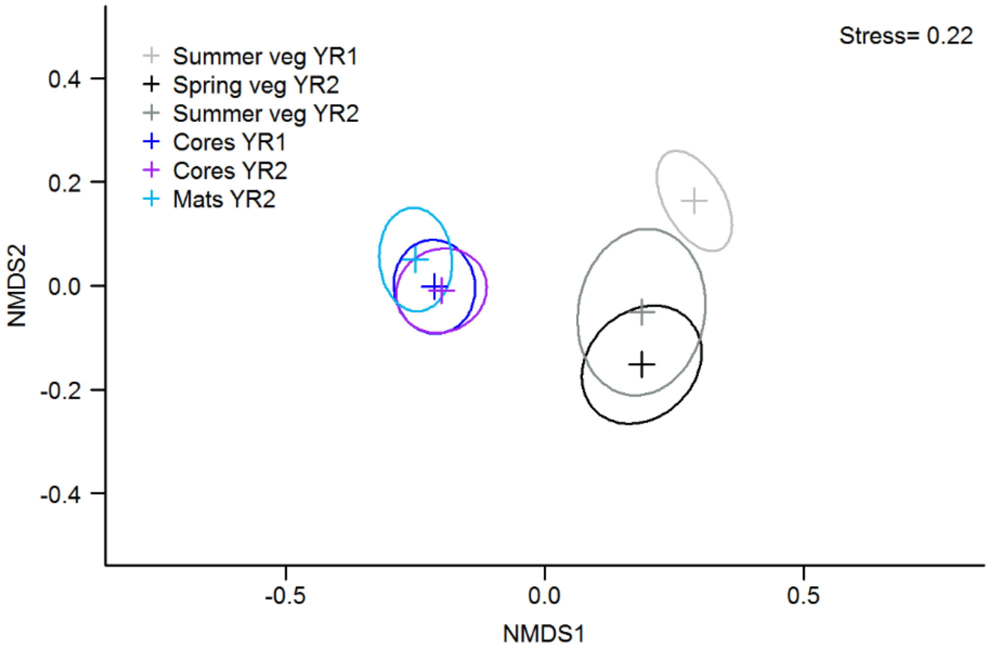

Fig 5. Non metric multidimensional scaling diagram (NMDS) of the above-ground species composition of sites along 20 rivers. Symbols indicate the mean community composition for above-ground vegetation in summer YR1, spring Yr2 summer Yr2, and propagule composition in soil cores YR1 and Yr2 and mats Yr2, surrounded by ellipses representing ± CI.

Sorensen's index of dissimilarity (SDI) showed little difference between the permutations of comparison in both spring and summer (Table 1) and was consistently high. Similarity between cores Yr1 or Yr2 and spring and summer standing vegetation was virtually unaffected by bank position. SDI on the mats compared to spring and summer standing vegetation revealed a greater dissimilarity at the top of the river bank.

Table 1. Average Sorensen's dissimilarity index between different components of the native subordinate (sub-native) propagule bank and above-ground native subordinate vegetation at different bank positions, in spring and summer 2014. Bank position Q1= water's edge, Q2= mid-bank height and Q3= the bank top.

	Mats Sub-native	Core Yr1 Sub-native	Core Yr2 Sub-native
Spring			
Q1	0.76	0.74	0.75
Q2	0.78	0.77	0.76
Q3	0.82	0.76	0.75
Site	0.78	0.76	0.75
Summer			
Q1	0.75	0.72	0.73
Q2	0.80	0.79	0.78
Q3	0.81	0.73	0.71
Site	0.79	0.75	0.74

The effect of native dominant and IAP cover on the similarity of propagule bank and above-ground vegetation communities (SDI) exceeded the effect of abiotic factors in summer, closest to the water's edge (Q1) (Table 2). Overall, greater dissimilarity between propagule bank and above-ground vegetation in summer Yr2 was associated with greater IAP and native dominant species cover closest to the water's edge (Q1), as well as greater sediment deposition at the top of the riparian bank (Q3) (Fig. 6). There was a greater negative effect of IAP compared to native dominant species cover on community similarity between mat propagules Yr2 and above-ground summer Yr2 vegetation at the water's edge. Greater IAP cover was also associated with increased dissimilarity when comparing the cores Yr1 and mats to the above-ground summer Yr2 vegetation, but in these cases the IAP effect was similar to that of native dominant species. At the top of the bank (Q3), furthest from the water's edge, plant communities in the cores Yr1 and 2 and mats were more dissimilar to the above-ground summer Yr2 vegetation when sediment deposition was higher (Fig. 6). In spring there was greater dissimilarity between above ground vegetation and propagules on mats when flow variability was higher (not illustrated; see Appendix Table 6).

Table 2. Comparison of models derived from *a priori* hypotheses about processes capable of influencing similarity between the propagule bank and above-ground vegetation in spring and summer, at different riparian bank zones. Models were fitted using general linear models. For each candidate model, Akaike's Information Criterion (AICc) and Akaike weights (*Wi*) are presented. Model numbers represent various fitted predictors: Mod2: Global model; Mod3: dominant native cover + IAP cover; Mod4: short term CoV + sediment; Mod5: suspended solids + phosphorus; Mod6: channel slope + sediment; Mod7: sediment; Mod8: short term CoV; Mod9: dominant native cover + IAP cover + soil moisture.

		Spring						Summer					
		Core Yr1		Mats		Core Yr2		Core Yr1		Mats		Core Yr2	
Bank position	Model	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*
Q1	Null	-36.26	0.19	**-29.41**	**0.46**	**-23.73**	**0.47**	-29.94	0.10	-31.86	0.29	-28.39	0.01
	Mod2	-15.76	0.00	-5.32	0.00	0.37	0.00	-12.84	0.00	-13.74	0.00	-16.88	0.00
	Mod3	-33.53	0.05	-23.89	0.03	-20.55	0.10	**-33.35**	**0.55**	**-32.10**	**0.33**	**-36.59**	**0.69**
	Mod4	-34.63	0.09	-24.93	0.05	-18.59	0.04	-24.96	0.01	-27.49	0.03	-23.99	0.00
	Mod5	-30.52	0.01	-25.86	0.08	-18.79	0.04	-25.16	0.01	-27.36	0.03	-33.06	0.12
	Mod6	-36.32	0.20	-24.83	0.05	-18.78	0.04	-24.92	0.01	-26.44	0.02	-25.23	0.00
	Mod7	**-37.71**	**0.39**	-27.34	0.16	-20.99	0.12	-27.85	0.04	-29.06	0.07	-26.12	0.00
	Mod8	-33.48	0.05	-27.44	0.17	-21.72	0.17	-27.48	0.03	-30.64	0.16	-26.51	0.00
	Mod9	-32.20	0.03	-20.49	0.01	-17.52	0.02	-31.83	0.26	-29.22	0.08	-33.73	0.17
Q2	Null	-40.78	0.31	-41.78	0.16	**-36.61**	**0.56**	**-22.59**	**0.44**	**-31.56**	**0.36**	**-22.79**	**0.43**
	Mod2	-20.04	0.00	-24.52	0.00	-7.91	0.00	2.76	0.00	-11.24	0.00	2.32	0.00
	Mod3	-35.54	0.02	-37.60	0.02	-31.53	0.04	-19.80	0.11	-30.44	0.20	-21.67	0.24
	Mod4	-38.07	0.08	-41.07	0.11	-30.79	0.03	-17.92	0.04	-27.49	0.05	-16.85	0.02
	Mod5	-37.51	0.06	-37.81	0.02	-30.83	0.03	-17.95	0.04	-23.30	0.01	-17.22	0.03
	Mod6	-38.00	0.08	-40.89	0.10	-31.30	0.04	-17.68	0.04	-24.64	0.01	-17.25	0.03
	Mod7	-38.10	0.08	-39.04	0.04	-33.90	0.14	-20.83	0.18	-28.02	0.06	-20.00	0.11
	Mod8	**-41.06**	**0.36**	**-44.19**	**0.54**	-33.87	0.14	-20.07	0.13	-30.66	0.23	-20.02	0.11
	Mod9	-31.92	0.00	-34.07	0.00	-29.74	0.02	-16.27	0.02	-28.73	0.09	-18.27	0.04
Q3	Null	**-16.57**	**0.37**	**-37.05**	**0.52**	-24.56	0.24	-27.09	0.19	-29.90	0.17	-23.46	0.00
	Mod2	7.40	0.00	-11.86	0.00	-0.49	0.00	-5.02	0.00	-13.76	0.00	-13.68	0.00
	Mod3	-12.99	0.06	-32.71	0.06	-19.95	0.02	-21.73	0.01	-28.05	0.07	-20.85	0.00
	Mod4	-12.83	0.06	-31.10	0.03	-22.57	0.09	-25.62	0.09	-28.70	0.09	-34.23	0.43
	Mod5	-11.93	0.04	-31.43	0.03	-23.70	0.16	-21.77	0.01	-25.36	0.02	-24.10	0.00
	Mod6	-10.90	0.02	-32.53	0.05	-22.38	0.08	-27.14	0.20	-29.79	0.16	-31.33	0.10
	Mod7	-13.88	0.10	-34.26	0.13	**-25.03**	**0.31**	**-28.76**	**0.44**	**-31.84**	**0.44**	**-34.33**	**0.46**
	Mod8	-15.95	0.27	-34.27	0.13	-22.60	0.09	-24.39	0.05	-27.19	0.04	-22.85	0.00
	Mod9	-13.75	0.09	-32.48	0.05	-18.43	0.01	-18.21	0.00	-24.43	0.01	-18.38	0.00

