Linkages between riparian invasive plants, hydromorphology and salmonid fish in Scottish rivers

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September 2018

Submitted to Biological and Environmental Sciences
School of Natural Sciences
University of Stirling
Scotland

For the degree of Doctor of Philosophy

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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.

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Word count: 47607

“We must make no mistake: we are seeing one of the greatest historical convulsions in the world’s fauna and flora.”

Charles S. Elton, The ecology of invasions by animals and plants (1958)

‘Day of the Balsaminaceae’ © Nigel Willby

Acknowledgements

First and foremost, I would like to thank my supervisors, Colin Bull and Nigel Willby, for their invaluable and unwavering support throughout this PhD. You both gave me an incredible opportunity to pursue a subject that I am truly passionate about, and the wisdom, knowledge and technical skills that you have passed on over the past four years has been absolutely invaluable. Thank you both.

Thank you to Scottish Natural Heritage for funding this project, and thank you to both Phil Boon and Julia Stubbs-Partridge for their guidance and support during this PhD process. I am fortunate to have been supported by a wonderful technical team during my PhD; thank you in particular to Ronnie Balfour, James Weir, Stuart Bradley and Scott Jackson for your advice and support. I have also had a number of field and laboratory assistants during this project, whose help I am incredibly grateful for. Thank you to Fergus McFarlane for supporting and working with me during my second field season, to Jack Shelton and Thomas Edmondson for numerous contributions to field and lab work, and to Sophie Eastwood for enduring many painful days crawling through brambles and stinging nettles in the aid of pitfall trapping!

The postgraduate department at Stirling University encourages and promotes research and collaboration, and has been an excellent place to work. I have been fortunate to work with a number of people who have supported and encouraged me over the past four years. Thank you to Zarah Pattison for your invaluable help and advice from day one, and for keeping me sane over the final year of analysis and writing. Thank you to Anna Doeser, Alan Law and Robbie Whytock for your patient advice with both taxonomy and statistical analyses, and to Anwen Bill and Renée Kerkvliet-Hermans for your support and motivation.

This PhD has often been challenging, and I have been grateful for the constant support from my parents, Phil and Rosemary, who not only enabled me to pursue this opportunity, but have always been there to offer advice, motivation and a source of self-belief. You have both always convinced me that I could achieve this, and I would not have been able to do so without your love and support – thank you. Thank you also to my partner, Jodie Simmons: you have been there through the difficult times

and provided words of encouragement and support to keep me going throughout this process.

This thesis is dedicated to my parents, Phil and Rosemary, who instilled in me the belief that I could achieve whatever I set my mind to, and have given their love and unconditional support from day one. I cannot thank you both enough.

General Abstract

Invasions by non-native species are reported as one of the greatest threats to global biodiversity, and the invasion of riparian ecosystems by invasive non-native plants (INNP) presents a common and difficult challenge for river and fishery managers. Whilst the various impacts of INNP are well-documented in a range of global studies, the type and extent of ecological changes that riparian INNP invasions induce in invertebrate and salmonid fish communities remains poorly understood. To address these gaps in the literature, this thesis assesses: (1) how riparian INNP alter the abundance, diversity and composition of freshwater macroinvertebrate communities, in relation to environmental variables; (2) how the structure of riparian terrestrial invertebrate communities differs at heavily invaded sites, and whether there is evidence of a difference in INNP species effect and (3) how juvenile salmonids utilise the altered aquatic and terrestrial prey resources at sites with greater INNP cover, and the relative importance of INNP to prey selection in relation to population dynamics and environmental stressors.

Recent field survey data was used to quantify changes in the freshwater and terrestrial invertebrate communities of 24 low order streams in central Scotland. Analyses indicated that whilst greater INNP cover reduced local freshwater macroinvertebrate diversity, their effects were generally subordinate to that of physicochemical variables, though there was evidence of a legacy effect of invasion that presents a constant pressure on freshwater macroinvertebrate communities. Similarly, greater INNP cover reduced terrestrial morphospecies diversity, but also reduced abundance and increased spatial heterogeneity through loss of species at the site scale. INNP cover was found to be the strongest predictor across all assessments of terrestrial invertebrate communities. Juvenile salmonids were observed to change their predatory selection of two taxonomic orders at more heavily invaded sites, but broadly changed their feeding patterns in response to community and environmental stressors, indicating a lesser effect of riparian INNP invasions on salmonid communities.

The findings presented in this thesis suggest that riparian INNP are important and significant contributors to reductions in the diversity and overall quality of both freshwater and terrestrial invertebrate communities. However, it appears that the impacts of riparian INNP are less severe for salmonid fish compared to invertebrate

communities, perhaps due to their resilience and adaptability in a highly stressful environment. This thesis suggests that efforts to improve the quality of low order streams by actively managing severe riparian INNP invasions are merited, and suggests that there is a scale of community responses which may provide guidance when planning INNP management strategies. However, there is clearly a trade-off between the often significant economical investment required to treat INNP invasions and the relative uncertainty concerning any recovery that may be achieved post-treatment.

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Chapter 1: General introduction

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1.1 General overview

The following chapter presents some of the important current issues surrounding freshwater ecosystems and invasive non-native plants. The first section introduces invasive alien species, their impacts across ecosystems, methods through which they may facilitate environmental change and, more specifically, invasive non-native plants. Following this, the importance of river systems is discussed with relation to riparian zones, and the concept of freshwater extinctions is introduced and linked to invasive alien species as potential drivers of freshwater community change. The key species studied in this thesis are introduced and finally, the research questions addressed by this thesis are presented and briefly discussed.

1.2 Nomenclature

The following is a list of key and/or frequently used terms throughout this thesis

Native species: A species that has been observed to be naturally occurring and self-sustaining (European Union 1979). A native species is most commonly defined simply as a species that occurs “within its natural range” (Crees and Turvey 2015), though more complex and context-dependent definitions exist (e.g. a species that migrated after the last ice age, without the assistance of humans (Scottish Natural Heritage 2014)).

Invasive alien species (IAS): An invasive alien species is defined as a non-native species that threatens an ecosystem, habitat or species (Pejchar and Mooney 2009). They are often considered to be key drivers of change on a global scale, and pose one of the more prominent challenges to the conservation of biodiversity and natural resources (Simberloff et al. 2013).

Invasive non-native plant (INNP): Invasive non-native plants are a particularly damaging group of invasive alien species that possess a number of mechanisms through which they are able to outcompete and suppress native plant species. They spread rapidly, particularly through waterways, and can have ecosystem-level effects, particularly in riparian habitats. Their resilient and adaptable nature can often make invasions particularly costly and difficult to treat, and many INNP species are listed in the Wildlife and Countryside Act (1981) as causes of ecological, environmental or socio-economic harm (Wildlife and Countryside Act 1981).

Novel weapons hypothesis: The novel weapons hypothesis suggests that some INNP are able to gain advantages over native plant species through the use of novel allelopathic, defence, or antimicrobial chemicals (Ni et al. 2012). In this case, the invading plant faces fewer pressures from natural "enemies" compared to native plants, as these enemies have not had time to adapt to the novel biological weapons that INNP possess (Callaway and Ridenour 2004).

1.3 Invasive alien species

An invasive alien species (IAS hereafter) is generally defined as a species that has arrived outside of its native location, established populations, and spread (Simberloff 2013). The introduction of IAS is often an important event that has ecological consequences for the affected ecosystem (Gallardo et al. 2016). These species are able to flourish in their introduced habitats due to the absence or comparatively low prevalence of environmental factors which may hinder their growth – known as the Enemy Release Hypothesis (ERH) (Prior and Hellmann 2015). However, the contribution of the ERH to overall IAS success may be overstated, particularly given that this concept is an assessment of the number of enemy species, rather than a quantification of their overall effects (Colautti et al. 2004). The ERH may also be skewed towards specialist "enemies", and the perceived fewer number of these enemies in the introduced range of an IAS may simply reflect a poorer richness of insect herbivores compared to the native range (Liu and Stiling 2006). IAS are often spread unintentionally as consequences of travel and trade (Bonanno 2016). However, the rapid spread of a species throughout an ecosystem is not necessarily justification for an 'invasive' tag. Introductions and the subsequent spread of non-native trout and salmon species to create new populations for recreational angling are examples of ecological "invasions" that would not necessarily require management intervention (Keller et al. 2015).

Quantifying the impact of IAS and determining their relative importance as threats to native ecosystems is made difficult by their varying effects on different ecosystem types. For example, invasive non-native plants (INNP hereafter) have differing effects on grazing and detrital groups within terrestrial food webs, and show further differentiation between terrestrial food webs in woodland and wetland systems (McCary et al. 2016). This can prove problematic when trying to develop and prioritise management strategies, as attempts to treat INNP invasions and restore native flora may not be as successful regionally when compared to a more local scale (Maskell et al. 2006). Success of invasion by INNP may also correlate with environmental variables and as such, the magnitude and impact of INNP invasions differs across a range of ecosystem sizes and structures (Zelnik et al. 2015). It is also likely that studies assessing the impacts of non-native species invasions will be carried out when these IAS have already become established and dominant (Vila et al. 2011), highlighting a niche for studies that are able to reliably predict the location and magnitude of invasions.

Whether invasions by non-native species are intentional or not, they are one of the most important anthropogenic factors modifying the earth, through extinctions and global ecosystem modifications (Simberloff 2015). Such can be the magnitude of non-native species invasions, they can create issues of global concern. For example, two species of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) have invaded and spread rapidly throughout the western Atlantic. Due to their voracious feeding nature and ecological dominance, they have decimated reef fish populations, with catastrophic long-term impacts forecast for local prey fish species biomass (Green et al. 2012) and disastrous consequences for the diversity and survivability of coral-reef communities (Albins and Hixon 2011). Attempts to rectify the ecological damage caused by IAS through restoration are often met with resistance, as changes at an ecosystem level may take a long time to reverse (Becker and Robson 2009; Rodewald et al. 2015). Shifts in species distributions and fragmentation of habitat may hinder or completely prevent ecosystem recovery (Suding 2011), and legacy effects of invasion may still be detectable several decades after IAS clearance (Maclean et al. 2018).

Ecosystem impacts of invasive species

Invasions represent a multifaceted threat to biodiversity, ecosystem services, and the health and economic wellbeing of the communities that they affect (Ricciardi et al. 2017). Invasive species colonise rapidly and with the ability to change through genetic adaptations, adapting efficiently to a vast range of environmental conditions and threatening many native species in the process (Estoup et al. 2016). In an ever-changing and advancing world, there is now also evidence to suggest that in addition to negatively affecting our ecosystems directly, anthropogenic changes may also promote invasion. Species populations that are able to adapt to the constant pressure of human disturbance show an increased likelihood to increase in abundance within these heavily-disturbed areas, increasing their chances of being transported to a novel range (Hufbauer et al. 2012).

Invasive species are represented by a diverse range of species of organisms, which utilise a number of different life history strategies to invade, colonise and monopolise an ecosystem. These invasions have significant implications for the ecosystems that they colonise, with the potential to change their fundamental structure and function (Ehrenfeld 2010). The invasive European bird cherry (*Prunus padus*) contributes a subsidy to stream-dwelling coho salmon (*Ohcorhynchus kisutch*) that is two to three times lower than native trees (Roon et al. 2016), whilst the spiny water flea (*Bythotrephes longimanus*) has caused a decline in water clarity of nearly 1m in North American Great Lakes through the suppression of Cladoceran grazers (Walsh et al. 2016). These potentially drastic changes can occur at either end of the size spectrum, with chytrid fungi decimating global frog and toad populations (Blaustein and Kiesecker 2002), and larger herbivores at the upper end of the size spectrum exerting top down regulatory effects on native forest composition (Nugent et al. 2001).

The impacts of invasive species are context-dependent (Gallardo et al. 2016), varying between different species and habitats. Invasive species may become particularly problematic when they are deliberately introduced, particularly as it is often difficult to predict which species may present further problems once they become naturalised (Brunel et al. 2013). This issue can be further complicated by the interaction between science and politics, whereby overly optimistic rhetoric may push forward the introduction of a non-native species under the assumption that the organism will have a beneficial impact. A classic example of this is the introduction of four carp species to the Mississippi Valley since the 1880s, which were introduced as a potential method of biocontrol for various aquatic algae, weeds and parasites, and have subsequently become widespread and classified as harmful to native organisms (Sandiford 2015). These fish can have ecosystem level impacts, for example through the alteration of river zooplankton communities (Sass et al. 2014), or by unbalancing native food webs and facilitating unpredictable interactions with native species (Collins et al. 2017).

The impact of IAS may also increase with time since invasion, as both the magnitude of their local effects and their overall distribution continue to increase (van

Wilgen et al. 2008). Not only are IAS ecosystem engineers, they are also particularly opportunistic and able to take advantage of degraded ecosystems and poorer environmental conditions which may be unfavourable to native species (MacDougall and Turkington 2005). IAS may also act together to facilitate further invasions, both through mutual interactions with other IAS, and also through modification of habitat (Simberloff and Von Holle 1999). The stranglehold that IAS can exert on important resources such as light, space and nutrients can alter the relative abundance of native species, significantly changing the composition of invaded communities without necessarily being the driving force (Didham et al. 2005).

The increasing prominence of ecological studies focusing on restoration of damaged ecosystems is partly due to the need to understand the long-term damaging effects of IAS invasions, and the disproportionate amount of resources that are often required to manage invasions and enable post-invasion recovery following management efforts (Simberloff 2015). Further still, the long-term impacts of IAS remain relatively unpredictable, and surprising consequences and ecological changes resulting from IAS colonisations are not uncommon. An recent study describes the replacement of kokanee salmon (*Oncorhynchus nerka*) by lake trout (*Salvelinus namaycush*) as the dominant fish species in a lake in Montana, due to the introduction of a particularly virulent shrimp species (opossum shrimp, *Mysis diluviana*) and its competition with *O. nerka* for prey (Vitule et al. 2012). Furthermore, invasive species removal may not always be the best approach when the end-goal is conservation. The long-term invasive status of some exotic species may mean that they have not only replaced native species, but have also assumed their ecological niches. At this point, removal of the invader may also remove functions that are required for other organisms in the same system (Zavaleta et al. 2001).

Lastly, there is a risk of underestimating the ecosystem-level impacts of invasive species, as coupled with the lag phenomenon that is commonplace in invasions, relatively subtle and/or indirect impacts of invasions may mean that a number of responses to invasive species simply remain undetected thus far (Simberloff 2011). Some invasive species may simply be unpredictable, such as the emergence of common cordgrass (*Spartina anglica*), following the introduction of smooth cordgrass (*Spartina alterniflora*) in Europe (Daehler and Strong 1996). Attempts to control invasive species through biological means may also indirectly exacerbate their effects, such as the introduction of moth species to control spotted knapweed (*Centaurea maculosa*), which indirectly increased its negative impacts on other native plants (Callaway et al. 2004). Invasive species may also co-exist, interact and facilitate each other in freshwater ecosystems, such as in the case of the invasive largemouth bass (*Micropterus salmoides*) consuming invasive Louisiana crayfish (*Procambarus clarkii*), subsequently reducing competitive pressure on the invasive European carp (*Cyprinus carpio*) (Britton et al. 2010). The potentially unpredictable or undetectable nature of some species invasions presents a hurdle for their short- and long-term control, particularly when funding for intervention and management work may rely on sufficient evidence.

Can IAS have beneficial impacts?

In contrast to a plethora of research that highlights the global negative impacts of IAS (e.g. Gallardo *et al*., 2016; Schirmel *et al*., 2016; Dick *et al*., 2017), there is also a body of literature discussing their potential for facilitation of native species due to their proficiency as ecosystem engineers. Example studies suggest that there is potential for "tolerating" IAS, particularly when these introduced species may have long-term positive impacts (Walther et al. 2009). Modification of habitat may have negative consequences for taxa that are sensitive to disturbance, but it may also generate new niches for opportunistic taxa to colonise invaded systems (Rodriguez 2006). The introduction of exotic species may even be necessary to enable habitat restoration, such as the use of fast-growing grasses to quickly establish cover in areas prone to soil erosion (D'Antonio and Meyerson 2002). The inclusion of IAS in biodiversity assessments has also been suggested (Schlaepfer 2018), although this is contentious given the large body of literature documenting negative impacts of IAS globally.

The arbitrary removal of IAS due to perceived negative impacts of invasion may have unforeseen negative consequences, such as enabling other undesirable monocultures or the colonisation of other exotic species (Zavaleta et al. 2001). There is evidence to support a taxonomic focus in restoration efforts, as opposed to relying on the "invasive versus native" rhetoric to define the quality of an ecosystem. For example, Davis *et al.* (2018) demonstrated that some INNP may support a greater abundance and diversity of flower-visiting insects than uninvaded plant communities, supporting a case-by-case approach to IAS management (Davis et al. 2018). IAS may be passengers as well as drivers of change (MacDougall and Turkington 2005; Greenwood and Kuhn 2014; Greenwood et al. 2018), and the functional roles of species should be considered in addition to the local effects of IAS in determining necessary management strategies (Bonanno 2016).

Invasive non-native plants

Invasive non-native plants (INNP hereafter) are an important group within IAS ecology, largely due to the negative impacts they have on native plant communities through direct competitive effects and changes to local biotic and abiotic conditions (van Oorschot et al. 2017). INNP such as Japanese knotweed (*Fallopia japonica*) and Himalayan balsam (*Impatiens glandulifera*) can alter the structure of native plant communities (Tanner and Gange 2013), whilst aquatic invasive species such as Eurasian water-milfoil (*Myriophyllum spicatum*) can form dense surface mats of vegetation, blocking out light and reducing the diversity of native aquatic plants (Havel et al. 2015).

Through plant community changes, INNP such as *Salix* sp. may affect aquatic communities by altering the quality, quantity and timing of allochthonous plant and invertebrate inputs to river systems (McInerney and Rees 2017). Invasive knotweed species are able to colonise habitats to such a high density that they drastically reduce the density and richness of native flora (Duquette et al. 2016), which subsequently has negative impacts on the nutrient quality of leaf litter (Urgenson et al. 2009). They can also directly affect terrestrial invertebrate communities through changes to the local microclimate and diversity of habitat and leaf litter (Scherber et al. 2010). INNP also exert morphological changes, promoting soil erosion at invaded sites after the winter dieback (Greenwood and Kuhn 2014) as riverbanks are left exposed to surface runoff and mechanical stress. However, there is an argument to be made for potential ecosystem benefits provided by INNP, particularly when they are able to provide similar inputs as those of native plants to terrestrial and aquatic ecosystems. Fogelman et al. (2018) showed that freshwater macroinvertebrates may be able to utilise invasive *F. japonica* leaf litter due to the novel weapons hypothesis (Fogelman et al. 2018), whereby *F. japonica* inhibits microbial colonisation, slowing the rate of litter breakdown in rivers. The findings of Christopher (2014) support this, demonstrating no preference for native or exotic litter shown by macroinvertebrate functional feeding groups in *F. japonica* dominated streams.

In addition to the effects of INNP on a variety of native flora and fauna, there are also economic considerations to take into account. A study published in 2010 estimated the total annual cost of three key riparian invasive plants in Great Britain, giant hogweed (*Heracleum mantegazzianum*), *I. glandulifera* and *F. japonica* at nearly £169 million (Williams et al. 2010). Similarly, the cost of saltcedar (*Tamarix* spp.) to the western United States was estimated at $127-291 million per year (Zavaleta 2000). INNP also have the potential to leave a costly legacy effect as a result of their invasions, whereby the effects of the these plants may persist long after their removal, continuing to influence community composition and ecosystem properties in both aquatic and terrestrial habitats (Corbin and D'Antonio 2017).

With financial costs such as these, it is clear that invasive plants can have large economic impacts, and that removal of these invaders will require a substantial investment of both time and money. The preferable method of treatment is prevention, as this is also likely to be much less costly (Mack et al. 2000). The value of ecosystem services should not be underestimated, particularly when such an area can be influential in determining public opinion and policy decisions (Loomis et al. 2000). The importance of these services makes species-specific studies particularly important, as this allows problem plants in certain geographical locations to be removed through targeted treatment plans.

1.4 River systems

The freshwater network in Scotland is comprised of over 6000 rivers with a combined length in excess of 100,000 km (Gilvear et al. 2002). In addition to providing a number of ecosystem services with both social and economic value, they are highly biodiverse, supporting a disproportionately high number of species (Strayer and Dudgeon 2010). Rivers are some of the most endangered ecosystems globally, and as such many indices exist to monitor their ongoing status and rate and direction of change in their conditions (Li et al. 2010). These indices frequently incorporate freshwater macroinvertebrates, due to their diversity, ubiquity, and range of responses and sensitivities to common environmental stressors such as sedimentation, acidity/alkalinity and hydraulic habitat (Sundermann et al. 2013).

In recent years, research into riverine ecology has advanced to assess the combined roles of different ecological process, enabling us to better understand factors driving spatial variation in river communities (Tonkin et al. 2018). This is particularly useful considering the requirement to restore the ecological status of water bodies under the EC Water Framework Directive (WFD) (Council of the European Communities 2000). Studies have more recently begun to incorporate fish into the ecological assessment and classification of water bodies under the WFD (Fiona and Trevor 2016), highlighting their importance in river systems. There is however a lack of understanding concerning exactly how stressors caused by IAS contribute to the overall classification of a water body. There is therefore a niche for studies which aim to quantify the pathways through which IAS exert their effects – particularly as their presence may carry significant management implications, depending on the risks posed (Cardoso 2008).

The riparian zone

Riparian ecosystems are complex, dynamic and diverse habitats which offer a variety of resources, ecological niches and habitats for a wide range of species. They contribute to and modify aquatic food webs through the provision of allochthonous plant and animal material (Valente-Neto et al. 2015), and influence the environmental conditions of stream ecosystems through processes such as shading, buffering surface runoff (Leps et al. 2015), and providing aquatic habitat diversity through the input of woody debris (Gurnell 2013). Riparian systems are the focus of a wide variety of studies globally, demonstrating influences on aquatic invertebrate composition (O’Toole et al. 2016), fish assemblages (Teixeira-de Mello et al. 2015) and terrestrial invertebrates and associated subsidies (Collins et al. 2016), amongst many others.

However, the changeable nature of riparian zones and their positioning at the interface of aquatic and terrestrial ecosystems also makes them particularly vulnerable to both natural and anthropogenic stressors (Zelnik et al. 2015), whilst the connected nature of waterways makes riparian zones particularly susceptible to invasion by alien species (Walker et al. 2008). Riparian zones are considered to be particularly susceptible to invasion by non-native species (Tickner et al. 2001), due to the dynamic nature of the environment and variety of organisms, life-history strategies and disturbance regimes occurring over both temporal and spatial scales (Naiman and Decamps 1997). Exotic plants spread preferentially via riparian corridors and river networks (Gurnell 2013) and the adaptive nature of many of these plants allow seeds and other plant fragments to disperse across various distances. Combined with a superior competitive ability (Bradford et al. 2007), riparian invasive plants are able to undergo large population surges at the expense of native plant assemblages. Given that the hydromorphology of riparian areas is typically influenced by factors such as plant structure, height and density (van Oorschot et al. 2017), riparian invaders have the capacity to change the overall morphology of rivers that they invade.

Global studies demonstrate the importance of the riparian zone in understanding and addressing multiple stressors that can potentially impact river ecosystems. Modification to the structure of riparian vegetation can alter the abundance and diversity of terrestrial invertebrates associated with native vegetation, causing knock-on effects on the abundance and diversity of larger fauna that rely on these sources of invertebrate prey (Mosher and Bateman 2016). These changes in vegetation can also alter aquatic macroinvertebrate composition, leading to spatial homogenisation of communities which take significant lengths of time to recover with restorative efforts (Becker and Robson 2009). Changes to riparian canopy can affect both the quantity and quality of allochthonous terrestrial inputs entering rivers, which can have cascading effects on the abundance and diversity of prey items available to keystone fish species such as brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) (Ryan and Kelly-Quinn 2015). More complex interactions between riparian vegetation and river systems may also occur, as the structure and size of vegetation and woody debris entering the river may alter the local hydrological conditions, which may consequently affect aquatic invertebrate assemblages (Lawson et al. 2015).

1.5 Freshwater extinctions

Rivers are considered to be one of the most sensitive ecosystems to climate change (Durance and Ormerod 2007, 2009), particularly through interactions with other environmental stressors (Jackson et al. 2016). Given the fundamental importance of freshwater ecosystems, it is particularly alarming to note that extinctions amongst freshwater species are becoming more common (Pimm et al. 2014), particularly in relation to climate change (Ormerod et al. 2010; Woodward et al. 2010). Populations of brook trout (*Salvelinus fontinalis*) for example may be negatively affected by elevated temperatures and extreme seasonal variations in rainfall (Kanno et al. 2015), whilst multiple salmonid species in North America are at risk of extirpation and/or extinction if predicted climate change trends continue (Katz et al. 2012). North America has a particularly high extinction rate for freshwater fish, with between 53 and 86 species expected to be extinct by 2050 (Burkhead 2012). In South America, populations of *Arapaima* spp. are historically overfished and recorded as depleted in just over three-quarters of the fishing communities in the Amazon Basin (Castello et al. 2015). These trends continue globally, with 87% of freshwater fish species in Malaysia considered to be under threat (Chong et al. 2010), and multiple endemic freshwater fish species in China considered to be critically endangered (Dudgeon 2010). Extinctions are further compounded by our failure to notice them until it is too late, with studies often reporting the loss of species as opposed to pre-emptively highlighting their threatened status (Regnier et al. 2009). The consequences of loss of species within these systems is likely to be significant, particularly given their disproportionately high contribution to biodiversity (Ormerod and Durance 2012), and the likely high number of species that may be affected by another’s removal.

Freshwater systems are constantly changing via pressures from human-mediated change, aquatic invasive species, land-use changes and associated chemical inputs, and economic or recreational uses (Carpenter et al. 2011). Fragmentation of habitat is a key driver of species loss, and loss of species diversity at lower trophic levels may have knock-on effects that drive extinctions at higher trophic levels. Examples include reductions of accessible habitat following dam construction and the exclusion of populations of lamprey (*Lampetra* spp.), eels (*Anguilla* spp.) and shads (*Alosa* spp.) (Hall et al. 2010; Liermann et al. 2012). Modifications to land use that impinge on riparian zones may negatively impact terrestrial invertebrate taxa and squeeze out specialists that have more specific habitat requirements (Sinnadurai et al. 2016). Human-induced changes to freshwater habitats are also particularly important, and are likely to be one of the most important causes of freshwater invertebrate extinctions (Strayer 2006). Reductions in hydrological connectivity are responsible for extirpations and/or risk of extinction in North American mussel and salmon and steelhead (*Oncorhynchus* spp.) fish species, which would have potentially significant consequences for other organisms which depend on them (Pringle 2003).