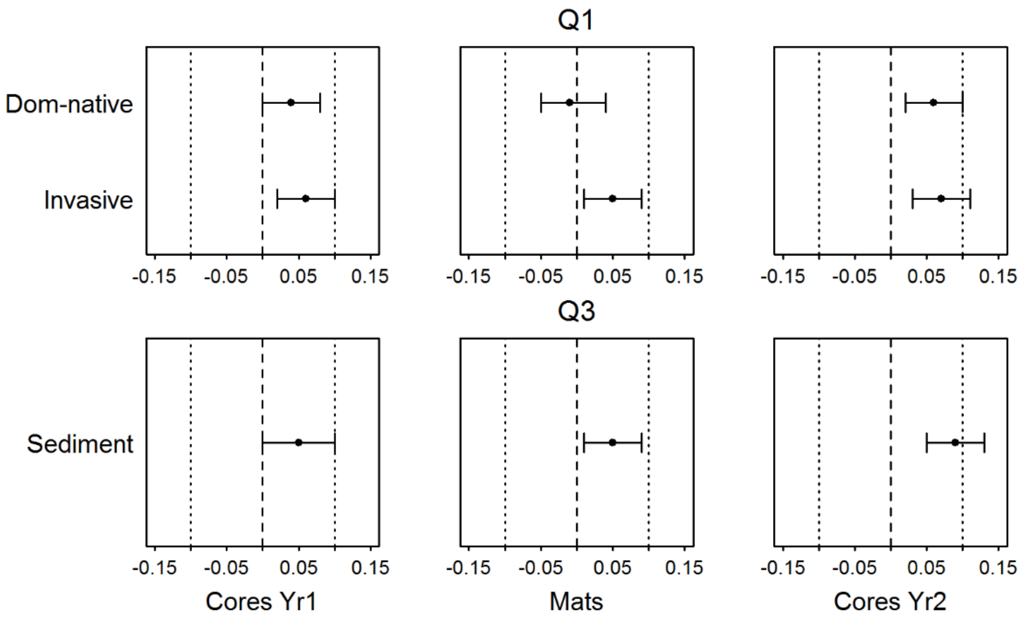

Fig 6. Parameter estimates ± 95% confidence intervals. Model response was Sorenson's Dissimilarity Index between summer 2014 above-ground subordinate vegetation and cores Yr1 (left), mats (centre) and cores Yr2 (right), at bank zone Q1 (water's edge) and Q3 (bank top). All explanatory variables Dominant native and IAP % cover and sediment (kg) were standardised to 1SD prior to analyses. Dotted lines represent an effect size of 0.1.

5.4.3 Seedbank contribution to standing vegetation cover

Over the duration of the germination trials, a total of 44693 seedlings germinated from the soil seed bank samples with 15650, 12830 and 16213 germinating from cores (Yr1), mats and cores (Yr2) respectively. Subordinate native species accounted for 84% of total viable seeds.

Overall, there was little effect of increasing density or richness of propagules on IAP cover (Table 3; Appendix Table7). More native propagules deposited over-winter (mats) was associated with lower IAP cover in spring at the upper most bank elevation (Fig. 7a), but in summer Yr2 this relationship was reversed (Fig. 7b).

Native dominant species cover was negatively associated with subordinate species richness in the propagule bank in spring (Fig. 7c) and summer (Fig. 7d), further from the water's edge (Q2, Q3), although species richness of mat propagules was positively associated with native dominant species cover at the top of the riparian bank in summer

(Fig. 7e). There was also a negative association between native dominant species and density of native subordinate species in the Yr2 soil cores in spring (Fig. 7f) and mats in summer (Fig. 7g).

In spring and summer, above-ground subordinate species cover (Fig. 7h) and richness (Fig.7 i, j) was positively associated with subordinate propagule richness in Yr2 cores, close to the water's edge. The density of propagules on the mats was positively associated with above-ground subordinate species cover in spring (Fig. 7k), however greater mat propagule species richness was negatively associated with above-ground subordinate cover (Fig. 7l).

Table 3. Comparison of models derived from a priori hypotheses about propagule bank richness and abundance influencing above-ground vegetation in spring and summer, at different riparian bank zones. Models were fitted using general linear models for IAP, dominant native and subordinate cover. Negative binomial models were fitted for subordinate native richness. For each candidate model, Akaike's Information Criterion (AICc) and Akaike weights (Wi) are presented. Model numbers represent various fitted predictors. Mod2: global model; Mod3: mat seedling abundance + core Yr2 seedling abundance; Mod4: mat species richness + core Yr2 species richness; Mod5: mat seedling abundance + mat Yr2 species richness; Mod6: core Yr2 seedling abundance + core Yr2 species richness; Mod7: mat seedling abundance; Mod8: core Yr2 seedling abundance; Mod9: mat species richness; Mod10: core Yr2 species richness.

		Spring '14								Summer '14							
Bank zone	Model	IAP cover		Dom-native cover		Sub-native cover		Sub-native richness		IAP cover		Dom-native cover		Sub-native cover		Sub-native richness	
		AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*	AICc	*Wi*
Q1	Null	**82.82**	**0.39**	**48.17**	**0.22**	96.23	0.19	137.37	0.07	**91.93**	**0.42**	**28.56**	**0.31**	95.75	0.19	**149.39**	**0.13**
	Mod2	94.23	0.00	54.10	0.01	104.07	0.00	143.76	0.00	104.53	0.00	37.24	0.00	104.10	0.00	157.58	0.00
	Mod3	87.29	0.04	53.17	0.02	97.70	0.09	140.32	0.02	97.19	0.03	32.69	0.04	98.37	0.05	153.68	0.02
	Mod4	88.05	0.03	51.42	0.04	96.99	0.13	136.01	0.13	97.27	0.03	31.24	0.08	97.59	0.08	149.99	0.10
	Mod5	88.09	0.03	49.06	0.14	101.78	0.01	141.49	0.01	97.38	0.03	32.99	0.03	101.15	0.01	154.51	0.01
	Mod6	88.04	0.03	48.96	0.15	98.54	0.06	136.40	0.11	97.33	0.03	32.73	0.04	97.62	0.07	149.80	0.11
	Mod7	85.39	0.11	50.04	0.09	98.75	0.05	139.57	0.02	94.68	0.11	30.10	0.15	98.44	0.05	151.94	0.04
	Mod8	85.11	0.13	50.92	0.06	96.40	0.17	137.17	0.07	94.38	0.12	31.31	0.08	96.34	0.14	150.52	0.08
	Mod9	85.51	0.10	49.36	0.12	98.70	0.05	138.34	0.04	94.25	0.13	30.41	0.12	98.35	0.05	151.35	0.05
	Mod10	84.89	0.14	49.07	0.14	**95.61**	**0.25**	**133.24**	**0.53**	94.70	0.11	30.19	0.14	**94.47**	**0.36**	146.85	0.47
Q2	Null	**95.03**	**0.28**	47.80	0.02	90.70	0.00	**126.03**	**0.27**	98.24	0.04	48.97	0.02	97.89	0.24	**141.20**	**0.36**
	Mod2	103.96	0.00	47.92	0.02	84.57	0.02	135.28	0.00	101.23	0.01	51.99	0.00	106.31	0.00	153.04	0.00
	Mod3	97.36	0.09	48.68	0.01	95.67	0.00	129.52	0.05	95.39	0.18	54.13	0.00	103.77	0.01	146.31	0.03
	Mod4	100.90	0.02	42.67	0.20	79.07	0.37	129.08	0.06	102.02	0.01	44.65	0.14	100.05	0.08	145.66	0.04
	Mod5	98.62	0.05	51.88	0.00	93.70	0.00	130.17	0.03	96.11	0.12	54.10	0.00	103.40	0.02	146.27	0.03

	Mod6	98.35	0.05	41.97	0.28	81.52	0.11	128.62	0.07	102.93	0.00	44.40	0.16	99.54	0.11	145.69	0.04
	Mod7	96.03	0.17	50.53	0.00	93.20	0.00	127.07	0.16	**93.00**	**0.58**	51.24	0.01	100.61	0.06	143.14	0.14
	Mod8	95.73	0.20	45.58	0.05	92.62	0.00	128.59	0.07	100.00	0.02	51.31	0.01	100.68	0.06	143.97	0.09
	Mod9	97.77	0.07	49.64	0.01	92.41	0.00	127.96	0.10	98.87	0.03	51.76	0.00	100.55	0.06	143.86	0.10
	Mod10	97.79	0.07	**41.20**	**0.42**	**78.52**	**0.49**	126.79	0.18	101.03	0.01	**41.50**	**0.67**	**97.07**	**0.36**	142.58	0.18
Q3	Null	79.93	0.08	45.86	0.13	87.46	0.08	**126.19**	**0.27**	**101.81**	**0.31**	55.49	0.05	93.50	0.17	**126.15**	**0.32**
	Mod2	85.62	0.01	52.87	0.00	89.96	0.02	136.12	0.00	112.12	0.00	54.50	0.08	100.11	0.01	137.00	0.00
	Mod3	79.18	0.12	45.77	0.14	84.87	0.28	130.64	0.03	106.48	0.03	53.27	0.14	93.96	0.13	131.37	0.02
	Mod4	84.97	0.01	51.78	0.01	91.88	0.01	129.13	0.06	105.27	0.06	61.30	0.00	97.52	0.02	129.44	0.06
	Mod5	77.85	0.23	50.96	0.01	**84.85**	**0.28**	131.04	0.02	106.50	0.03	**50.88**	**0.46**	95.19	0.07	130.96	0.03
	Mod6	85.81	0.00	46.07	0.12	88.68	0.04	128.55	0.08	105.47	0.05	59.88	0.01	94.46	0.10	129.62	0.06
	Mod7	**76.40**	**0.48**	48.29	0.04	86.81	0.11	128.97	0.07	103.77	0.12	52.21	0.23	95.18	0.07	128.93	0.08
	Mod8	82.72	0.02	**43.29**	**0.48**	86.47	0.13	127.47	0.14	104.42	0.08	57.03	0.02	**92.42**	**0.29**	128.21	0.11
	Mod9	81.97	0.03	48.64	0.03	90.15	0.02	128.25	0.10	104.57	0.08	58.25	0.01	95.95	0.05	128.18	0.11
	Mod10	82.66	0.02	48.63	0.03	88.78	0.04	126.61	0.22	102.30	0.24	58.16	0.01	94.63	0.09	126.95	0.21