Role of invasive species in freshwater extinctions

IAS cause significant changes in ecosystems globally, but whilst there are many studies that provide evidence for roles of IAS in the extinction of native species, these are not necessarily applicable in a wider context (Gurevitch and Padilla 2004). Furthermore, their effects may often be dependent on the trophic position of the invader (Gallardo et al. 2016), suggesting that the impact of a particular IAS may differ between ecosystems and also depend on interactions with other species. However, IAS are recognised and reported as an extinction threat to native species. A report by Clavero & Garcia-Berthou (2005) concluded that in an analysis of recent worldwide animal extinctions, IAS were either one of the factors or the only factor in 74% of cases where the cause of extinction was assessed. Examples of IAS-driven extinctions include the threat posed to North American freshwater mussels (Unionoida) by the invasive zebra mussel (*Dreissena polymorpha*) (Ricciardi et al. 1998), whilst the invasion of Nile Perch (*Lates niloticus*) in Lake Victoria is a classic example of the potentially devastating impact of introduced fish species on native populations (Goldschmidt et al. 1993). Hermoso *et al.* (2011) found invasive species to be the best predictor of the decline of native freshwater fish assemblages, whilst the tropical signalgrass *Urochloa subquadripara* is shown to cause small scale habitat homogenisation and reduced richness of native macrophytes (Michelan et al. 2010; Thomaz and Cunha 2010). This could have consequences both for aquatic invertebrate communities which feed on macrophyte leaf material (Newman 1991) and for fish species which feed on these invertebrates and use macrophyte cover as refuge from predation (Wilson et al. 2015). INNP in particular lend themselves to disruption of freshwater ecosystems due to a general superiority in important performance-related traits (such as physiology and growth rate) when compared to native plants (van Kleunen et al. 2010).

There is still debate concerning a definitive role of IAS on species extinctions in freshwater ecosystems, as the impacts of invasive species on ecosystem services remain largely unquantified, and are rarely defined in terms that are useful to decision makers (Walsh et al. 2016). Whilst the individual impacts of invaders may be relatively small, these can combine in the event of multiple invasive species introductions, leading to drastic reductions or even extinctions in native species populations. These ecosystem engineers are capable of causing localised and regional-scale modifications to habitats and associated community assemblages, and as such should be carefully considered in studies relating to the persistence of freshwater biodiversity. Future research must incorporate efforts to disentangle the impacts of invasive species from other environmental stressors, particularly when the impacts of both vary spatially and temporally (Jackson et al. 2017).

1.6 Study species

Impatiens glandulifera

Himalayan balsam (*Impatiens glandulifera* Royle) was first introduced from the Himalayas in the early 1800s (Perrins et al. 1993), and has subsequently become one of the most widespread invasive plants in the UK (Pattison et al. 2016) due to its ability to thrive in disturbed environments (Greenwood and Kuhn 2015). As an annual plant, *I. glandulifera* is able to affect vegetation composition by displacing native ruderal species (Tanner et al. 2013), which combined with the detrimental effects of disturbance makes *I. glandulifera* a common and successful invader of riparian systems (Čuda et al. 2017) (Figure 1.1).

Impatiens glandulifera displaces native plant species through direct competition for resources, such as water and light, though research has shown that displacement may also manifest through competition for pollinators (Thijs et al. 2011). Its competitive success is due in part to its tolerance for a wide range of climates and soil types (Chittka and Schurkens 2001), and partly due to its explosive seed dispersal system, which facilitates its spread throughout river corridors. The consequences of winter frosts are particularly devastating for *I. glandulifera*, which dies back and exposes the riverbank to the elements. This is in part due to the ability of *I. glandulifera* to outcompete and displace native plant species that would contribute to bank stability (Cockel and Tanner 2012), promoting erosion and increased sedimentation through surface run-off, and also depriving the bank of a solid structural root network with which to resist shear stress (Pollen and Simon 2005). Increased rates of fine sediment ingress can in turn clog interstitial spaces within the benthos, reducing permeability and local oxygen concentrations (Wildhaber et al. 2014).

Figure 1.1 *Impatiens glandulifera* flowers (left) and an invaded bank of the Pow burn on the South Esk catchment (right).

Fallopia japonica

Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decraene) is a herbaceous, perennial plant native to China, Japan, Korea and Taiwan, but which is now widely established in Europe after its introduction in the early 19th century (Beerling et al. 1994). It is able to recruit via several modes, including through clonal, rhizomatous growth, (Aguilera et al. 2009) and can quickly form monocultures, particularly in disturbed habitats. However, *F. japonica* is also able to spread via seed bank, and can over-winter without any negative impact on germination success the following spring (Gowton et al. 2016). Similarly to *I. glandulifera*, *F. japonica* displaces native vegetation to alter the composition of riparian plant communities (Figure 1.2), with consequences for aquatic and terrestrial invertebrate communities which utilise the allochthonous inputs and habitat offered by native vegetation (Braatne et al. 2007). Studies have also shown that in addition to standard methods of competition (e.g. shading, monopolisation of nutrients), *F. japonica* also excludes other native plants through allelopathy, whereby it produces chemicals that have significantly negative impacts on the growth of native plants (Siemens and Blossey 2007; Murrell et al. 2011).

The persistent nature of this plant provides a significant threat to infrastructure and native flora and fauna, particularly bordering waterways, with negative ecological, economic and social impacts (Babic and Trkulja 2014). An estimated £1.7 million was spent in 2010 to control riparian *F. japonica* in Scotland (Williams et al. 2010).

Figure 1.2 A stand of *Fallopia japonica* on the Argaty burn (Forth catchment), demonstrating the dense canopy and riparian overhang.

Freshwater macroinvertebrates

Aquatic macroinvertebrates are some of the most ubiquitous and commonly-studied freshwater taxa, as their diverse nature and range of responses to a suite of environmental indicators make them excellent organisms for biomonitoring indices (Everall et al. 2017). Orders of invertebrate taxa such as Ephemeroptera and Plecoptera (Figure 1.3) are generally pollution intolerant (Hodkinson and Jackson 2005), whereas the Chironomidae family are able to survive under near-anoxic conditions, and are used as indicators of freshwater pollution (McGeoch 2007). Many of these taxa also play important roles in the overall functioning of river communities, such as linking the algal and detrital energy sources with higher trophic levels, through herbivorous feeding methods such as grazing and shredding (Usseglio-Polatera et al. 2000a), and providing an abundant and essential food source for fish that forage in the benthos and drift (Dobrin and Giberson 2003).

Figure 1.3 *Dinocras cephalotes*, a member of the Plecoptera order and an important indicator of water quality.

Similarly to native vegetation communities, changes to river hydromorphology and environmental conditions caused by INNP can affect aquatic invertebrate communities (Ellis and Jones 2014). Increased erosion and sediment run-off as a result of INNP may negatively impact benthic macroinvertebrates, increasing the volume of suspended sediment and increasing risk of predation (Bilotta and Brazier 2008). Furthermore, fluctuations in freshwater macroinvertebrate communities in response to stressors can echo through the aquatic food web, as changes in the abundance and spatial distribution of taxa may result in disproportionate responses by other species in an attempt to compensate (Covich et al. 1999).

Given their abundance, diversity and range of responses to environmental variation, freshwater macroinvertebrates are an excellent focal group for monitoring the condition of aquatic ecosystems and forecasting environmental change. From being incorporated into natural studies to predict future effects of global warming (Woodward et al. 2010) to their use as overall predictors of environmental conditions and community composition (Clarke et al. 2003), the importance of this broad range of taxa in ecological studies cannot be overstated.

Terrestrial invertebrates

Terrestrial invertebrates are a diverse, multifunctional group of organisms (Figure 1.4) that play significant roles in ecosystems globally (Ramey and Richardson 2017). They can be used as indicators of environmental quality (although perhaps not as regularly or efficiently as aquatic macroinvertebrates) (Hodkinson and Jackson 2005), and are a key component of biodiversity monitoring studies (Andersen et al. 2004). Terrestrial invertebrates are particularly responsive to variations in the local microclimate and habitat structure, with many species demonstrating habitat specificity, and are also important in a variety of ecosystem processes such as pollination, seed dispersal and the breakdown of organic materials (Taylor and Doran 2001). Similarly to aquatic macroinvertebrates, terrestrial invertebrate taxa can be used to infer information about habitat quality. For example, both Acari and Collembola communities show variations in species composition in response to *I. glandulifera*, demonstrating that INNP can alter nutrient cycling through the modification of arthropod community composition (Rusterholz et al. 2014).

Terrestrial invertebrates are part of an important subsidy that links aquatic and terrestrial systems, particularly in riparian habitats. They provide a vital energy source to supplement the diets of juvenile salmonid fish such as *Salmo trutta* (brown trout) and *Salmo salar* (Atlantic salmon), and the size of the subsidy they provide is correlated with the size of riparian canopy (Collins et al. 2016). This allochthonous energy input can become even more important to fish in the event of aquatic pollution, when the abundance of drifting invertebrates may be lessened by stressors such as trace metals (Kraus et al. 2016). Terrestrial invertebrates can also be used as indicators of aquatic subsidies to demonstrate the flow of nutrients from aquatic to terrestrial food webs. Hoekman *et al*. (2011) demonstrated a measurable change in terrestrial arthropod communities in response to midge (Chironomidae) emergences in an Icelandic lake system, highlighting the transfer of resources across ecosystems.

Figure 1.4 Examples of the more common terrestrial invertebrate morphotypes. Coleoptera (top-left), Hemiptera (top-right), Diptera (bottom-left), Hymenoptera (bottom-right).

Salmonid fish

Salmonids are often significant keystone species in river ecosystems, both as predators of lower trophic levels and as a food resource for terrestrial vertebrate predators and scavengers (Willson and Halupka 1995). The presence and persistence of salmonids in a river system can have consequences for aquatic macroinvertebrate communities, such as the suppression of grazing invertebrate taxa and subsequent bloom in algal productivity (Townsend 2003). Baxter et al. (2004) showed that introduced non-native rainbow trout (*Oncorhynchus mykiss*) outcompeted native Dolly Varden charr (*Salvelinus malma*) for terrestrial invertebrate subsidies, forcing the latter to switch to aquatic grazing insects as a prey source. The resulting reduction in emerging adult aquatic insects led to a reduced density of riparian-specialist spiders, demonstrating the ability of keystone salmonid species to alter resource flow between ecosystems. A similar study by Benjamin *et al*. (2011) also found reductions in the abundances of terrestrial spiders in response to the replacement of native cutthroat trout (*Oncorhynchus clarkii*) with the non-native brook trout (*Salvelinus fontinalis*).

The brown trout (*Salmo trutta* L) and Atlantic salmon (*Salmo salar*) are two anadromous salmonid fish species; S. *trutta* is indigenous to Europe, whilst *S. salar* is distributed throughout Europe and the eastern coast of North America (Jensen et al. 2012). Both species contribute significantly to the Scottish economy (Butler et al. 2009) and as such are the focus of numerous ecological studies that monitor their responses to anthropogenic and environmental pressures across a range of ages and population sizes (e.g. Metcalfe et al., 1988; Bridcut & Giller, 1995; Elliott & Hurley, 2000). Both species are also included in assessments of water bodies for the Water Framework Directive (Council of the European Communities 2000), which considers the impacts of barriers to migratory fish, and *S. salar* is incorporated in the designation of Special Areas of Conservation as a protected species (HMSO 1994).

Studies also frequently consider *S. trutta* and *S. salar* concurrently, as it is common to find both species living in sympatry due to a large overlap in their preferred habitat (Armstrong et al. 2003; Johansen et al. 2011). However, variations that arise from competition between and within populations of these two species mean that their utilisation of both aquatic and terrestrial invertebrate prey resources differ, both between species and amongst fish of different ages. For example, *S. trutta* are likely to be more aggressive than and dominant over *S. salar* individuals of a similar size, and as such will be more likely to control the surface drift and associated invertebrate inputs from terrestrial sources (Höjesjö et al. 2010). This heterospecific interaction can also alter the feeding behaviour of subordinate *S. salar* individuals, which may forgo their preferred nocturnal feeding strategy during the summer and winter months in favour of more diurnal feeding in order to maintain a suitable growth rate (Nislow et al. 2010). This may have the disadvantage of increasing natural mortality rates.

Salmonids may be affected by a range of biotic and abiotic stressors (Jackson et al. 2001), which may have implications for their ability to persist in river systems. Both species are visual predators (Kemp et al. 2011), and their ability to successfully attack and consume prey items may be impeded by factors such as sedimentation, which can reduce visibility and the efficiency of their foraging exertions (Chapman et al. 2014). Given the established link between riparian INNP and increased rates of sedimentation in rivers (Greenwood and Kuhn 2014), it is possible that reductions in visibility and the consequential reduction in foraging success by salmonids may have wider, whole ecosystem consequences. Similar trophic cascades have been observed before, where changes in the voracity and methods of feeding of a keystone predatory fish can alter the biomass of herbivorous invertebrate consumers via predation pressures on predatory invertebrates (Woodward et al. 2008).

Salmonids are a particularly important group when considering the effects of INNP on riparian systems. Although they are opportunistic feeders and are able to adapt to changes in the quantity and quality of prey available to them (Johansen et al. 2011), INNP may exert pressure through alternative pathways, such as through changes to the hydrology and morphology of the river. Alterations to local habitat heterogeneity through changes to substrate and flow diversity may alter the abundance and diversity of aquatic invertebrate prey in both benthic and drift food sources (Naman et al. 2017), both of which are important to *S. trutta* and *S. salar*. The dense riparian canopy afforded by INNP such as *F. japonica* may alter salmonid feeding behaviour – significant changes in *S. trutta* diet have been observed in response to riparian canopy (Ryan and Kelly-Quinn 2015).

Figure 1.5 The focal salmonid species for this study: *Salmo salar* (top) and *Salmo trutta* (bottom).

1.7 Research questions

Changes in freshwater macroinvertebrate communities in response to riparian invasive non-native plants

Freshwater macroinvertebrates respond in a variety of ways to a suite of environmental and anthropogenic pressures. Their inclusion in a vast array of biomonitoring indices is an indication of their ecological significance, and is testament to their importance in aquatic ecosystems on a global scale. The annual nature of riparian plant invasions (Tanner et al. 2013) suggests that their impact may persist through seasonal variations in hydromorphological habitat. Whilst the abundance and density of INNP stands is clear during the summer period of peak growth, their impact during the winter months following dieback (Greenwood and Kuhn 2015) is less clear, with the exception of a riverbank devoid of vegetative cover. Whilst there is a significant body of literature discussing the impacts of INNP (Simberloff et al. 2013), there remains a need to quantify their effects on invertebrate communities, particularly compared to the environmental variables that are responsible for natural fluxes in invertebrate community composition. Chapter 2 examines the effect of INNP on freshwater macroinvertebrate communities, and provides some context of these effects in relation to environmental drivers of community change in river systems.

Question: To what extent do riparian INNP alter the abundance, diversity and composition of freshwater macroinvertebrate communities?

Hypothesis: Higher riparian INNP cover will homogenise the composition of aquatic invertebrate communities through changes to allochthonous inputs and local instream habitat. Aquatic invertebrate communities at sites with higher INNP cover will exhibit reduced diversity as a result of these physical and chemical changes.

Changes in the structure of terrestrial invertebrate communities in invaded riparian systems

The terrestrial environment is an important part of riparian ecosystems. It is linked to the aquatic food web through plant matter inputs and invertebrate subsidies, both of which provide a significant allochthonous energy source for aquatic organisms. Recent studies demonstrate the ability of invasive riparian flora to modify river systems through processes such as altered quality and quantity of allochthonous leaf litter inputs (Fargen et al. 2015). However, the effective use of terrestrial invertebrates in biomonitoring assessments is less developed and perhaps less effective than aquatic invertebrate equivalents (Hodkinson and Jackson 2005). One potential explanation for this is that taxonomic and logistic constraints can make traditional taxonomic identification for terrestrial invertebrates more difficult (Oliver and Beattie 1996).

It is possible that INNP will exert their effects on terrestrial invertebrates through different pathways than those which alter aquatic invertebrate communities. Studies have demonstrated variations in the effects that invasive plants have on different types of terrestrial food web (McCary et al. 2016), and factors such as local litter microhabitat and woody debris may significantly alter terrestrial invertebrate communities (Taylor and Doran 2001); factors which are likely to be affected by significant changes to the local vegetation community. Chapter 3 addresses this by assessing the variation in terrestrial invertebrate communities at heavily invaded riparian sites. In particular, potential pathways and important indicator species are highlighted and discussed with respect to INNP.

Question: How do the diversity and heterogeneity of riparian terrestrial invertebrate communities differ at sites invaded by INNP, and is there evidence of a difference in effect between *Fallopia japonica* and *Impatiens glandulifera*?

Hypothesis: High levels of INNP cover will reduce the diversity of above-ground terrestrial invertebrate communities through changes to local microhabitat conditions. Whilst *F. japonica* and *I. glandulifera* exert similar dominant effects on riparian vegetation communities, the biological differences between these two species are expected to cause differing effect sizes on the assessed invertebrate community indices.

Relative importance of invertebrate prey sources in salmonid diets

Salmonid fish are particularly important in the ecological assessment of rivers (Pehlivanov et al. 2012) and as indicators of the success of restoration attempts (Pander and Geist 2013). They are opportunistic foragers (Syrjänen et al. 2011), and as such they may be able to adapt to local variations in prey availability. However, less is known about how salmonids respond to changes in their local environment and physical habitat as a result of terrestrial and aquatic morphological changes following riparian INNP invasions. Whilst studies exist that examine the effects of invasive species on salmonids (either directly or indirectly), these tend to focus on salmonids as invaders (Simon and Townsend 2003), competition with other fish (Hasegawa and Maekawa 2006), or the associated introduction of disease (Vitule et al. 2009; Strayer 2010). In particular, fisheries managers may attempt to block upstream invasions with movement barriers (Fausch et al. 2009), but the resulting isolation can often be detrimental to the native salmonid populations that they are trying to preserve.

Understanding how these important keystone predators respond to changes in bankside vegetation following INNP invasions is vital in assessing how best to manage these invasions should they affect important salmonid nursery/spawning streams. Chapter 4 assesses how the presence of *F. japonica* and *I. glandulifera* alters the relative selection of a range of terrestrial and aquatic invertebrate taxa by juvenile *S. trutta* and *S. salar*, and quantifies the relative effect of both INNP species on salmonid diet, compared to environmental variables.

Question: Do any impacts of INNP on either freshwater or terrestrial invertebrates affect the dietary selections of juvenile salmonid fish, and how important are these changes in relation to population dynamics and environmental stressors?

Hypothesis: Given the opportunistic and adaptable nature of salmonids, changes in the local availability of invertebrate prey will be offset by the acquisition of alternative prey sources.

General discussion

Freshwater and riparian systems are constantly under pressure from a suite of environmental and anthropogenic pressures, and these often form the basis of policy and management plans to protect and/or restore threatened ecosystems. In recent years, the increase in size and prevalence of the invasion biology niche has popularised and widely publicised the threat posed to native ecosystems by invasive non-native species (Simberloff 2015). However, there is still a pressing need to incorporate the threats posed and effects exerted by these invaders in methods of ecological assessment, particularly in riparian systems. By their very nature, these dynamic habitats enable the rapid spread of invasive species that are able to adapt to regular disturbance and spread throughout river systems.

Studies that present methods of including invasive non-native species into methods of ecological assessment (Cardoso 2008; Hulme et al. 2008) provide a framework upon which research such as that presented here may build. Chapter 5 gives an overview and in-depth discussion of the findings of this thesis, limitations of the studies presented within, and suggestions for future research that will continue to improve our understanding of the impacts of invasive non-native plants in riparian ecosystems.

Chapter 2: Responses of aquatic invertebrates to invasion of river banks by non-native plants

Surber sampler *in situ* for the collection of benthic macroinvertebrate samples.

2.1 Introduction

Riparian zones are diverse, complex habitats that provide an ecologically important buffer between land and water, regulating the health and quality of the waterways they border. The dynamic nature of riparian zones increases their susceptibility to invasion, particularly by non-native plants, which can spread quickly throughout catchments (Richardson et al. 2000) and are associated with negative ecosystem-wide impacts (Simberloff 2015) that are repeated on a global scale. The impact of invasive non-native plants (INNP) has been demonstrated on native plant communities (Pysek et al. 2012; Pattison et al. 2017). Other studies suggest that invasive alien trees may alter the structure of secondary consumer assemblages (McInerney and Rees 2017) and promote long-term changes in macroinvertebrate community structure (Becker and Robson 2009; Roon et al. 2014).

Management of the riparian zone has been shown to influence stream and riparian trophic productivity by altering in-stream conditions (Wootton 2012; Mehler et al. 2014; Wallace et al. 2015). The River Continuum Concept (Vannote et al. 1980) highlights the importance of riparian vegetation and identifies a number of ways through which riparian plants can affect river system processes. Through this we see that a general understanding of the biological strategies and dynamics of river systems requires a synoptic knowledge of the physical factors (and the magnitude of their effects) acting upon the river system. The riparian zone is of particular importance to this, as riparian modifications may alter processes such as primary production in small, low order streams, consequently affecting macroinvertebrate density and biomass (Graça 2001), as well as key predators such as fish (Wipfli and Baxter 2010). Other localised effects, such as nutrient interception, storage and release (Pusey and Arthington 2003), as well as larger scale changes such as the modification of channel structure through sediment retention and alterations to the hydraulic and mechanical properties of the substrate (Gurnell 2013) are also typical of these invaded ecosystems.

Currently, river and fisheries managers, local authorities and environmental protection agencies devote significant resources to managing riparian plant invasions, but without strong evidence of impact, it is challenging to justify these resources or envisage the potential ecological gains arising from management.

Freshwater macroinvertebrates are excellent indicators of environmental conditions, as their presence and abundance reflect a variety of instream physical and chemical characteristics (Li et al. 2010). In recent years biomonitoring has expanded to include other anthropogenic stressors alongside organic pollution (Murphy et al. 2015) and likely impacts on ecosystem processes such as organic matter decomposition and secondary production (Usseglio-Polatera et al. 2000b; Bonada et al. 2006). Given these advances, there remains a pressing need to assess the importance of riparian INNP cover as a driver of aquatic macroinvertebrate community structure, relative to the suite of environmental variables already known to influence macroinvertebrates. The effects of riparian INNP cover are particularly relevant when considering the ecological status of water bodies as prescribed under the EC Water Framework Directive (WFD) (Council of the European Communities 2000). The WFD prescribes that assessments of ecological status reflect the ability of a water body to support various biota (e.g. benthic macroinvertebrates and flora) characteristic of undisturbed conditions. As such, assessments must take into account the presence of INNP and their outcomes may be influenced by the impacts of invasive non-native species more generally (Macneil et al. 2013; Mathers et al. 2016). Since European countries are required under the WFD to restore failing water bodies to good ecological status, the presence of INNP may carry significant management implications, depending on the risks posed (Cardoso 2008).

Invasive plants such as *Fallopia japonica* (Japanese knotweed) and *Impatiens glandulifera* (Himalayan balsam) are now widely established on river banks across the northern hemisphere. They influence the aquatic environment via shading, lowering of water temperature, and by altering the quality, quantity and timing of terrestrial carbon input (Claeson et al. 2013). Rapid growth enables INNP to outcompete native plants, leading to the formation of dense monocultures. These may reduce the ability of riparian vegetation to filter contaminants (Duquette et al. 2016), whilst early winter dieback potentially exposes river banks to erosion by floods (Greenwood and Kuhn 2015). Disturbances to native riparian vegetation can also permeate aquatic food webs: riparian shading modulates water temperatures (Broadmeadow et al. 2011), which, together with changes to the nutritional quality of allochthonous leaf litter (Kuglerová et al. 2017), may affect the diversity and abundance of aquatic macroinvertebrates, thereby altering decomposition rates

(Lagrue et al. 2011; Claeson et al. 2013). Additionally, clearing of INNP along rivers has recently been shown to promote some recovery of vulnerable stream macroinvertebrate taxa (Mcneish et al. 2015).

The aim of this study was to assess whether riparian INNP affect the structure and turnover of aquatic macroinvertebrate communities, using field surveys to isolate the magnitude and direction of any effect from those of other environmental variables driving aquatic macroinvertebrate community structure. It was hypothesised that changes to riparian vegetation caused by INNP would affect the composition of aquatic invertebrate communities through changes to allochthonous inputs and by modifying local environmental conditions. Aquatic invertebrate communities at sites with higher INNP cover were predicted to exhibit reduced diversity as a result of these physical and chemical changes.

2.2 Methods

Study sites

Sites were located on six low (1st to 4th) order streams (Strahler 1957) in catchments across central and southern Scotland (Appendix, Figure 1), providing a range of geographically and environmentally varied sampling locations. On each stream, a pair of control (uninvaded) sites were located upstream from a pair of invaded sites containing established stands of either *F. japonica* or *I. glandulifera*, the sites in each pair being separated by an average of 0.35km (Figure 2.1). There were 24 study sites in total (Appendix, Table S1). Sites were limited by the size of INNP stands present, and as such were standardised to a 20m length of channel. Invaded sites were chosen according to the criteria that INNP coverage should exceed 50% of the vegetation cover on at least one bank, their characteristics otherwise being similar to those of upstream uninvaded sites (Sax et al. 2005). INNP cover at a site often fell below this threshold when considering the total INNP cover across both banks. Both *I. glandulifera* and *F. japonica* were assessed collectively, the focus of the study being on overall effects of invasion-related disturbances rather than differences between similar INNP species. Distances between sites and the downstream main stem river varied from 0.2-8.7km, to fulfil the need to match physicochemical characteristics and ensure suitable riparian invasive cover.

Figure 2.1 A representative pair of study sites – a typical native woodland stream (left) and an invaded counterpart (right).

Macroinvertebrate sampling and processing

Benthic invertebrates were collected by hand raking Surber samples (collecting area 0.3 x 0.3m) for 30 seconds. To remove potential bias in the field (Hulme et al. 2013), sampling locations were randomly allocated prior to collection. Sites were sampled during spring and autumn 2015 to allow seasonal changes in invertebrate composition to be assessed before and after the summer peak of INNP growth. Eight Surber samples were collected per site in each season to allow investigation of spatial heterogeneity in invertebrate composition. Samples were preserved in the field with 70% industrial methylated spirits and subsequently sorted and identified to the lowest practicable taxonomic level (normally species) with the aid of taxonomic keys (Hynes 1977; Edington and Hildrew 1981; Wallace et al. 2003; Elliott and Humpesch 2010; Tachet et al. 2010; Foster and Friday 2011; Dobson et al. 2012; Foster et al. 2014) (Appendix, Table S2).

Physico-chemical variables

Environmental data were obtained through on-site measurements. Conductivity and pH were measured at each site in tandem with stream macroinvertebrate samples using a combimeter (HANNA instruments HI-98130 Pocket EC/TDS and pH Tester). Land use at both the 5m and 50m scale was categorised based on visual assessment and supplemented by aerial photography accessed via Google Earth. The proportion of the channel that was shaded was estimated visually, and the total number of trees in the study reach exceeding 5m in height was recorded as a proxy for the amount of channel shading caused specifically by riparian trees. Sites were surveyed using an electronic distance measuring instrument (Theomat Wild TC1000 electronic total station, Leica Geosystems Ltd, Milton Keynes, UK) to map the thalweg profile at each site and to derive an accurate measure of channel slope (Jones 2010).

To investigate the diversity of the substrate, a Wolman count of 100 particles was made in summer using a gravelometer (Wolman 1954), which categorises particle sizes according to their intermediate axis. Shannon's diversity index was then calculated for the substrate particle size composition at each site, treating each size class as a 'species', using the "diversity" function in the vegan (Oksanen et al. 2017) R package (R Core Team 2017). Water velocity and depth were recorded for each specific Surber sample, using a flowmeter (SENSA RC2 Water Velocity Meter, Aqua-data Ltd, UK) and metre rule. To utilise these physical measurements in the analysis of macroinvertebrate species turnover, a Bray-Curtis (B-C) dissimilarity index was calculated using depth and velocity at the Surber level. Used together, these variables enabled dissimilarity between sample locations to serve as a proxy for hydraulic habitat heterogeneity.