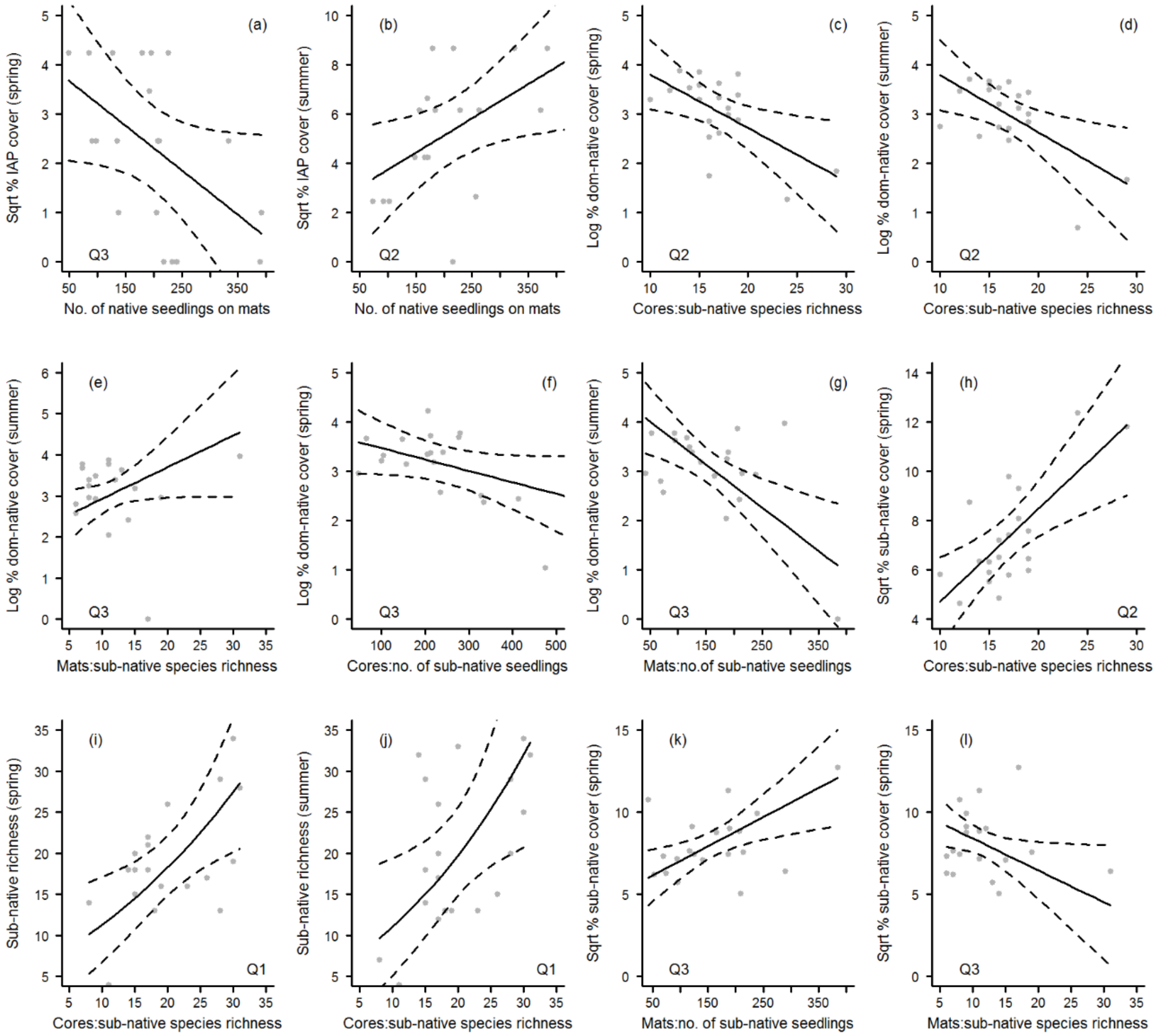

Fig 7. Best model fits, from multiple regression models, to the field data (circles) are visualized by continuous lines. The 95% confidence intervals of the modelled relationships are displayed by the dotted lines. Q represents the positon along the riparian bank where a quadrat was placed. Q1 = closest to the water's edge, Q2= middle of the riparian bank and Q3 = top of the riparian bank denoted by the trash line.

5.5 Discussion

Our study showed that species composition of the above-ground riparian vegetation and propagule bank is generally dissimilar, increasingly so when assessing the contribution of over-winter deposited propagules to standing vegetation at higher bank elevations. Community dissimilarity in this study was associated to a greater extent with IAP and native dominant plant cover compared to environmental variables, emphasizing the importance of competitive interactions in structuring riparian vegetation. Propagule bank density and richness had little impact on above-ground IAP cover, which may serve to perpetuate invasions even in situations where invasive plants are actively managed.

5.5.1 Similarity between propagule bank and above-ground vegetation

Results showed no distinct differentiation between the similarity of spring or summer above-ground vegetation versus the soil propagule bank, or with increasing bank elevation. Generally, dissimilarity between the propagule bank and vegetation was high, as observed in other studies, such as Capon & Brock (2006), where the propagule bank is dominated by few species not present in the standing vegetation. However, when comparing spring and summer above-ground vegetation to propagules deposited over-winter on mats, the communities were less similar with increasing bank elevation. This is indicative of establishment from water-borne seed occurring primarily at lower bank elevations (Richardson *et al.* 2007). Above-ground vegetation and propagule bank composition was also more dissimilar at the top of the bank in situations where sediment deposition was higher. Previous studies have shown that greater sediment deposition along riparian zones is associated with increased species richness and abundance within the propagule bank (Cockel & Gurnell 2011, Pattison & Willby (Ch4)). However, above-ground vegetation in less disturbed areas of the bank is often maintained by a predominantly vegetative propagule bank (Goodson *et al.* 2003). Native dominant and IAP species may therefore emerge and establish prior to germination of a more speciose propagule bank often dominated by ruderal, annual species (Gurnell *et al.* 2008). Greater sediment deposition at these sites may mean greater opportunities for dispersal but not necessarily for germination (Goodson *et al.* 2003), as our results suggest that the main limitation to native species establishment is equally invasion by IAPs and competition with native dominant species rather than underlying environmental conditions at these sites. Environmental conditions may however affect the balance between sexual and clonal reproduction for many species, with fewer perennial, vegetatively reproducing species being represented in the propagule bank from disturbed sites (Casanova 2015). This may therefore reflect the greater dissimilarity seen between the propagule bank and standing vegetation at higher elevations with greater sediment deposition.

The prevalence of low to moderate similarity between regenerative and established components of wetland vegetation may be attributed to varying hydrology and the presence of both transient and persistent seed bank species (Hopfensperger 2016). Plant communities closer to the water's edge are structured more strongly by abiotic factors and are generally dominated by flood-tolerant and annual species which can complete their life cycles between major flood events (Abernethy & Willby 1999; Capon 2005). Based on previous studies we therefore expected greater similarity between the propagule bank and above-ground vegetation, in flood-disturbed areas. However, closest to the water's edge banks with greater cover of IAP or native dominant species were more dissimilar, suggesting that large stands of IAP and native dominant species are indicative of less disturbance. Invasion by IAPs is generally seen as an indicator of disturbance (Willby 2007), with the initial colonisation by IAPs often driven through increased flood frequency (Pattison, Minderman & Willby (Ch2)), urban habitat fragmentation (Gaertner *et al.* 2016), nutrient enrichment (Lake & Leishman 2004) and sediment deposition (Goodson *et al.* 2003). Whilst the initial arrival and establishment of IAPs is well documented within the literature, there is still uncertainty as to how IAP populations are maintained and persist within dynamic environments such as riparian zones (Richardson *et al.* 2007). Indeed, once-formed, dominant stands of IAPs should persist best under *less* disturbed conditions, such as stable hydrological regimes during the growing season. Therefore, greater coverage by competitive species in intermittently disturbed areas of the riparian zone suggests intrinsic local stability rather than continued disturbance, as the similarity between summer vegetation and propagule bank was higher under low cover of IAP and dominant native species.

Less similarity in species composition between components may also be driven by IAP and native dominant species suppressing recruitment of subordinate native species, as this same effect was lacking in spring, when the height and cover of IAPs and native dominant species are much lower (Pattison, Vallejo-Marin & Willby (Ch3)). Although environmental factors in these more disturbed areas of the riparian zone are generally thought to control species composition, Fraaije et al. (2015) showed that timing of seed arrival was the primary mechanism for plant germination and establishment in the riparian zone, consistent with the lack of competitive effect we observed in spring. At the top of the bank, which is less-fluvially disturbed, biotic factors such as competitive exclusion can be more important in structuring the plant community (Capon 2005). Unexpectedly, however, our results showed no effect of IAP or native dominant species cover on similarity between above-ground vegetation and propagule bank species at the top of the bank. This may because the top of the bank is generally so much less disturbed that there is already a high dissimilarity between the propagule bank and standing vegetation and the gradient of dissimilarity is therefore characteristically short. In this location established vegetation was generally less diverse, presumably due to reduced fluvial disturbance, increased competition and less effective water-borne dispersal (Gurnell *et al.* 2008) and fewer opportunities for recruitment, resulting in less variation in species composition both within and between sites. This is in contrast to areas closest to the water's edge which are more dynamic (Renöfält *et al.* 2005), and hence show greater variation in both the density and richness of both above-ground and propagule bank vegetation.

5.5.2 Influence of propagule bank on above-ground vegetation

Levine & D'Antonio (1999) proposed that species-rich communities would be less invasible due to lack of available resources, although contrary evidence has also been produced (for example Maskell *et al.* 2006). Within riparian zones IAPs can have a negative effect on the propagule bank (Gioria & Osborne 2009) and propagule banks in heavily invaded sites are often dominated by seeds of a few agricultural weed species and rushes (Gioria & Osborne 2010). Therefore, alterations in soil seed banks as a consequence of plant invasions could, in turn, facilitate further colonization by other invasive species (Gioria & Osborne 2010), thus reducing the effectiveness of treatment or removal programmes. However, despite the potentially important influence of seed banks on plant invasions, quantitative evidence that seed banks actually promote invasiveness and invasibility is rather scarce (Gioria, Pyšek & Moravcova 2012).

Our results showed no consistent pattern of suppression of above-ground IAP cover in the riparian zone where there was greater native species richness or density of propagules in the propagule bank. A similar effect was found when experimentally adding more diverse seeds to a tallgrass prairie restoration site in the US (Larson *et al.* 2013). Greater species richness in the seed bank did not reduce the above-ground cover of the IAP *Cirsium arvense*, however, greater abundance of grasses such as *Elymus canadensis* and *Elymus trachycaulus* did have a negative impact on *C. arvense* (Larson *et al.* 2013). In our study, in spring, a greater number of propagules of native species deposited over-winter was negatively associated with above-ground IAP cover. This may be indicative of an upstream catchment being uninvaded or poorly suited to IAPs, hence less establishment of IAPs at these sites from freshly deposited propagules. Sarneel et al. (2016) showed that the presence and relative abundance of subordinate species depends on arrival time at a site. Priority effects driven by arrival time (Sarneel *et al.* 2016), may thus enable colonisation and establishment of less competitive species in spring within areas previously dominated by high IAP cover. However, by summer, a negative relationship with IAP cover was no longer evident, perhaps due to their superior competitive ability (Bottollier-Curtet *et al.* 2013). Indeed, across the middle of the bank (Q2), there was a positive association between the amount of native seed deposited over winter and above-ground IAP cover. This is an unexpected result that we attribute to deposition favouring both IAP and native propagules at some sites, particularly those within a heavily invaded catchment.

In both spring and summer, above-ground native dominant species cover was negatively associated with the density and species richness of native subordinate seedlings in the propagule bank closest to the water’s edge. This relationship did not, however, apply to IAPs. This suggest that conditions such as flood events or sediment deposition which favour abundance of native subordinate species in the propagule bank (Gioria & Pyšek 2015), may prevent native dominant species, not IAPs, from reaching high cover in the established vegetation. Conversely, the loss of transient species from a community, such as ruderal, annual species, inevitably affects the probability of colonization and establishment of species such as IAPs after a disturbance event (Grime 1998). Our results, however, offer no evidence that a larger subordinate propagule bank will support more subordinate native species in the above-ground vegetation, particularly in summer, or that it increases resistance to invasion.

5.5.3 Conclusion

Our study demonstrates the importance of IAP and dominant native species in explaining similarity between the propagule bank and above-ground vegetation. Even in flood disturbed areas of the riparian zone, prevailing environmental conditions were not the primary driver of similarity. Spring vegetation was less constrained by competitive effects, suggesting the importance of arrival time of propagules and germination prior to onset of growth by more competitive species (Sarneel *et al.* 2014). One of the primary objectives in determining the relationship between IAPs and the propagule bank is to inform decisions behind restoration. However, the native propagule bank had no consistent effect on the above-ground cover of IAPs and therefore cannot be relied upon to increase rate of recovery or resistance to invasion. Restoration efforts after invasive species removal may require additional seed input if seed banks are depleted or differ strongly in composition from the desired endpoint due to invasion (Kundel, van Kleunen & Dawson 2014). Our study indicates that a high density and richness of subordinate native species in the propagule bank does not guarantee these attributes in the above-ground community. Alongside this effect the deposition of sediment in riparian zones provides opportunities for colonisation, but local conditions and the abundance of IAPs and dominant native species will likely regulate establishment success.

Chapter 6: General discussion

6.1 Invasion ecology so far

The literature on biological invasions has grown rapidly since Charles Elton's seminal work "The ecology of invasions by animals and plants." in 1958 (Elton 1958). Scientists, managers, policy makers and the public have become increasingly aware of the many applied issues of managing invasive species, as well as the fundamental ecological questions raised by biological invasions. Numerous questions in invasion science have been highlighted over recent years, often around the various hypotheses that attempt to explain biological invasions, such as the evolution of increased competitive ability hypothesis (Blossey & Nötzold 1995). Many experimental studies have tested these hypotheses, particularly in the context of propagule pressure and enemy release (for reviews see Colautti, Grigorovich & MacIsaac 2006; Liu & Stiling 2006). Many studies have assessed the impacts of invasion on native ecosystems and the consequences of biological control (for reviews see Messing & Wright 2006; Simberloff *et al.* 2013). Terrestrial systems are most strongly represented within this literature, with far fewer studies focused on freshwater systems (Lowry *et al.* 2013). Studies on plants dominate the invasion biology literature and many advances have been made in understanding the causes of invasion and impacts of key invasive plant species on native ecosystems.

Freshwater systems, particularly rivers, are tremendously important both economically and biologically, with our reliance on freshwater ecosystem services being unquestionable (Capon *et al.* 2013). Within riparian habitats native vegetation plays a key role in many abiotic and biotic processes (Gurnell *et al.* 2012), such as sediment retention, nutrient uptake, temperature regulation, and the global interest in understanding the cause and impacts of invaders in such habitats has grown rapidly, particularly in the face of climate change (Lowry *et al.* 2013). Within Europe, countries such as the Czech Republic (Pyšek *et al.* 2012), Ireland (Gioria & Osborne 2014) and Great Britain have made significant progress in advancing our knowledge of *I. glandulifera*, *F. japonica* and *H. mantegazzianum* and Britain has played a key role in research on the biological control of these species (Pratt *et al.* 2013; Tanner *et al.* 2015).

Although many advances have been made in understanding various aspects of plant invasions, contention still surrounds the impact of the key invaders on native species, particularly within naturally dynamic riparian environments. The questions addressed in this thesis are a result of literature reviews, observations made in the field or inspired by the ongoing debate regarding the impact of IAP species on native communities, relative to native dominant plant species and set against a backdrop of ongoing environmental change. This thesis addresses these questions using sites covering a gradient of invasion intensity and environmental conditions. In this respect it departs from direct comparisons of invaded versus uninvaded sites (for example see Hejda, Pyšek & Jarošík 2009), which, though useful, carry some major limitations (Sax, Kinlan & Smith 2005).

Fig 1. Bank of the River Teith invaded by *Fallopia sachalinensis*, *Heracleum mantegazzianum* and *Impatiens glandulifera*, May 2014.

6.2 Conditions promoting growth of IAP and native species

Chapter 2 challenges findings from recent studies (see Maskell *et al.* 2006; Thomas & Palmer 2015) which assess the impact of plant invasions over large spatial and temporal scales, and have suggested a lack of negative impact on native flora. In our study it was not only the overall impact on native communities that was of interest, but also the extent of this impact relative to other environmental variables. Although an increasing abundance of IAPs was associated with a decline in native plant diversity, land use had the greatest effect on turnover of native vegetation over time. However, over the last 30 years there has been an increase in the presence of IAPs within riparian zones, particularly along lowland rivers where reduced native diversity is also evident. Change in river flow regime, such as an increase in high flow events, were also associated with an increase in the incidence of IAPs along lowland rivers. In contrast, longer low flow periods have increased the abundance of native dominant plants along lowland rivers, highlighting the conditions favourable to both IAP and native species success on a national scale. This study also highlighted the progression of IAP colonisation into upland rivers, which could pose risks to native flora of greater conservation significance and potentially create further impact downstream.

On a local patch scale environmental variables also differentially affected the abundance of IAP (particularly *I. glandulifera*) and native dominant species along lowland rivers. Chapter 3 demonstrated the opposing associations between IAP and native dominant species with greater soil moisture. In spring, native dominant species cover was greater closest to the water's edge compared to IAP cover. Across study sites, native dominant species, such as *Phalaris arundinacea*, formed dense stands along the water's edge, able to persist in damp conditions. Therefore, although increased flood frequency may improve opportunities for dispersal and colonisations of IAPs, high soil moisture due to frequent inundation is unfavourable for IAP growth. This suggests that pressures on riparian zones such as drought, abstraction, channel incision and sedimentation will tend to favour IAPs at the expense of native dominant species. In chapter 5 dense stands of IAPs along the water's edge were associated with more stable conditions and IAPs attained greater cover within low energy environments, further highlighting a need for low disturbance. This suggests that disturbance, such as flooding or habitat alteration, can promote the spread of IAPs, but for them to attain high abundance stable conditions are required.

6.3 Competitive effects of IAPs and native dominant species

Throughout this thesis the importance of competitive interactions between IAPs and native species has been demonstrated in chapters 3, 4 and 5. Experimental studies have addressed whether or not native dominant species are as competitive as IAPs (see review Daehler 2003), however, there is still little consensus on this subject. Field-based observations can enable us to assess the effect of IAP and native dominant species abundance on the vegetation community as a whole, compared to experimental studies. Chapter 3 showed that IAPs generally had little or no effect in spring when their abundance was substantially lower compared to native species, particularly native dominant species such as *Aegopodium podagraria* and *Urtica dioica* which emerge early in spring. Native dominant species had a greater negative effect in spring closer to the water's edge where they frequently dominate. In comparison IAPs have a greater negative effect in summer at the top of the riparian bank, where they can maintain large monospecific stands. Although both native dominant and IAP species were negatively associated with subordinate species cover, species richness of the subordinate species community was less affected. Our results highlight previous questions raised by studies such as those of Gurevitch and Padilla (2004), which ask whether there is an association between IAPs and the extinction of native flora. In areas where species richness declined following invasion by *Impatiens glandulifera*, Hulme and Bremner (2006) have suggested that the species lost were common and not permanently excluded to the extent where extinction of the species was a concern. This suggests that a focus on how native plant communities differ between those dominated by IAPs or by native dominant species, would be a better basis for understanding the impact of invasions on native flora.