To quantify riparian INNP cover, vegetation surveys were conducted during August to coincide with peak growing season. Using three transects running perpendicular to the channel, three 1m^2 quadrats (where space permitted) were placed equidistantly on each transect between the foot and top of each bank, giving a total of 18 quadrats per site. The percentage cover of INNP in each quadrat was calculated and averaged over both banks to provide an estimate of invasive plant cover for the site.

Macroinvertebrate metrics

Several macroinvertebrate metrics were focused on because of their relevance to national methods for assessing ecological status for WFD purposes (UKTAG 2014). Macroinvertebrate community richness was expressed using the sample level alpha diversity based on the full complement of taxa recorded per Surber sample. The Whalley Hawkes Paisley Trigg (WHPT) index (Paisley et al. 2014), a reformulation of the Biological Monitoring Working Party scoring system, was used to assess water quality. Values for this index range from 13 (most pollution-sensitive macroinvertebrates) to 1 (least sensitive). Due to strong variation in individual sample abundances and the representation of different taxa, the abundance-weighted WHPT score was used, whereby the index value for a sample is the log-abundance weighted average of the scores of the taxa present.

The proportion of sediment-sensitive invertebrates (PSI) (Extence et al. 2013) was calculated at each of the study sites in both spring and autumn, to assess whether taxa present at invaded sites indicated a greater degree of sediment loading.

Additionally, the Bray-Curtis dissimilarity index was used to express spatial heterogeneity in stream macroinvertebrate communities. A series of pairwise Bray-Curtis dissimilarities was generated for each season x site (comparing the first sample to each of the rest, then the second to the rest, etc.). The average of these pairwise comparisons served as a measure of dissimilarity between a specific sample and the remaining samples from that site. Higher average values indicated greater spatial dispersion in composition between samples at a location on a given date. The total number of individuals per sample was also considered as a measure of invertebrate abundance.

Statistical analysis

Four linear mixed effects models (LMMs) were used to investigate drivers of variation in the selected macroinvertebrate metrics (response variables: Simpson’s diversity index, WHPT score, spatial dissimilarity and raw abundance). Predictors used in these models were channel shade, invasive cover, number of trees, channel slope, conductivity, habitat heterogeneity and substrate diversity. River identity was treated as a random effect.

To test for an effect of season, each model was run with season as a fixed effect. If this model output showed evidence of a significant seasonal effect ($p < 0.05$) season was then included as an interaction term to determine whether predictors had seasonally-dependent effects. Prior to modelling, predictors were scaled to one standard deviation to allow their effects to be directly compared. All possible combinations of predictors were identified using the “dredge” function in MuMIn (Barton 2017). Models were then ranked by their corrected Akaike information criterion (AICc) to account for small sample sizes. To identify the top set of models, a threshold of ΔAICc < 2 was set (Burnham and Anderson 2002). From this top set (Appendix, Table S3), a fully averaged model was chosen for interpretation of coefficients (Barton 2017). To assess variation explained solely by the fixed effects, as well as variation explained by both the fixed and random effects together, both marginal and conditional R^2 values are reported for each model (Nakagawa et al. 2013) (Table 1).

PSI scores were generated following the methodology described by Extence *et al.* (2013). Macroinvertebrates were assigned a score based on their abundance at a site, and which related to their sensitivity to sediment. From these values, scores from each sensitivity group (ranging from highly sensitive to highly insensitive) were obtained for each site, which were used to assess the degree of pressure from fine sediment loading.

Species characteristics of invaded and uninvaded sites were identified using indicator species analysis (IndVal; Dufrêne & Legendre, 1997) applied to species abundance data at the individual Surber sample level from the 12 invaded or uninvaded sites. The indicator value represents the specificity and fidelity of aquatic invertebrate species for invaded and uninvaded sites. The index ranges from 0% (no presence in a survey group), to 100% (present in only one group, and in all samples within that group). The significance of these values was tested using a Monte Carlo randomisation procedure (Dufrêne and Legendre 1997).

Variation in macroinvertebrate species composition between invaded and uninvaded sites in spring and autumn samples was compared using non-metric multidimensional scaling (NMDS) (Kruskal and Wish 1978). To minimise the influence of highly abundant taxa, data were converted to presence/absence data (Borcard et al. 2011). To evaluate the contribution of individual environmental variables to overall macroinvertebrate community composition, a redundancy analysis (RDA) by season was performed, including INNP cover and all environmental attributes (channel shade, invasive cover, number of trees, channel slope, conductivity, habitat heterogeneity and substrate diversity) as explanatory variables. RDA was applied to Hellinger transformed macroinvertebrate species abundance data, and rare species were down-weighted (Borcard et al. 2011). The global model was reduced using forward selection based on AICc, to adhere to rules of model parsimony.

All statistical analyses were conducted using R 3.4.3 (R Core Team 2017), with the additional packages vegan (Oksanen et al. 2017), reshape2 (Wickham 2007), biotic (Briers 2016), labdsv (Roberts 2016), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), effects (Fox 2003), MuMIn (Barton 2017) and r2glmm (Jaeger 2017).

2.3 Results

Response	**Model parameters**	**R^2m**	**R^2c**
Simpson's diversity	Channel slope (1) + depth*flow B-C (1) + invasive cover (1) + season (0.79) + channel shade (0.77) + substrate diversity (0.18)	0.14	0.22
WHPT	Channel shade (1) + conductivity (1) + depth*flow B-C (1) + invasive cover (1) + season (1) + substrate diversity (1) + nº trees (1) + channel shade*season (1) + conductivity*season (1) + depth*flow B-C (1) + season*substrate diversity (1) + season*nº trees (0.74) + invasive cover*season (0.31)	0.28	0.49
Abundance	Channel shade (1) + invasive cover (1) + season (0.56) + conductivity (0.37)	0.07	0.39
Spatial dissimilarity	Channel shade (1) + channel slope (1) + depth*flow B-C (1) + invasive cover (1) + substrate diversity (1) + nº trees (1) + season (0.78) + conductivity (0.48)	0.19	0.64

Table 2.1 The best, fully-averaged models for models with ΔAICc < 2. Relative variable importance is given in brackets, followed by marginal (R^2m) and conditional (R^2c) values.

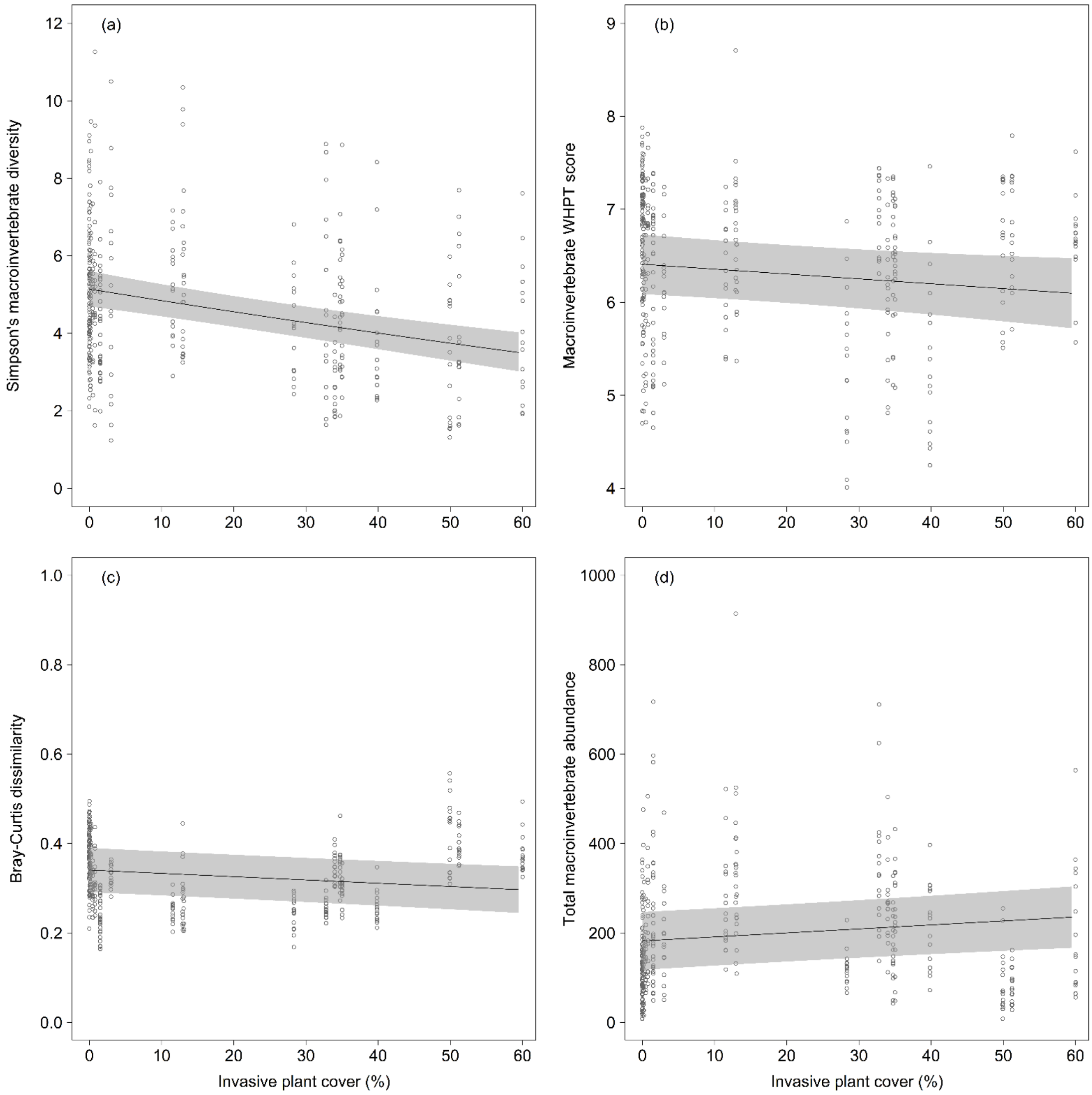

Figure 2.2 Full model predicted values (shaded polygon shows ± 95% confidence intervals) from the LMM analyses of (a) Simpson's macroinvertebrate diversity, (b) macroinvertebrate WHPT score, (c) spatial dissimilarity for individual Surber samples and (d) macroinvertebrate abundance for individual Surber samples, all plotted against invasive cover.

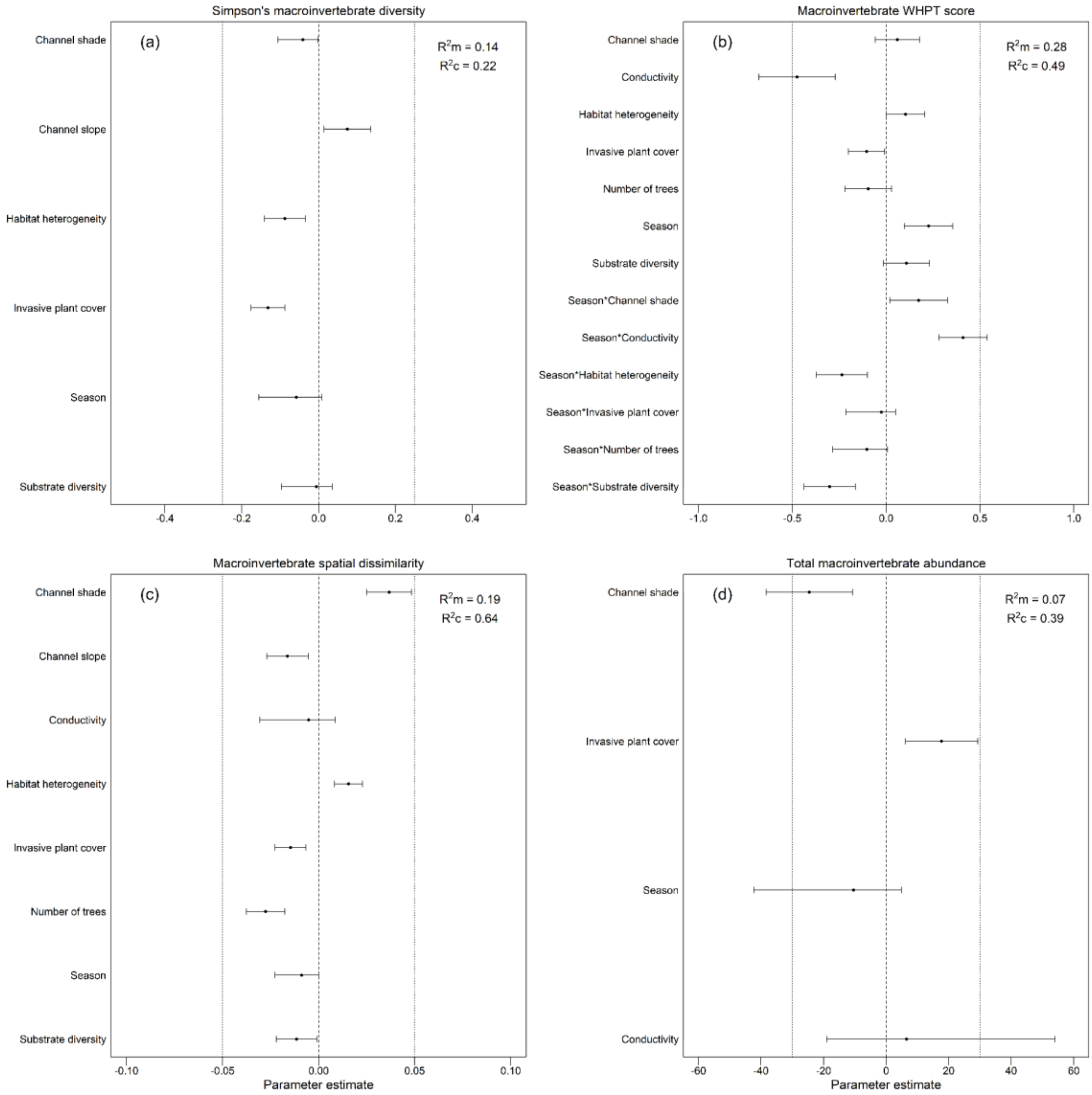

Figure 2.3 Full, model-averaged parameter estimates ± 95% confidence intervals. Modelled responses were (a) Simpson’s diversity index, (b) macroinvertebrate WHPT score, (c) spatial dissimilarity and (d) macroinvertebrate abundance. Marginal (R^2m) and conditional (R^2c) values are given.