Fig 2. Bank of the River Teith dominated by a monoculture of *Impatiens glandulifera,* August 2015 © Nigel Willby.

6.4 Changes in plant communities

The naturally dynamic nature of riparian zones suggests there may be an environmental "see-saw" effect in which different species are favoured intermittently over time, without there being a clear trajectory of change. Chapter 2 showed that over the past 30 years plant communities have changed partly in response to agricultural land use in lowland catchments, as well as indirectly due to the changing dominance of IAPs and native dominant plants under varying river flow conditions. Riverbanks now feature more trees, such as *Salix* spp., and tall herb vegetation. This has led to shadier, and to some extent moister habitat conditions and a resultant loss of shade intolerant species. In Chapter 3, when assessing plant communities at a local scale, differences in species composition were evident between stands dominated by either IAPs or native dominant plants. Sites invaded by *I. glandulifera* were associated with *Salix* spp. and other IAPs namely *F. japonica* and *H. mantegazzianum,* suggesting that invaded sites are hot spots for further invasion. In comparison uninvaded sites dominated by *Petasites hybridus* or *P. arundinaceae,* were associated with a greater variety of native species, signifying that invasion may lead to homogenisation of native flora able to coexist alongside IAPs.

The importance of trees along river banks is a recurring theme. Chapter 3 showed that in spring, tree-lined banks were associated with greater IAP cover, potentially due to additional sediment trapping following over-winter flood events. In chapter 4 there was a positive association between the amount of IAP cover in the year prior to over-winter deposition and the amount of sediment deposited at those sites. This association may be due to characteristics of a heavily invaded river catchment, such as a greater incidence of trees along invaded river banks. Perhaps this suggests that tree-lined banks are potential hotspots for sediment deposition, although, in principle, increased tree cover might be expected to reduce bank erosion and intercept sediment close to source. Chapter 4 also revealed a positive association between sediment deposition and propagule supply, of both IAP and native species. Sediment patches in competitive riparian environments may offer a unique competition-free, resource-rich habitat ideal for the establishment of fast growing, shade tolerant IAPs (Baattrup-Pedersen *et al.* 2013a).

Fig 3. Over winter sediment deposition along a tree lined bank of the River Isla, March 2014.

6.5 Role of propagule bank contribution to above ground vegetation

Chapters 4 and 5 showed the importance of propagule transport by hydrochory, with greater abundance and diversity of propagules being associated with sediment deposited over winter. However, contrary to expectations of greater recruitment from the propagule bank in disturbed areas, the amount and diversity of propagules within the propagule bank had minimal influence on above-ground vegetation. In Chapter 5 there was little similarity between the above-ground and propagule bank vegetation, supporting findings from previous studies (Tabacchi *et al*. 2005). This relationship was exaggerated at sites which were heavily invaded closest to the water's edge, suggesting that large monocultures of IAPs are more likely to be representative of stable, rather than disturbed conditions. Chapter 5 also showed that IAPs and native dominant species cover were the most important determinants of both recruitment from the propagule bank and turnover of the above-ground plant community, compared to local environmental conditions.

Chapter 4 revealed that although over-winter deposition has the ability to provide riparian zones with an abundance of propagules, this itself is not enough to determine recruitment along invaded river banks. Rather it is competitive interactions which determine community structure, particularly once IAP and native dominant species have established in the summer months. However, there are potentially more opportunities for recruitment from the propagule bank in spring when competition is lower (Sarneel *et al.* 2016). Interestingly IAPs only formed a very small proportion of the total propagule bank (< 1%) despite amounting to 26% of the total cover of the above-ground vegetation. This was equivalent to the amount of native dominant species within the total above-ground vegetation, although the density of native dominate propagules were proportionally greater than IAPs (15%). This suggests that IAPs have a high success of establishment which is not reliant on a large propagule supply from the soil propagule bank, further highlighting the greater competitive ability of IAPs.

6.6 Study limitations

Across both coarse and local scales competition between IAPs and native dominant species in riparian plant communities is evidently of crucial importance in understanding community changes and to refine strategies for managing IAPs. There is, however, a need for long term monitoring within riparian habitats, as well as thorough assessments of sediment characteristics and channel geomorphology. In chapter 2 annual monitoring of vegetation would reveal whether or not cyclical changes occur. Comparing fixed points over time is useful to understand how communities have changed, both pre- and post-invasion and how such changes are associated with prevailing abiotic factors. Studies of temporal change at individual sites would also avoid criticisms relating to the use of the space-time substitution method, when inferring IAP impacts on communities for which the pre-invasion state was unknown (Sax *et al.* 2005).

In chapters 3-5 samples were taken on downstream communities at river sites in central Scotland, as these were assumed to be most prone to invasion. Surveys carried out across the length of selected rivers would have enabled detection as to where IAPs are most likely to impact native communities. This would enable inferences to be made about the state of invasion and native diversity upstream of heavily invaded sites and to what degree this influences downstream communities. Although chapter 5 suggested that locally, recruitment from the propagule bank was low.

6.7 Management considerations

The focus of management in highly invaded habitats is now to control the areas worst affected by IAPs and reduce the likelihood of further spread (Hulme 2009). This thesis has highlighted some opportunities for targeted management within riparian zones. Areas under most pressure from IAPs are those which are more stable and drier, i.e. the top of the bank and along rivers with more stable flow conditions; and an absence of grazing which enables the formation of dense stands (Marty 2005). An important finding from this research was that IAP cover was generally lower in areas with greater soil moisture. *I. glandulifera,* in particular, has been reported to favour damp and even waterlogged conditions (Schmitz & Dericks 2010) and is often prolific in woodlands which can be shaded and damp (Beerling & Perrins 1993). This finding was therefore unexpected. It may be that *inundation* by flooding does not favour this species, particularly in spring when young plants are often smaller than native species. Management efforts may need to target earlier stages of plant development in the spring, when environmental conditions are particularly important in determining establishment success of plant species (Fraaije *et al.* 2015; Sarneel *et al.* 2016). As wetter conditions will favour native species, alterations to regulated flow regimes in spring may also reduce abundance of IAP cover. Similarly, in river restoration projects, shallow bank profiling that increases the extent of inundation and reduces bank dewatering would be expected to favour native dominant species over IAPs.

When comparing the differences in plant community composition between invaded and uninvaded sites, there was a reoccurring theme of the potential role of grasses. Site assessments showed that areas with minimal invasion were often densely populated by common grass species, such as *Lolium perenne* and *Arrhenatherum elatius*. In the literature, Larson et al. (2013) provided evidence of greater grass species cover in less invaded areas and Gioria and Osborne (2010) showed that invaded propagule banks supported less grass species. This suggests that the high density of stems in grass-dominated riparian areas may potentially restrict recruitment of IAPs, due to the lack of gaps for colonisation. Grass seeding may therefore offer an important restoration tool post removal of IAPs, in order to reduce re-colonisation of alien species.

Fig 4. From left to right: A 100 m bank of the River Kelvin invaded by *Impatiens glandulifera.* Less than 10 m upstream an uninvaded bank dominated by grasses.

6.8 Key outstanding questions

This research has provided important insights into the factors affecting the success of IAPs in riparian zones and their relative impacts on native plant diversity. However, a number of key questions remain. Firstly, chapter 2 showed changes in the vegetation at upland sites across Great Britain and indicated that *I. glandulifera* was present in some of these communities. The effect of invasion in the uplands may vary due to temperature and altitude. *I. glandulifera* can be intolerant to early frost conditions (Skálová & Pyšek 2009) which may constrain growth and reduce potential negative impacts on upland flora. However, IAPs may add additional pressure in these habitats where environmental stressors play a key role in determining the community structure.

Secondly, one of the biggest challenges in understanding the impact of IAPs on native communities is whether or not IAPs are the drivers or passengers of environmental change (Ricciardi *et al.* 2013). In recent decades the establishment of IAPs in riparian zones has increased (Pattison, Minderman & Willby (Ch2)) and is perhaps one of the most profound changes to have occurred in riparian habitats. Whether an increase in IAP spread is the main driver of change in native vegetation over time is still unclear. This thesis did, however, elucidate some of the environmental constraints to the dominance of IAPs, which could then indirectly affect native communities. This highlights the importance of assessing the interactions between IAPs and environmental variables when assessing their impact on native communities.

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Supporting Information

Table 1. Model selection summary for models which had ΔAICc values of <4 for each of the 5 Response variables: invasive alien plant (IAP) presence or absence (GLMER), native diversity, BCI, native subordinate species % cover and native dominant species % cover (LMER). Parameters in the models were eastings (East), flood frequency (FRE_5), number of low flow days (LF), PC1 (representing site altitude and slope), invasive alien % cover (IAP), native dominant species % cover (Dom), survey and each predictors interaction with survey. Superscript 2 indicates a squared quadratic term. Models are ranked by AICc weight (W_i), where higher weighted models have more support. Marginal (R^2m) and conditional (R^2c) R^2 and log-likelihood ratio values are given.

Response	Model parameters	R^2m	R^2c	logLik	AIC_c	Δ_i	W_i
IAP Presence/Absence	FRE_5 + FRE_5^2 + PC1 + Survey + FRE_5 x Survey + FRE_5^2 x Survey +PC1 x Survey	0.57	0.80	-239.54	499.49	0.00	0.68
	FRE_5 + FRE_5^2 + LF + LF^2 + PC1 + Survey + FRE_5 x Survey + FRE_5^2 x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey	0.58	0.83	-236.66	502.11	2.62	0.18
	FRE_5 +FRE_5^2 +LF +PC1 +Survey + FRE_5 x Survey + FRE_5^2 x Survey + LF x Survey + PC1 x Survey	0.57	0.82	-239.01	502.61	3.12	0.14
Native diversity	East + LF + LF^2 + PC1 + IAP + IAP^2 + Survey + East x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey + IAP^2 x Survey	0.27	0.44	-174.35	383.9	0.00	0.87
	East + FRE_5 + LF + LF^2 + PC1 + IAP + IAP^2 + Survey + East x Survey + FRE_5 x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey+ IAP^2 x Survey	0.27	0.44	-174.08	387.6	3.73	0.13
BCI	East + PC1 + LF	0.23	0.39	223.39	-434.46	0.00	0.20
	East + PC1 + LF + Dom + IAP	0.25	0.39	223.99	-433.55	0.91	0.13
	East + PC1 + LF + Wood	0.23	0.39	223.96	-433.49	0.96	0.13
	East + PC1 + LF + Dom	0.24	0.39	223.62	-432.82	1.63	0.09
	East + PC1 + LF + Dom + IAP + Wood	0.25	0.39	224.49	-432.44	2.02	0.07
	East + PC1 + LF + LF^2	0.23	0.39	223.41	-432.39	2.07	0.07
	East + PC1 + LF + Dom + IAP	0.25	0.39	224.28	-432.01	2.45	0.06
	East + PC1 + LF + Dom + Wood	0.24	0.40	224.22	-431.90	2.56	0.06
	East + PC1 + LF + LF^2 + IAP	0.24	0.39	224.00	-431.46	3.00	0.05
	East + PC1 + LF + LF^2 + Wood	0.23	0.39	223.97	-431.39	3.06	0.04
	East + PC1	0.13	0.38	220.69	-431.15	3.30	0.04
	East +PC1 + LF + Dom + IAP + Wood	0.25	0.39	224.81	-430.92	3.53	0.03
	East + PC1 + LF + LF^2 + Dom	0.24	0.39	223.63	-430.70	3.75	0.03

Native subordinate sp % Cover	East + FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + IAP + Dom + Dom^2+ Survey + East x Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey + Dom x Survey + Dom^2 x Survey	0.35	0.56	-740.23	1528.59	0.00	0.38
	East + FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + IAP + IAP^2 + Dom + Dom^2+ Survey + East x Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey + IAP^2 x Survey + Dom x Survey + Dom^2 x Survey	0.36	0.57	-738.17	1528.86	0.28	0.33
	East + FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + IAP + IAP^2 + Dom + Dom^2+ Survey + Wood + East x Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey + IAP^2 x Survey + Dom x Survey+ Dom^2 x Survey + Wood x Survey	0.36	0.57	-736.69	1530.33	1.74	0.16
	East + FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + IAP + Dom + Dom^2 + Wood + Survey + East x Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey + Dom x Survey + Dom^2 x Survey + Wood x Survey	0.35	0.56	-739.05	1530.61	2.03	0.14
Native dominant sp % Cover	FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + IAP + Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey	0.24	0.76	-599.68	1234.53	0.00	0.26
	FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey +LF^2 x Survey + PC1 x Survey	0.24	0.76	-602.19	1235.28	0.76	0.18
	LF + LF^2 + PC1 + Survey + LF x Survey + LF^2 x Survey + PC1 x Survey	0.22	0.69	-606.40	1235.29	0.77	0.18
	LF + LF^2 + PC1 + IAP + Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey	0.22	0.70	-604.69	1236.06	1.54	0.12
	East + LF + LF^2 + PC1 + Survey + East x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey	0.20	0.69	-605.10	1236.88	2.35	0.08
	East + FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + IAP + Survey + East x Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey	0.22	0.76	-598.82	1237.09	2.57	0.07
	East + FRE$_5$ + FRE$_5^2$ + LF + LF^2 + PC1 + Survey + East x Survey + FRE$_5$ x Survey + FRE$_5^2$ x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey	0.22	0.75	-601.17	1237.50	2.98	0.06
	East + LF + LF^2 + PC1 + IAP + Survey + East x Survey + LF x Survey + LF^2 x Survey + PC1 x Survey + IAP x Survey	0.19	0.69	-603.37	1237.65	3.12	0.05

Table 2. The location of each river used in this study for both invaded and uninvaded sites.

Site	River	Location	Latitude	Longitude
Invaded	Almond	South Queensferry, Edinburgh	55.952092	-3.3767
	Annick Water	Dreghorn, North Ayreshire	55.614311	-4.643453
	Avon	Old Polmont, Falkirk	55.998912	-3.686592
	Bannock Burn	Bannockburn, Stirling	56.113967	-3.887941
	Black Cart Water	Johnstone, Renfrewshire	55.844892	-4.495599
	Carron	Bainsford, Falkirk	56.020883	-3.791697
	Dean Water	Blairgowrie, Perthshire	56.599114	-3.163649
	Devon	Tillicoultry, Clackmannanshire	56.147622	-3.748654
	Earn	Dunning, Perthshire	56.342651	-3.612989
	Eden	Cupar, Fife	56.321496	-2.995423
	Endrick	Drymen, Stirlingshire	56.063982	-4.486721
	Forth	Craigforth, Stirling	56.137189	-3.980235
	Gryfe	Johnstone, Renfrewshire	55.868136	-4.505754
	Irvine	Drybridge, Irvine	55.600081	-4.633034
	Isla	Blairgowrie, Perthshire	56.534417	-3.332573
	Kelvin	Torrance, East Dunbartonshire	55.936747	-4.209249
	Ruthven	Aberuthven, Perthshire	56.327413	-3.653021
	Teith	Bridge of Allan, Stirling	56.144372	-3.990134
	Tweed	Horncliffe, Berwick-upon-Tweed	55.752726	-2.105794
	White Cart Water	Paisley, Renfrewshire	55.83982	-4.406034
Uninvaded	Almond	South Queensferry, Edinburgh	55.952643	-3.378437
	Annick Water	Dreghorn, North Ayreshire	55.613444	-4.642065
	Carron	Bainsford, Falkirk	56.026196	-3.781988
	Earn	Dunning, Perthshire	56.340964	-3.610953
	Eden	Cupar, Fife	56.320576	-2.995826
	Endrick	Drymen, Stirlingshire	56.063684	-4.488443
	Isla	Blairgowrie, Perthshire	56.534482	-3.331884
	Kelvin	Torrance, East Dunbartonshire	55.93623	-4.207081
	Ruthven	Aberuthven, Perthshire	56.328964	-3.649229

Table 3. The name of each river used in this study, ranked in descending order of their percentage increase in flow over the period 1990-2012.

River	% flow increase
Dean Water	26.9
Avon	20.9
Forth	20.8
Almond	17.8
Endrick	17.7
Eden	16.7
Teith	15.5
Devon	14.1
Gryfe	13.2
Black Cart Water	12.2
Carron	12.1
Bannock Burn	11.2
Ruthven	11.2
Isla	10.9
Annick Water	10.9
Tweed	9.8
Earn	8.1
Kelvin	7.3
Irvine	4.6
White Cart Water	4.1

Table 4. Model selection summary for LMER models which had ΔAICc values of <4 for each of the four response variables: invasive alien plant percentage cover, dominant native plant species percentage cover, subordinate native plant species percentage cover and subordinate native plant species richness. Parameters in the models were soil moisture (moisture), flow variability (COV), water phosphorus (P), water suspended solids (SS), distance from trees along the riparian bank (tree), native dominant species percentage cover (dominant native), invasive alien species percentage cover (invasive), season, bank position (quad) and each predictors interaction with season and bank position. Models are ranked by AICc weight (W_i), where higher weighted models have more support. Log-likelihood ratio values are also given.

Response	Model parameters	logLik	AIC_c	Δ_i	W_i
Invasive alien plant cover (%)	Moisture + channel slope + COV + P + SS + tree +quad + season + moist x season + channel slope x quad + COV x quad + tree x quad + tree x season + P x season + SS x season	-1741.83	3528.66	0.00	0.34
	Moisture + channel slope + COV + P + SS + tree +quad + season + moist x season + channel slope x quad + tree x quad + tree x season + P x season + SS x season	-1744.26	3529.35	0.69	0.24
	Moisture + channel slope + P + SS + tree +quad + season + moist x season + channel slope x quad + COV x quad + tree x quad + tree x season + P x season + SS x season	-1745.44	3529.63	0.97	0.21
	Moisture + channel slope + COV + P + SS + tree +quad + season + moisture x quad + moist x season + channel slope x quad + COV x quad + tree x quad + tree x season + P x season + SS x season	-1740.97	3531.14	2.48	0.10
	Moisture + channel slope + COV + P + SS + tree +quad + season + moisture x quad + moist x season + channel slope x quad + tree x quad + tree x season + P x season + SS x season	-1743.47	3531.95	3.28	0.07
	Moisture + channel slope + P + SS + tree +quad + season + moisture x quad + moist x season + channel slope x quad + tree x quad + tree x season + P x season + SS x season	-1744.67	3532.25	3.59	0.06
Dominant native plant cover (%)	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + COV x season + tree x quad + SS x season	-1577.56	3198.03	0.00	0.12
	Moisture + channel slope + COV + SS + tree +quad + season + channel slope x quad + COV x quad + tree x quad + tree x season + P x season + SS x season	-1580.83	3198.34	0.31	0.10
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + tree x quad + tree x season + P x season + SS x season	-1578.92	3198.68	0.64	0.09
	Moisture + channel slope + COV + SS + tree +quad + season + channel slope x quad + COV x quad + COV x season + tree x quad + SS x season	-1580.20	3199.15	1.12	0.07
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + tree x quad + SS x season	-1580.24	3199.23	1.19	0.07
	Moisture + channel slope + COV + SS + tree +quad + season + moisture x season + channel slope x quad + COV x quad + tree x quad + SS x season	-1580.24	3199.24	1.21	0.07
	Moisture + channel slope + COV + P + SS + tree +quad + season + moisture x season + channel slope x quad + COV x quad + COV x season + tree x quad + SS x season + P x season	-1577.47	3199.95	1.91	0.05
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + COV x season + tree x quad + SS x season	-1579.59	3200.02	1.99	0.04
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + COV x season + tree x quad + tree x season + SS x season + P x season	-1577.53	3200.06	2.03	0.04
	Moisture + channel slope + COV + SS + tree +quad + season + channel slope x quad + COV x quad + tree x quad + tree x season + SS x season	-1580.68	3200.12	2.08	0.04
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + moisture x season + COV x quad + tree x quad + SS x season	-1578.63	3200.18	2.14	0.04
	Moisture + channel slope + COV + P + SS + tree +quad + season + moisture x season + channel slope x quad + COV x quad + tree x quad + SS x season	-1579.70	3200.24	2.21	0.04
	Moisture + channel slope + COV + SS + tree +quad + season + channel + moisture x season + slope x quad + COV x quad + COV x season + tree x quad + SS x season	-1579.78	3200.39	2.35	0.04
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + tree x quad + season x tree + SS x season + P x season	-1578.83	3200.58	2.54	0.03
	Moisture + channel slope + COV + P + SS + tree +quad + season + channel slope x quad + COV x quad + tree x quad + season x tree + SS x season	-1580.08	3201.00	2.97	0.03
	Moisture + channel slope + COV + SS + tree +quad + season + channel slope x quad + COV x quad + COV x season + tree x quad + tree x season + SS x season	-1580.10	3201.03	2.99	0.03
	Moisture + channel slope + COV + SS + tree +quad + season + moisture x season + channel slope x quad + COV x quad + tree x quad + tree x season + SS x season	-1580.16	3201.16	3.12	0.03