Simpson’s macroinvertebrate diversity

Macroinvertebrate diversity was positively associated with channel slope and negatively associated with habitat heterogeneity (Figure 2.3a), indicating that fewer macroinvertebrate species were tolerant of increased spatial variation in water velocity and depth. Macroinvertebrate diversity was also negatively associated with invasive cover (Figures 2.2a and 2.3a), which had the greatest overall effect size (-

0.13), with Simpson's macroinvertebrate diversity being on average approximately 33% (± 5.6%) lower at 60% invasive cover (the maximum cover recorded in this study), compared to uninvaded sites. There was no evidence of any seasonal interaction.

Macroinvertebrate WHPT and PSI scores

Macroinvertebrate WHPT score was positively associated with habitat heterogeneity and negatively associated with conductivity (Figure 2.3b) and invasive cover (Figures 2.2b and 2.3b). Conductivity (-0.47) and season (0.23) had the greatest overall effects on WHPT score. Macroinvertebrate WHPT score was on average approximately 5% (± 2.4%) lower at 60% invasive cover, compared to uninvaded sites. There was a positive interaction between season and conductivity, and season and channel shade. Higher conductivity and channel shade were associated with a higher WHPT score in spring compared to autumn, indicating the presence of more sensitive taxa at sites with these conditions in spring. There was a negative interaction between season and habitat heterogeneity, and season and substrate diversity. Greater habitat heterogeneity and substrate diversity were associated with a lower WHPT score in spring compared to autumn, perhaps in response to greater hydrological disturbance over the preceding winter.

The PSI scores ranged between 74.4 and 100, indicating that all study sites in both spring and autumn were classed as minimally sedimented or unsedimented, with a small number being classified as slightly sedimented (Extence et al. 2013). Additionally, there was no evidence of a trend in PSI scores associated with either invaded or uninvaded sites.

Macroinvertebrate spatial dissimilarity

Spatial dissimilarity in macroinvertebrate composition between samples at a site was positively associated with channel shade and habitat heterogeneity, indicating a more spatially diverse community at shaded and hydraulically diverse habitats. Spatial dissimilarity between samples at a site was negatively associated with number of trees, channel slope, substrate diversity (Figure 2.3c) and invasive cover (Figures 2.2c and 2.3c). Channel shade (0.04) and number of trees (-0.03) had the greatest overall effects on macroinvertebrate spatial dissimilarity. The effect of invasive cover was marginal, on average reducing spatial dissimilarity by approximately 12% (± 3.4%) at

60% invasive cover, compared to uninvaded sites. There was no evidence of any seasonal interaction.

Macroinvertebrate abundance

Macroinvertebrate abundance was positively associated with invasive cover (Figures 2.2d and 2.3d) and negatively associated with channel shade (Figure 2.3d), indicating a limiting effect of overhead shading on the availability of suitable habitat conditions for macroinvertebrates at our sites. At 60% invasive cover, sites on average had approximately 33% (± 11.0%) more macroinvertebrates than uninvaded sites. No other variables were significant and there was no evidence of any seasonal interaction.

Indicator species

A larger number of macroinvertebrate taxa were significantly associated with invaded sites compared to uninvaded sites in both spring and autumn (Table 2.2). In addition, marginally more macroinvertebrate taxa were significant indicators in autumn compared to spring. The strongest indicators of invaded sites in both spring and autumn were Gammaridae and *Dicranota* spp. (Indicator values (IV) = 0.46-0.56), with the addition of *Serratella ignita* (IV = 0.63) in the spring. These taxa are indicative of a generalist preference for a range of substrates and slow to medium flow conditions (Usseglio-Polatera et al. 2000a), and suggest an in-stream habitat characterised by a moderate leaf litter input. Uninvaded sites were most strongly characterised by members of the Baetidae and Rhyacophilidae families in spring (IV = 0.40-0.47), indicating a preference for more rheophilic and oligosaprobic conditions, and the presence of a suitable food source for predatory invertebrates. In autumn, uninvaded sites were most strongly characterised by Hydropsychidae and Nemouridae (IV = 0.33-0.36), again indicating greater flow and less organic matter entering the stream.

Site type	**Species**	**Observed Indicator Value**	**Biological/ecological trait group**	**Functional feeding group**
Invaded, spring	*Serratella ignita****	62.7	f/C1	Deposit feeder
	Gammaridae***	55.7	b1/C1	Shredder
	Dicranota spp.***	49.8	c1/D1	Predator
	Elminthidae***	37.0	e3/B1	Scraper
	*Drusus annulatus****	26.1	f/A	Shredder
	*Ancylus fluviatilis**	21.0	e2/C1	Scraper
	*Ecclisopteryx guttulata**	12.7	f/A	Shredder
Uninvaded, spring	*Baetis rhodani***	47.3	e2/C1	Scraper
	*Rhyacophila dorsalis**	40.4	c1/B2	Predator
	*Lepidostoma hirtum****	15.7	f/C1	Grazer
	*Rhyacophila munda**	6.3	c1/B2	Predator
Invaded, autumn	*Dicranota* spp.**	55.0	c1/D1	Predator
	Gammaridae*	46.2	b1/C1	Shredder
	*Silo pallipes****	44.5	e2/B1	Scraper
	*Limnius volckmari****	37.3	e3/B1	Scraper
	*Ecclisopteryx guttulata**	36.0	f/A	Shredder
	*Ancylus fluviatilis****	35.3	e2/C1	Scraper
	Lymnaea spp.*	16.7	c2/F3	Scraper
	*Baetis scambus**	11.8	e2/C1	Scraper
	Paraleptophlebia spp.**	11.7	f/C1	Deposit feeder
Uninvaded, autumn	*Hydropsyche siltalai**	36.1	e1/C1	Filter feeder
	*Protonemura meyeri****	33.1	f/A	Shredder
	*Amphinemura sulcicollis**	21.4	f/A	Shredder
	*Capnia bifrons***	13.5	e2/B2	CPOM feeder
	*Philopotamus montanus***	8.3	e2/A	Filter feeder

Table 2.2 Significant indicator species for invaded and uninvaded sites. Observed Indicator Value shows the indicator value for each species (0 = no fidelity or specificity; 100 = complete fidelity and specificity). Asterisks indicate the probability of that Indicator Value occurring by chance based on permutation tests (*** <0.001, ** <0.01, * <0.05). Biological and ecological group classifications are included after Usseglio-Polatera *et al.* (2000a), and broad functional feeding group classifications are included after Murphy and Giller (2000).

Macroinvertebrate community composition

Analysis of compositional data by NMDS showed a partition between invaded and uninvaded sites in autumn (Appendix, Figure S2). No distinction could be found between invaded and uninvaded sites in spring (Appendix, Figure S1).

The RDA model for spring and autumn was a significant fit between the predictor variables and species abundance matrix, with conductivity and invasive cover being the only significant explanatory variables in both seasons. Consistent with the indicator species analysis, the autumn RDA triplot (Appendix, Figure S3) showed clustering of taxa such as Gammaridae and *Ancylus fluviatilis* at higher invasive cover, while taxa such as *Chloroperla tripunctata* and *Protonemura meyeri* were associated with higher conductivity. Axes 1 and 2 explained 4% of the total variation.

2.4 Discussion

Effects on macroinvertebrate metrics

Riparian INNP cover had the strongest association with Simpson's macroinvertebrate diversity across both seasons, suggesting that high INNP cover in summer has a legacy effect on macroinvertebrate diversity which extends to the following spring. Additionally, INNP cover was positively associated with macroinvertebrate abundance and negatively associated with WHPT score, though the latter effect size was relatively minor in comparison to other environmental predictors (conductivity, habitat heterogeneity and substrate diversity). This suggests overall that invaded sites foster a greater abundance, but lower diversity of pollution-tolerant, low-scoring WHPT taxa. This suite of responses will be reflected in lower average ecological status, as inferred from invertebrates, at invaded stream sites. The indication that habitat quality for macroinvertebrates is lower at invaded sites is also consistent with the decreased spatial dissimilarity in composition between samples. The indicator species analysis adds further support for this, demonstrating that more taxa with lower WHPT scores showed fidelity to invaded sites (including Gammaridae, *Dicranota* spp. and Elmidae taxa), whilst more taxa with higher WHPT scores showed fidelity to uninvaded sites (including *Rhyacophila* spp., *Lepidostoma hirtum*, *Protonemura meyeri* and *Amphinemura sulcicollis*).

Reductions in riparian macroinvertebrate abundance, richness and biomass have previously been demonstrated in response to invasions by *Fallopia* species (Gerber et al. 2008), and these reductions may ultimately lead to changes in aquatic food web dynamics, as other species attempt to adjust to declines in more sensitive taxa (Covich et al. 1999).

The relationship between INNP cover and macroinvertebrate diversity may also reflect local changes in the chemical and physical properties of the leaf litter available to invertebrates, as well as variation in nutritional quality or palatability. Riparian INNP invasions may alter rates of litter decomposition by aquatic macroinvertebrates, but these changes appear to depend more on the type and quality of litter than invasive status *per se* (Kuglerová et al. 2017). Less palatable INNP litter or a reduction in the supply of preferred litter types might help to explain the observed reduction in macroinvertebrate diversity found at sites with higher INNP cover.

Effects on macroinvertebrate community structure and heterogeneity

Macroinvertebrate composition was most heterogeneous at sites with little or no invasive cover. Heavily invaded river banks can be left exposed to winter flooding due to rapid dieback of plants at the first frost, while fragile senesced material is easily dispersed by floods (Gowton et al. 2016). This exposure lowers bank stability (Gurnell 2013) potentially increasing surface run-off and fine sediment entry and reducing water quality and primary production (Chapman et al. 2014). Fine sediment has well documented adverse effects on stream invertebrates (Jones et al. 2015), including reduced ability to utilise the hyporheic zone (Mathers et al. 2014), resulting in net loss of habitat. An increase in suspended sediment through the erosion of unprotected banks can adversely affect benthic invertebrates, increasing risk of predation (Bilotta and Brazier 2008), and homogenising sediments through fine sediment ingress (Burdon et al. 2013). However, the PSI analysis suggested that the benthic habitat at most sites in this study was minimally or only slightly sedimented, offering no evidence to link invertebrate community response to INNP cover via channel sedimentation. Nevertheless, whilst the actual process of change remains undetermined, these results highlight a homogenising effect of riparian INNP cover on stream macroinvertebrate community composition, in agreement with Becker & Robson (2009).

Invasive cover showed one of the strongest associations with macroinvertebrate spatial dissimilarity, but channel shade, habitat heterogeneity and number of trees also exerted strong effects. Although invasive cover appears to have some spatially homogenising effect on macroinvertebrates, it is clearly not the only environmental factor to do so. NMDS analysis showed evidence of differences in community composition between invaded and uninvaded sites in autumn, but not in spring. This is supported by the RDA analysis, which shows that community composition in the autumn is driven by invasive cover and conductivity. Macroinvertebrate taxa such as Gammaridae and *Ancylus fluviatilis* are associated with invaded sites, and are generally regarded as shredders and scrapers respectively (Murphy and Giller 2000). Taxa such as *Lepidostoma hirtum* are associated with uninvaded sites, and are regarded as grazers (Usseglio-Polatera et al. 2000a). These associations are in agreement with the indicator species analysis. This community variation in autumn is supported by the loss of several high-scoring WHPT taxa from Surber samples, including the heptagenid mayfly *Ecdyonurus* spp., the taeniopterygid stonefly *Brachyptera risi* and individuals from the philopotamid caddisfly *Wormaldia* spp.

The indicator species analysis did not provide support for reductions in availability or palatability of leaf litter at invaded sites, as both invaded and uninvaded sites harboured multiple taxa associated with plant matter and detritus (including Gammaridae, *Baetis* spp., *Drusus annulatus* and *Ecclisopteryx guttulata*). The indicator species analysis does perhaps suggest that shredders present at invaded sites in the spring were being partially replaced by scrapers in the autumn. This pattern was not found at uninvaded sites. Stream macroinvertebrates may be characterised by their feeding guild (Rawer-Jost et al. 2000) and community responses to alterations in the availability and quality of useable food sources may be an important, yet cryptic driver of change. This apparent shift in feeding guild composition at invaded sites may be in response to the earlier dieback of INNP cover, reducing shading and allowing the re-establishment of biofilm (Sturt et al. 2011).

It seems that despite a clear negative effect on macroinvertebrate composition, riparian INNP cover explains a relatively small amount of variation in invertebrate community structure.

Management implications

It is difficult to state with confidence that any management action will yield a defined result, taking into account site-specific properties, interactions between stressors (Vinebrooke et al. 2004; Jackson et al. 2016) species-specific responses (Altermatt et al. 2013) and the external factors that drive stochastic variation in ecosystems. Caution must therefore be exercised when using these findings to inform management policy, as the improvement in conditions through removing riparian INNP cover at the local scale may deliver some ecological improvements, but may also yield a relatively low benefit-cost ratio if overwhelmed by effects of other anthropogenic stressors at coarser scales (Simberloff et al. 2013; Sundermann et al. 2013). Legacy effects of non-native invasions may also delay expected ecological responses (Cuddington 2012; Corbin and D'Antonio 2017), and certain treatment or removal approaches may themselves adversely affect native biota (Flory and Clay 2009; Kettenring and Adams 2011). Nevertheless, this study provides evidence that the presence of extensive riparian INNP cover does indeed affect stream macroinvertebrate communities, and thereby offers conditional support for actively managing severe riparian invasions, and gauging expected responses.