	Moisture + channel slope + COV + SS + P + tree +quad + season + moisture x season + channel slope x quad + COV x quad + COV x season + tree x quad + SS x season	-1579.22	3201.36	3.32	0.02
	Moisture + channel slope + COV + SS + tree +quad + season + + channel slope x quad + COV x quad + tree x quad	-1583.49	3201.58	3.55	0.02
	Moisture + channel slope + COV + SS + P + tree +quad + season + channel slope x quad + COV x quad + COV x season + tree x quad + tree x season + SS x season	-1579.49	3201.90	3.87	0.02
	Moisture + channel slope + COV + SS + P + tree +quad + season + moisture x season + channel slope x quad + COV x quad + COV x season + tree x quad + tree x season + SS x season + P x season	-1577.45	3202.00	3.97	0.02
Subordinate native plant cover (%)	Dominant native + invasive + quad + season + invasive x season + invasive x quad	-2384.59	4791.43	0.00	0.35
	Dominant native + invasive + quad + season + dominant native x season + invasive x season + invasive x quad	-2383.58	4791.46	0.03	0.35
	Dominant native + invasive + quad + season + dominant native x season + dominant native x quad + invasive x season + invasive x quad	-2382.38	4793.18	1.74	0.15
	Dominant native + invasive + quad + season + dominant native x quad + invasive x season + invasive x quad	-2383.41	4793.19	1.76	0.15
Subordinate native plant species richness	Dominant native + invasive + quad + season + dominant native x season + dominant native x quad + invasive x season	-2443.05	4908.36	0.00	0.54
	Dominant native + invasive + quad + season + dominant native x season + dominant native x quad + invasive x season + invasive x quad	-2441.15	4908.66	0.30	0.46

Table 5. All species recorded within the above-ground and propagule bank vegetation across seasons.

	Above-ground vegetation			Propagule bank seedlings		
Species	Summer Yr1	Spring Yr2	Summer Yr2	Cores Yr1	Cores Yr2	Mats
Native subordinate species						
Acer pseudoplatanus	0	X	0	0	0	0
Achillea millefolium	X	X	X	0	0	X
Aethusa cynapium	0	X	0	0	0	0
Agrostis canina	0	0	0	X	0	0
Agrostis capillaris	0	0	0	X	X	X
Agrostis gigantea	0	X	X	X	X	X
Agrostis stolonifera	X	X	X	X	X	X
Alliaria petiolata	0	X	X	X	X	X
Allium ursinum	0	X	0	0	0	0
Alnus glutinosa	0	0	X	X	X	X
Alopacurus pratensis	0	0	0	0	X	X
Alopecurus pratensis	X	X	X	0	0	0
Angelica sylvestris	X	X	X	0	X	0
Anthriscus sylvestris	X	X	X	X	X	0
Apium graveolens	0	X	0	0	0	0
Apium nodiflorum	0	0	X	0	0	0
Arabidopsis thaliana	0	0	0	X	X	X
Argentina anserina	X	X	X	X	X	X

Arrhenatherum elatius	X	X	X	X	X	X
Artemisia vulgaris	X	0	X	0	0	0
Aster x salignus	X	X	0	0	0	0
Asteraceae sp. A	0	X	0	0	0	0
Asteraceae sp. B	0	0	X	0	0	0
Atriplex patula	X	0	0	X	X	X
Avena strigosa	X	0	0	0	0	0
Barbarea vulgaris	0	0	X	0	0	0
Bellis perennis	0	0	0	0	X	X
Betula pendula	0	0	0	X	X	X
Bidens cernua	0	0	0	0	0	X
Brachypodium sylvaticum	X	X	0	X	0	X
Brassica napus	X	X	X	0	X	0
Brassica oleracea	X	X	0	0	X	0
Brassica rapa	0	0	0	X	X	X
Brassicaceae sp. A	0	0	0	0	0	X
Brassicaceae sp. B	0	0	0	0	0	X
Buddleja sp	0	0	0	X	X	X
Callitriche stagnalis	0	0	0	0	X	X
Caltha palustris	X	X	X	0	0	0
Calystegia sepium	X	X	X	X	X	X
Capsella bursa pastoris	X	0	0	0	0	0
Cardamine amara	0	X	X	X	X	X
Cardamine flexuosa	X	0	X	X	X	X
Cardamine hirsuta	0	X	X	X	X	X
Cardamine palustris	0	0	0	X	X	X
Cardamine pratensis	0	X	0	0	X	X
Carex hirta	0	X	X	0	X	X
Carex ovalis	X	0	0	0	0	0
Carex pendula	0	X	0	0	0	0
Carex rostrata nigra	0	0	0	X	X	0
Carex spp.	0	0	X	0	0	0
Centaurea nigra	X	X	X	X	0	0
Cerastium fontanum	0	X	0	X	X	0
Chamerion angustifolium	X	X	X	X	X	X
Chenopodium rubrum	0	0	X	0	0	0
Chrysosplenium oppostifolium	X	0	0	0	0	0
Cirsium arvense	X	X	X	X	X	X
Cirsium palustre	0	0	X	X	X	X
Conopodium majus	0	X	X	X	X	0
Corydalis spp.	0	X	0	0	0	0
Cytisus scoparius	0	X	0	0	0	0
Dactylis glomerata	X	X	X	X	X	X
Deschampsia cespitosa	X	X	X	X	X	X
Digitalis purpurea	0	0	0	X	X	0
Doronicum orientale	0	0	0	X	0	X

Elymus caninus	0	0	0	0	0	X
Elymus repens	X	X	X	X	X	X
Epilobium ciliatum	0	0	X	0	0	X
Epilobium montanum	X	X	X	X	X	X
Epilobium parviflorum	X	0	X	0	X	0
Epilobium spp.	X	0	0	0	0	0
Equisetum arvense	X	X	X	X	X	0
Eupatorium cannabinum	0	X	0	0	0	0
Fagus sylvatica	X	X	0	0	0	X
Festuca altissma	0	0	0	0	0	X
Festuca arundinacea	X	X	X	X	X	X
Festuca gigantea	X	0	X	0	X	0
Festuca ovina	0	0	0	0	0	X
Festuca rubra	0	0	0	0	X	0
Fragaria vesca	0	0	0	X	X	X
Fumaria spp.	X	0	0	0	0	0
Galeopsis tetrahit	X	X	X	X	X	X
Galium aparine	X	X	X	X	X	X
Galium cruciata	0	X	X	0	0	0
Galium palustre	X	X	X	0	0	X
Galium verum	0	0	X	0	0	0
Geranium dissectum	0	0	0	X	X	0
Geranium pratense	X	X	X	X	X	0
Geranium robertianum	0	X	X	X	X	X
Geranium sylvaticum	X	0	X	0	0	0
Geum rivale	X	X	X	0	0	0
Geum urbanum	X	X	X	X	X	X
Glechoma hederacea	0	X	X	X	X	X
Glyceria fluitans	0	0	X	X	X	X
Gnaphalium sylvaticum	X	0	X	X	X	X
Heracleum sphondylium	X	X	X	X	X	0
Hesperis matronalis	0	X	X	0	0	0
Hieracium lachenalii	0	0	0	0	X	0
Hieracium vulgatum	0	X	X	0	0	0
Holcus lanatus	X	X	X	X	X	X
Holcus mollis	X	X	X	X	X	0
Hyacinthoides non scripta	0	X	0	0	0	0
Hypericum perforatum	X	X	X	X	X	0
Hypericum spp.	X	0	0	0	0	0
Iris pseudacorus	0	X	0	0	0	0
Isolepis setacea	0	0	0	X	0	X
Juncus articulatus	0	0	0	X	X	X
Juncus bufonius	0	0	X	X	X	X
Juncus bulbosus	0	0	0	X	X	X
Juncus conglomeratus	X	0	0	0	0	0
Juncus effusus	X	X	X	X	X	X