Conclusions

This study found that invasive non-native riparian plants have a unique and measurable effect on stream macroinvertebrates. Invasive riparian cover constrained and homogenised macroinvertebrate communities, demonstrated by significant negative associations with spatial dissimilarity, Simpson’s macroinvertebrate diversity and WHPT score, and a positive association with abundance. Although the possibility that some other unmeasured but causal pressure covaried closely with INNP cover cannot be excluded, the effects reported here are consistent with negative associations noted for terrestrial INNP such as *Rhododendron ponticum* (Hladyz et al. 2011) and invasive species more generally (Roy et al. 2014; Gallardo et al. 2016). Furthermore, whilst this study demonstrates negative associations between INNP cover and macroinvertebrate communities, these effect sizes are reasonably small and as such may offer a low benefit-cost ratio as a result of any management efforts. Many other variables influenced macroinvertebrate communities, notably conductivity, channel slope, number of trees, channel shading and physical habitat heterogeneity, all of which themselves are prone to human modification.

Chapter 3: Responses of terrestrial invertebrates to invasion of riparian habitats by non-native plants

Adult *Tipula paludosa* on a *Fallopia japonica* leaf. New Abbey Pow, river Nith catchment, August 2016.

3.1 Introduction

Terrestrial invasive non-native plants (INNP) represent over 300 of the established plant species in Europe (Keller et al. 2011). INNP are often associated with reductions in overall biodiversity (Barney et al. 2015), lower abundance of terrestrial primary consumers (McCary et al. 2016) and disruption of above and below-ground fungal communities (Pattison et al. 2016). Negative impacts on ecosystem services such as pollination and biomass production may also be associated with INNP (Hulme et al. 2013), alongside altered rates of erosion and water use compared to their native counterparts (Pejchar and Mooney 2009). Impacts on ecosystem services and biodiversity comprise some of the main criteria for listing a species as an invasive alien species (IAS) under EU regulation No 1143/2014, which covers the prevention, management and spread of IAS (European Union 2014). INNP are also responsible for societal and economic losses, particularly when they colonise and disrupt agricultural land (Duncan et al. 2004), and often require costly investment to manage and/or repair ecological damage (such as flood damage following INNP colonisation) (Zavaleta 2000). Societal reactions to IAS may also depend on observable effects of visible invaders (Simberloff et al. 2013), which may hinder restoration efforts following colonisations by less prominent IAS.

The case for managing INNP is often built on evidence of their impacts, but such evidence can prove contentious. Conflicting arguments highlight potential benefits of INNP, such as use of *I. glandulifera* by pollinators (Bartomeus et al. 2010), or use of INNP biomass as feed for livestock (Van Meerbeek et al. 2015), but also invoke detrimental legacy effects of INNP introductions (Iacarella et al. 2015; Corbin and D'Antonio 2017). Naturally dynamic systems are particularly prone to invasion by non-native species (Catford et al. 2012); riparian habitats, characterised by fluvial disturbance and exposed to waterborne transport of propagules, are thus amenable to invasions (Lawson et al. 2015). However, little is known about how invasion of riparian habitats by INNP impacts their terrestrial invertebrate communities.

Terrestrial invertebrates account for a large proportion of the diversity found within riparian ecosystems. They serve as indicators of environmental conditions (Gerlach et al. 2013), perform various key functions, including pollination of invasive and native plant species (Bartomeus et al. 2010), and mediate the transfer of energy between aquatic and terrestrial food webs (Gustafsson et al. 2014; Ramey and Richardson 2017). Although studies do exist which assess the diversity and spatial distribution of terrestrial invertebrates, many of these assess specific taxa groups, such as Coleoptera (Topp et al. 2007), Acari (Báldi 2003) and Collembola (Rusterholz et al. 2014), rather than analysing the terrestrial invertebrate community as a whole and in context with the numerous anthropogenic and environmental stressors which impact them (Ramey and Richardson 2017).

Riparian vegetation may significantly alter the allochthonous subsidy provided by terrestrial invertebrates (Allan et al. 2003), affecting the energy resources available to fish (Bridcut 2000; Baxter et al. 2005). However, terrestrial invertebrate communities are also influenced by other anthropogenic and environmental pressures, including land use (Newbold et al. 2015), river discharge (Sinnadurai et al. 2016) and shading (Feld et al. 2018). These pressures may be further exacerbated by INNP, which thereby alter the structure and functioning of the ecosystems they invade (Ehrenfeld 2010). Gerber et al (2008) demonstrated that riparian habitats invaded by Fallopia species harboured a reduced abundance and morphospecies richness of terrestrial invertebrates, whilst Ruckli et al (2013) showed that *I. glandulifera* supported a higher abundance and species richness of gastropods compared to uninvaded plots. A range of responses by flower-visiting insect communities at sites colonised by INNP were demonstrated by Davis et al (2018), including higher insect diversity associated with *I. glandulifera* and lower abundance of solitary bees and hoverflies associated with *Heracleum mantegazzianum* (giant hogweed).These pressures may be further exacerbated by INNP, which alter the structure and functioning of the ecosystems they invade (Ehrenfeld 2010). For example, invasion of riparian areas by the aggressive giant reed (*Arundo donax*) reduces the abundance, biomass and richness of both terrestrial and aerial invertebrate species, which has implications on fauna that use these taxa as food sources (Herrera and Dudley 2003). Invasion and the subsequent introduction of novel terrestrial subsidies (i.e. novel plant-derived organic matter) into an aquatic food web has been shown to have negative effects on the survival of some freshwater macroinvertebrate taxa, thought to be due to significant reductions in pH and dissolved oxygen concentrations (Custer et al. 2017). Furthermore, alterations to terrestrial subsidies may depend on the size of the riparian canopy and associated inputs to stream food webs (Collins et al. 2016).

Riparian zones are disproportionately species rich (Gerber et al. 2008) and thus offer suitable habitats for studying the effects of INNP on invertebrate communities, especially as the structural complexity afforded by plant communities is directly linked to predator-prey dynamics (Grutters et al. 2015). Two key INNP species commonly associated with riparian habitats, *Fallopia japonica* and *Impatiens glandulifera*, feature prominently in studies assessing drivers of vegetation composition, with the former being listed among the world's 100 worst invasive alien species (Lowe et al. 2000). Both species can act as ecosystem engineers, with *I. glandulifera* triggering soil erosion in river systems (Greenwood and Kuhn 2015) and *F. japonica* reducing resident plant species diversity (Aguilera et al. 2009; Chmura et al. 2015) and lowering native plant cover through high propagule pressure (van Oorschot et al. 2017). However, despite apparent similarities in effect types and pathways between these two species, INNP can impact native biota through a variety of different mechanisms (Vila et al. 2011) and to varying degrees depending on the taxonomic level studied (Pysek et al. 2012).

The diversity presented by terrestrial invertebrate species and their functional significance makes them an excellent group for studying the impacts of INNP in riparian systems. Different broad groupings of terrestrial invertebrate taxa can be used as indicators for a variety of ecological conditions and environmental factors. For example – Isopoda for soil systems, ground-dwelling Hymenoptera and Coleoptera for the general surface layer, and more specific groupings such as Chrysomelid leaf beetles for indicators of foliage condition (Gerlach et al. 2013). Similarly to aquatic invertebrates, terrestrial invertebrate communities shows a degree of compositional variation between areas with distinctly different characteristics (Pik et al. 2002), demonstrating the ability to use terrestrial invertebrate community composition as a measure of conditions at invaded versus uninvaded habitats.

The aim of this study was to compare the effects of *F. japonica* and *I. glandulifera* on terrestrial invertebrate community composition, evaluating the relative effects of these two INNP species against those of other environmental factors, such as soil organic content and native plant community structure.

3.2 Methods

Study sites

Sites were located on low (1^{st} to 4^{th}) order streams in catchments across central and southern Scotland (Appendix, Figure S1), providing a range of geographically and environmentally varied sampling locations (Appendix, Table S1). On each stream, a pair of control sites were located upstream from a pair of invaded sites containing established stands of either *F. japonica* or *I. glandulifera*, the sites in each pair being separated by an average of 0.35km. Control sites were located on average between 0.6km to 2.9km upstream from invaded sites, and sites were chosen where the focal INNPs had been established for at least a 10 year period. There were 20 study sites in total; four invaded by *F. japonica* and six invaded by *I. glandulifera*, and the two INNP species did not co-occur at any study sites. Sites were limited by the size of INNP stands present, and as such were standardised to a 20m length of bank. Invaded sites were identified provisionally on the criteria that INNP coverage should exceed 50% of the vegetation cover on at least one bank (Figure 3.1), whilst other characteristics should as far as possible match those of upstream uninvaded sites (Sax et al. 2005). However in practice, INNP coverage fell below this threshold at some study sites.

Figure 3.1 Aerial photo of the Pow burn (South Esk catchment), showing dominant invasive *Impatiens glandulifera* (top bank) and native *Petasites hybridus* (lower bank) cover (© Nigel Willby).

Terrestrial invertebrate sampling and processing

Terrestrial invertebrates were collected at each site using pitfall traps, each comprising a 500ml plastic pot (10cm diameter) with a screw-top lid (Figure 3.2). To reduce the risk of flooding, four drainage holes were added near the top of the trap, and a ceramic tile was placed over the top of each trap, acting as a rain shelter and allowing a small vertical gap between the trap and the tile for invertebrate access. To avoid catching non-target fauna, an 85mm diameter hole was cut from the trap lid and replaced with heavy-duty garden mesh (mesh size 13mm). Traps were installed three weeks prior to the first proposed sampling session to minimise digging-in effects (Schirmel et al. 2010). At each site, 12 traps were installed at 75cm intervals along a linear transect running parallel to the river and located in the middle of an invasive stand at invaded sites. Traps were installed approximately between 1-2m horizontally from the water's edge (i.e. above the bankfull level) to minimise the risk of inundation by flood water. As traps were left collecting for one-week periods, antifreeze (approximately 60mm of 25% ethylene glycol) was used as a killing agent. Longer periods of trap exposure were rejected to reduce the risk of reduced trap catchability caused by evaporation of preservative (Schirmel et al. 2010). Sites were then sampled for one week during each of June and August to allow changes in invertebrate composition to be assessed in response to the summer peak of INNP growth. Upon collection, trap contents were preserved in the field with 70% industrial methylated spirits and invertebrates were thereafter assigned to morphospecies (Báldi 2003; Krell 2004) using light microscopy (up to x64 magnification). Parataxonomy and the use of morphospecies classifications was preferred to achieve accurate comprehensive estimates of terrestrial invertebrate diversity, whilst also minimising the risk of skewed estimates of individual abundance caused by errors in taxonomic identification (Oliver and Beattie 1996). Terrestrial invertebrate keys were used to guide the assignment of morphotypes (Chinery 1993; Tilling 2014), and guidance from experts was sought for the most commonly recorded groups (Diptera and Coleoptera) to ensure individuals were correctly partitioned into morphotypes.

Figure 3.2 The pitfall trap design (left) and a trap *in situ* with a tile cover (right).

Physico-chemical variables

Land use at each site was categorised at scales of both 5m and 50m from the water's edge based on a visual assessment and aerial photographs accessed via Google Earth, to give an estimate of the proportion of natural and artificial land use (as defined in the River Habitat Survey (Raven et al. 1998)). Site orientation (recorded as degrees from north) and site elevation were also obtained from Google Earth, and the total number of trees in the study reach exceeding 5m in height (henceforth tree density) was recorded in the field as a proxy for the amount of channel shading caused specifically by riparian tree cover.

Five soil cores (6cm depth, 4cm diameter) were taken at each site, spread equidistantly along the pitfall trap transect. Loss on ignition (LOI) was used to measure soil organic content (Heiri et al. 2001). Soil samples were aggregated and air dried at 100ºC overnight in a furnace, ground using a pestle and mortar, and passed through a 2mm sieve. They were then heated at 550ºC overnight to combust organic matter. Soil organic content was then defined as the change in mass before and after burning.

To quantify INNP cover, vegetation surveys were conducted during August to coincide with peak growing season. Using three transects running perpendicular to the channel, three 1m^2 quadrats were placed equidistantly on each transect between the foot and top of each bank containing pitfall traps, giving a total of nine quadrats on the bank (at seven sites it was not possible to place the full nine quadrats due to the narrowness of the riparian zone). The cover of all plants was estimated visually in each quadrat, and the percentage covers of *F. japonica* and *I. glandulifera* in each quadrat were averaged separately over the bank containing the pitfall traps to provide an estimate of the cover of each INNP. Plants recorded in the vegetation surveys were identified to species with the aid of taxonomic keys (Rose and O'Reilly 2006; Poland and Clement 2009).

Invertebrate indices

Terrestrial invertebrate community morphospecies diversity was expressed using both the sample level alpha and site level gamma diversity, based on the full complement of morphospecies in each pitfall trap and at each site respectively. Total invertebrate abundance per pitfall trap was also calculated for each weekly sampling period.

The Bray-Curtis dissimilarity index was used to express spatial dissimilarity in terrestrial invertebrate communities, giving a measure of turnover between individual pitfall traps at a given site, based on morphospecies composition. To assess spatial dissimilarity, a series of pairwise Bray-Curtis dissimilarities was generated for each site for a given sampling month (comparing the first sample to each of the rest, then the second to the rest, etc.). The average value for each of these pairwise comparisons was calculated and used as a measure of dissimilarity between a specific sample and the remaining population of samples from that site. Higher values indicated greater turnover in composition between samples. Given that distance between pitfall traps affects the capture rates of ground-dwelling arthropods (Zhao et al. 2013), pairwise Bray-Curtis dissimilarities were weighted based on distances between pairs of traps.