Lactuca serriola	0	0	X	0	0	0
Lamium album	X	X	X	0	0	0
Lapsana communis	0	X	X	X	X	0
Lathyrus pratensis	X	X	X	X	X	X
Lazula sylvatica	0	0	0	X	X	0
Leucanthemum vulgare	0	0	X	0	X	X
Lolium perenne	0	X	X	X	X	X
Lotus corniculatus	0	0	X	X	0	X
Luzula sylvatica	X	X	X	0	0	0
Lysimachia nummularia	0	X	X	X	0	0
Lythrum salicaria	X	0	X	0	0	0
Matricaria discoidea	X	X	X	0	0	X
Melampyrum arvense	0	0	X	0	0	0
Mentha aquatica	X	X	X	X	X	X
Mentha x piperita	0	0	X	0	0	0
Mercurialis perennis	0	0	X	0	0	0
Montia fontana	0	X	0	0	0	0
Myosotis discolor	0	X	X	X	X	0
Myosotis laxa	X	0	0	X	0	X
Myosotis scorpioides	X	X	X	X	X	X
Myosotis sylvatica	0	X	X	X	X	0
Myrrhis odorata	X	0	X	0	0	0
Narcissus poeticus	0	X	0	0	0	0
Pastinaca sativa	X	0	0	0	0	0
Persicaria amphibia	X	X	X	0	0	0
Persicaria hydropiper	X	X	X	X	X	X
Persicaria maculosa	X	X	X	X	X	X
Picris echioides	0	0	0	X	X	X
Plantago lanceolata	X	X	X	0	X	X
Plantago major	X	X	X	X	X	X
Poa annua	0	X	X	X	X	X
Poa nemoralis	0	0	0	0	X	X
Poa spp.	0	0	0	X	0	0
Poa trivalis	X	X	X	X	X	X
Polygonum aviculare	X	0	X	X	X	X
Pteridium aquilinum	X	0	X	0	0	0
Ranunculus ficaria	0	X	X	X	X	X
Ranunculus repens	X	X	X	X	X	X
Ranunculus sardous	0	X	0	0	0	0
Rhamnus frangula	0	0	0	X	X	0
Rorippa palustris	X	X	X	0	0	X
Rorippa sylvestris	0	X	0	0	0	0
Rosa canina	0	0	X	0	X	0
Rubia peregrina	X	0	0	0	0	0
Rubus idaeus	0	0	0	X	X	0
Rubus spp.	0	0	0	X	X	X

Rumex acetosa	X	X	X	X	X	X
Rumex acetosella	0	X	X	X	X	0
Rumex crispus	X	X	X	X	X	X
Rumex obtusifolius	X	X	X	X	X	X
Rumex sanguineus	X	0	X	0	0	0
Sagina procumbens	0	0	0	X	X	X
Salix alba	X	0	0	0	0	0
Salix spp.	0	X	X	0	X	0
Salix viminalis	X	0	0	0	0	0
Scenecio jacobaea	0	0	0	0	X	X
Scirpus sylvaticus	0	X	0	X	X	X
Scrophularia nodosa	0	0	X	0	0	X
Scrophularia umbrosa	0	0	X	X	X	X
Senecio jacobaea	X	0	X	X	X	X
Senecio vulgaris	0	X	0	X	X	0
Silene dioica	X	X	X	X	X	X
Silene latifolia	0	0	X	0	0	0
Solanum dulcamara	X	0	X	X	0	0
Solanum lycopersicum	0	0	X	0	0	0
Solidago canadensis	0	0	0	0	X	0
Sonchus arvensis	0	0	X	0	0	0
Sonchus asper	0	0	X	0	0	0
Sorbus spp.	0	X	X	0	0	0
Sparganium emersum	X	0	X	0	0	0
Spergula arvensis	0	X	0	X	X	X
Stachys palustris	X	X	X	X	X	0
Stachys sylvatica	0	X	X	X	X	X
Stellaria alsine	0	0	0	X	X	X
Stellaria graminea	0	X	X	X	X	X
Stellaria holostea	X	X	X	X	0	0
Stellaria media	X	X	X	X	X	X
Stellaria nemorum	0	X	X	0	X	X
Symphyotrichum novi belgii	X	0	X	0	0	0
Symphytum tuberosum	0	X	0	0	0	0
Tanacetum vulgare	X	X	X	X	X	X
Taraxacum officinale	X	X	X	X	X	X
Taraxacum spp.	X	0	0	0	0	0
Trifolium dubium	X	0	0	0	0	0
Trifolium repens	0	X	X	X	X	X
Tripleurospermum inodorum	X	0	X	0	0	0
Tussilago farfara	X	X	X	0	0	0
Ulex europaeus	0	0	0	X	0	0
Vaccinium uliginosum	0	0	0	X	X	0
Valeriana officinalis	X	X	X	X	X	0
Veronica beccubunga	0	X	X	X	X	X
Veronica catenata	0	0	0	X	X	X

Veronica chamaedrys	0	X	0	X	X	0
Veronica hederifolia	0	X	0	X	X	0
Veronica persica	0	X	0	0	0	0
Veronica serpyllifolia	0	0	0	0	X	0
Vicia sativa	X	X	X	0	X	0
Viola palustris	0	0	X	0	0	0

Native dominant species

Aegopodium podagraria	X	X	X	X	X	X
Epilobium hirsutum	X	X	X	X	X	X
Filipendula ulmaria	X	X	X	X	X	X
Glyceria maxima	X	X	X	X	X	X
Petasites hybridus	X	X	X	0	0	0
Phalaris arundinacea	X	X	X	X	X	X
Phragmites australis	X	X	X	0	0	0
Rubus fruticosus	X	X	X	X	X	X
Symphytum officinale	0	X	X	X	X	X
Urtica dioica	X	X	X	X	X	X

Invasive alien plant species

Claytonia sibirica	X	X	X	0	0	X
Epilobium brunnescens	0	0	0	X	X	X
Fallopia japonica	X	X	X	X	X	X
Fallopia sachalinensis	X	X	X	0	0	0
Fallopia x bohemica	X	0	0	0	0	0
Heracleum mantegazzianum	X	X	X	X	0	0
Impatiens glandulifera	X	X	X	X	X	X
Mimulus guttatus	X	X	X	X	X	X

Table 6. Parameters estimates and confidence intervals (CI) for the top SDI models, as judged using Akaike's Information Criterion. All regressions estimates in bold were significant ($P < 0.05$), with both the R^2 adjusted coefficients of determination ($adjR^2$) presented. Predictor variables retained in the top models were native dominant % cover, IAP % cover, sediment (kg) and short term flow variability. Model abbreviations are as in Table 3. Model numbers represent various fitted predictors: Mod3: dominant native cover + IAP cover; Mod7: sediment; Mod8: short term CoV.

	Mod	Intercept	± CI	Dom cover	± CI	IAP cover	± CI	Sediment	± CI	STV	± CI	R^2	$adjR^2$
Spring													
Core Yr1													
Q1	7	0.74	0.04	-	-	-	-	-0.04	0.04	-	-	0.19	0.15
Q2	8	0.77	0.03	-	-	-	-	-	-	0.03	0.03	0.14	0.10
Mats													
Q2	8	0.78	0.03	-	-	-	-	-	-	**0.04**	0.03	0.23	0.19
Core Yr2													
Q3	7	0.75	0.05	-	-	-	-	0.05	0.05	-	-	0.15	0.10
Summer													
Core Yr1		-	-	-	-	-	-	-	-	-	-	-	-
Q1	3	0.72	0.04	0.04	0.04	**0.06**	0.04	-	-	-	-	0.37	0.30
Q3	7	0.73	0.05	-	-	-	-	**0.05**	0.05	-	-	0.20	0.16
Mats													
Q1	3	0.75	0.04	-0.01	0.04	**0.05**	0.04	-	-	-	-	0.27	0.18
Q3	7	0.81	0.04	-	-	-	-	**0.05**	0.04	-	-	0.21	0.17
Core Yr2													
Q1	3	0.73	0.04	**0.06**	0.04	**0.07**	0.04	-	-	-	-	0.51	0.45
Q3	7	0.71	0.04	-	-	-	-	**0.09**	0.04	-	-	0.50	0.47

Table 7. Parameters estimates and confidence intervals (CI) for the most plausible model, as judged using Akaike’s Information Criterion and model weight (Table 5). All regressions estimates were significant ($P < 0.05$), with both the R^2 adjusted coefficients of determination (adjR^2) presented. Model numbers represent various fitted predictors. Mod5: mat’14 seedling abundance + mat’14 species richness; Mod7: mat’14 seedling abundance; Mod8: core’14 seedling abundance; Mod10: core’14 species richness.

	Model	Intercept	± CI	Abundance cores '14	± CI	Richness cores '14	± CI	Abundance mats ’14	± CI	Richness mats ‘14	± CI	R^2	adjR^2
Spring '14 Veg													
IAP cover													
Q3	7	2.33	0.63	-	-	-	-	-0.85	0.64	-	-	0.27	0.23
Dom-native cover													
Q2	10	4.85	0.55	-	-	-0.45	0.64	-	-	-	-	0.37	0.34
Q3	8	3.13	0.27	-0.34	0.28	-	-	-	-	-	-	0.24	0.19
Sub-native cover													
Q2	10	7.32	0.66	-	-	1.55	0.68	-	-	-	-	0.53	0.50
Q3	7	8.09	0.73	-	-	-	-	1.51	0.99	-1.13	0.99	0.35	0.27
Sub-native richness													
Q1	10	2.93	0.13	-	-	0.19	0.13	-	-	-	-		
Summer'14 Veg													
IAP cover													
Q2	7	5.39	0.95	-	-	-	-	1.48	0.97	-	-	0.33	0.29
Dom-native cover													
Q2	10	2.98	0.26	-	-	-0.48	0.27	-	-	-	-	0.40	0.37
Q3	5	3.05	0.31	-	-	-	-	-0.74	0.42	0.45	0.42	0.41	0.34
Sub-native richness													
Q1	10	2.99	0.18	-	-	0.23	0.18	-	-	-	-		