Plant community indices

Plant community richness (excluding *F. japonica* and *I. glandulifera*) was expressed using Shannon’s diversity index. Plant cover estimates were standardised to account for the number of quadrats sampled at each site.

Additionally, Ellenberg’s indicator scores (Ellenberg 1986) were used to express the ecological attributes of the native plant community. Ellenberg’s indicator scores are values assigned to vascular plant species for a range of environmental conditions including moisture, soil reaction and light regime (Schaffers and Sýkora 2000), which can be used to infer conditions at a site based upon the plant community.

Statistical analysis

Linear mixed effects models (LMMs) were used to investigate drivers of variation in the selected invertebrate metrics (response variables: invertebrate morphospecies diversity based on Simpson's index, invertebrate spatial dissimilarity based on Bray-Curtis, total invertebrate abundance and invertebrate morphospecies gamma diversity). The finalised list of predictors was refined based on preliminary analysis – predictors were checked for collinearity after Zuur et al (2010), model responses were assessed for normality, and normality of the model residuals was checked using normal probability plots. Final predictors included *F. japonica* cover, *I. glandulifera* cover, site elevation, mean Ellenberg indicator values for light (Ell-Light) and moisture (Ell-Moisture), tree density, percentage natural land use at the 50m scale, soil organic content and native vegetation diversity using Shannon's index. River, site and trap number were included as random effects in a multi-level nested design, with pitfall trap nested within site, and site nested within river. Residuals were checked for normality and heteroscedasticity (Zuur et al. 2010).

To test for an effect of sampling month, each model was run with month as a fixed effect. If this model output showed evidence of a significant month effect ($p < 0.05$), sampling month was then included as an interaction term to determine whether predictors had seasonally-dependent effects. Prior to modelling, predictors were scaled to one standard deviation to allow their effect sizes to be directly compared. All possible combinations of predictors were identified using the "dredge" function in MuMIn (Barton 2017). Models were then ranked by corrected Akaike information criterion (AICc) to account for small sample sizes. To identify the top set of models (Appendix, Table S4), a threshold of ΔAICc < 2 was set (Burnham and Anderson 2002). From this top set, a fully averaged model was chosen for interpretation of coefficients (Barton 2017). To assess variation explained solely by the fixed effects, as well as variation explained by both the fixed and random effects together, both marginal and conditional R^2 values are reported for each model (Nakagawa et al. 2013).

Whilst the concept of model averaging is well-reported and discussed (Symonds and Moussalli 2010; Zhang et al. 2014), some contention surrounds the suitability of such a technique for identifying the most ecologically sound conclusions from a starting model with multiple factors (Richards et al. 2010). To check the robustness of the model averaging technique, this approach was compared against a standard stepwise model selection protocol using AIC comparison (Burnham et al. 2010). The fully averaged model from the topset (Table 3.1) was re-built for each response, and stepwise removal of non-significant terms was carried out using AIC comparison to justify each removal. The predictor effect sizes from this approach are presented alongside the effect sizes from the fully averaged models in Figure 3.4.

Morphospecies characteristics of invaded and uninvaded sites were identified using indicator species analysis (IndVal; Dufrêne & Legendre, 1997) applied to morphospecies abundance data at the individual trap level for all pairs of invaded and uninvaded sites. The indicator value assesses the specificity and fidelity of terrestrial morphospecies for invaded and uninvaded sites. The index ranges from 0% (no presence in a survey group), to 100% (present in only one group, and in all samples within that group). The significance of these values was tested using a Monte Carlo randomisation procedure (Dufrêne & Legendre 1997).

All statistical analyses were conducted using R 3.4.3 (R Core Team 2017), with the additional packages vegan (Oksanen et al. 2017), reshape2 (Wickham 2007), labdsv (Roberts 2016), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), effects (Fox 2003), MuMIn (Barton 2017) and r2glmm (Jaeger 2017).

3.3 Results

Across all study sites, individual pitfall traps contained an average of 100 individuals, representing an average of 11 morphospecies per trap and 32 morphospecies per site. The most common taxonomic groupings (by abundance) were Acari (25%) and Coleoptera (24%), followed by Diptera (13%) and Collembola (12%). The remaining individuals comprised a mix of winged individuals such as Hemiptera and Hymenoptera, the lower catch rate of these taxa being typical of pitfall trapping studies (Schirmel et al. 2010).

Model coefficients from the topset of models with $\Delta AICc < 2$ are shown in Table 3.1. The relative variable importance, marginal (R^2m) and conditional (R^2c) values are also shown.

Response	**Model parameters**	**R^2m**	**R^2c**
Simpson's diversity	*I. glandulifera* cover (1) + *F. japonica* cover (1) + Ell-Light (1) + Ell-Moisture (0.71) soil organic content (0.19)	0.17	0.25
Total abundance	*I. glandulifera* cover (1) + *F. japonica* cover (1) + Ell-Light (1) + Ell-Moisture (0.40)+ month (0.38) + natural land use at 50m (0.12)	0.23	0.29
Spatial dissimilarity	*I. glandulifera* cover (1) + *F. japonica cover* (1) + Ell-Light (1) + month (1) + site elevation (0.17) + tree density (0.15) + Ell-Moisture (0.15) + soil organic content (0.15)	0.16	0.48
Gamma diversity	*I. glandulifera* cover (1) + Ell_Moisture (1) + soil organic content (0.84) + *F. japonica cove*r (0.22) + tree density (0.18)	0.39	0.50

Table 3.1 The best, fully-averaged models for models with ΔAICc < 2. Relative variable importance is given in brackets, followed by marginal (R^2m) and conditional (R^2c) values.

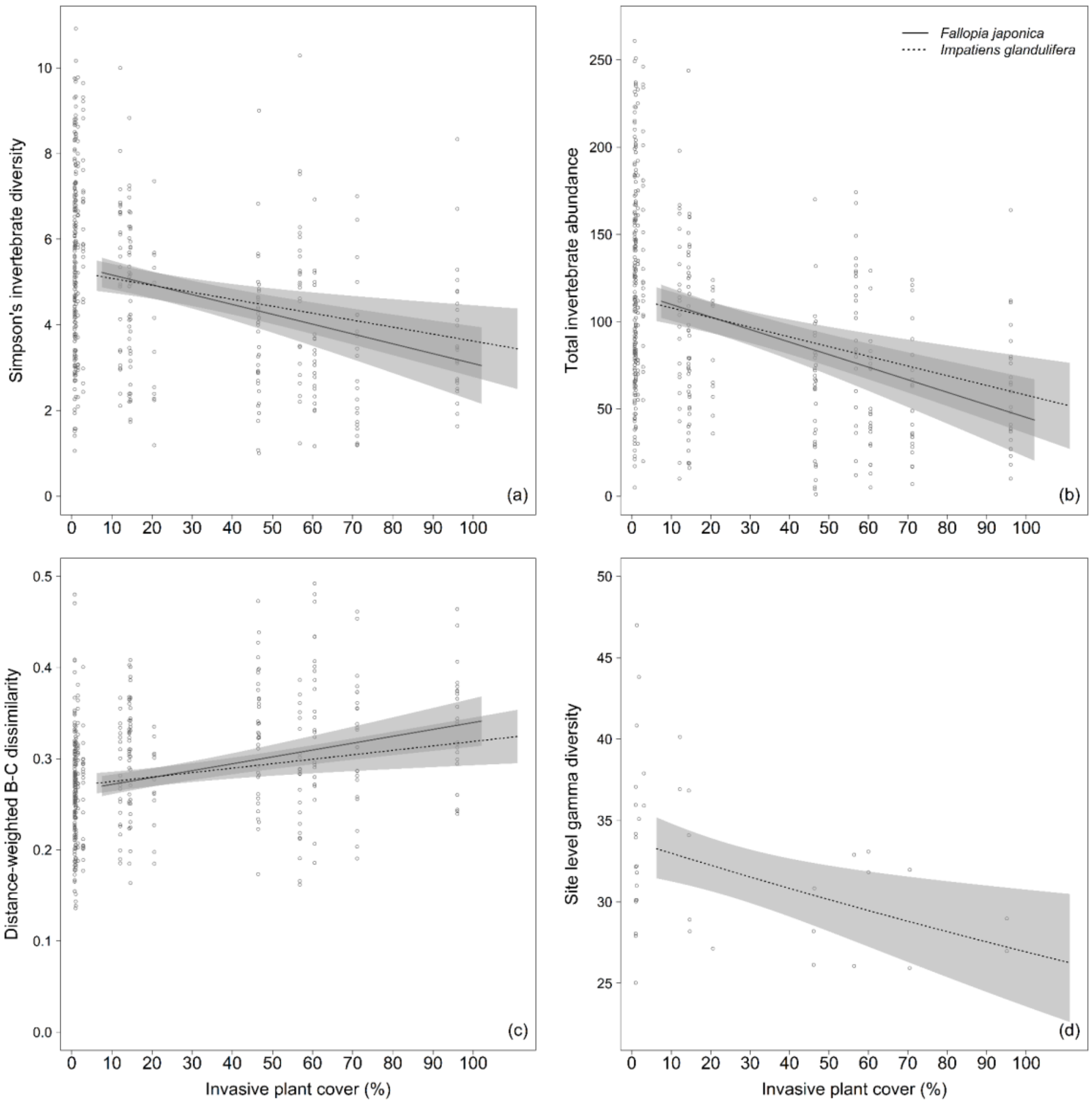

Figure 3.3 Full model predicted values (shaded polygon shows ± 95% confidence intervals) plotted over raw data from the LMM analyses of (a) Simpson's invertebrate diversity, (b) total invertebrate abundance, (c) spatial dissimilarity and (d) invertebrate gamma diversity, all plotted against invasive plant cover.

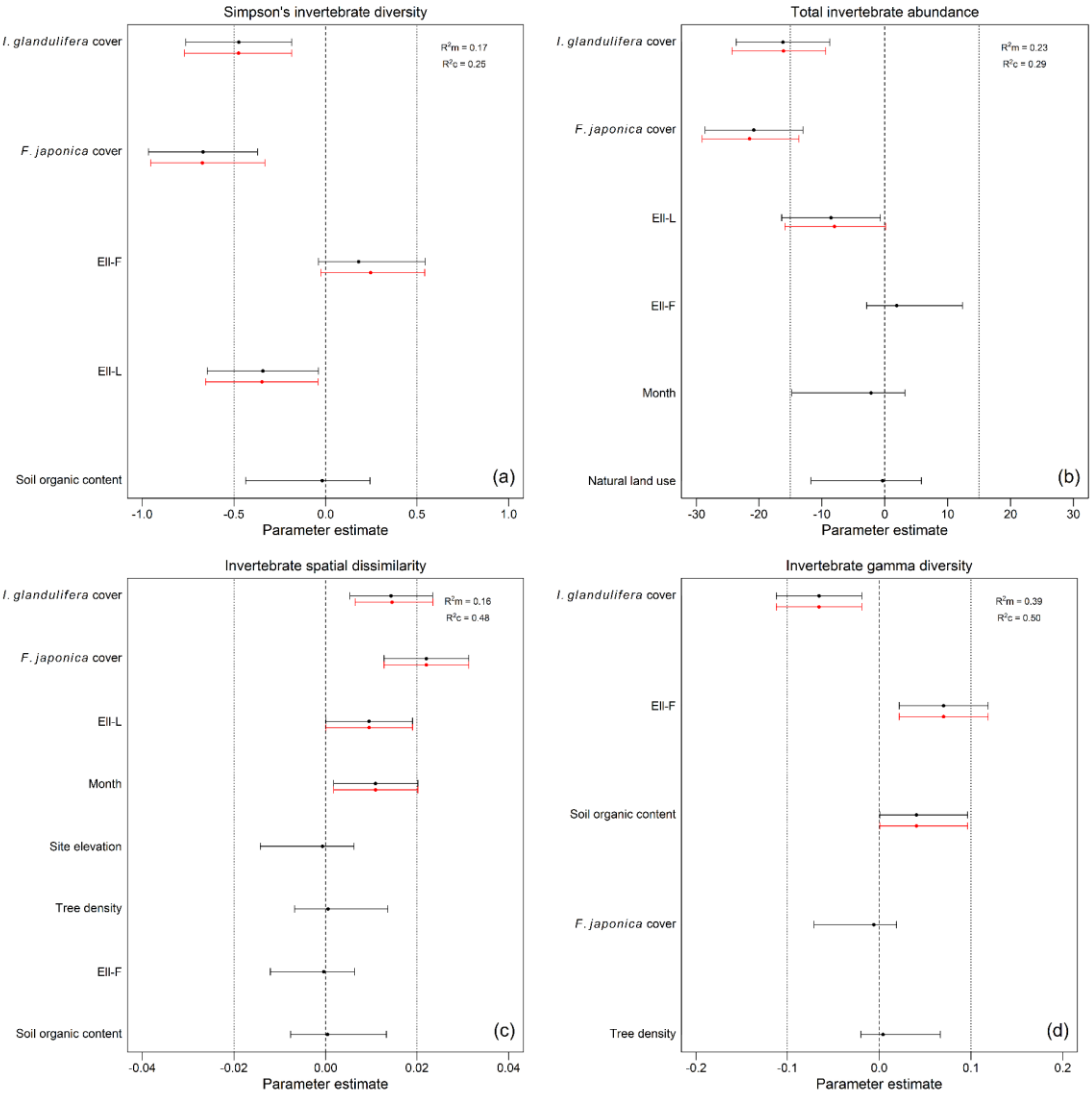

Figure 3.4 Full, model-averaged parameter estimates ± 95% confidence intervals. Modelled responses were (a) Simpson's invertebrate diversity, (b) total invertebrate abundance, (c) spatial dissimilarity and (d) invertebrate gamma diversity. Marginal (R^2m) and conditional (R^2c) values are given. Points and confidence intervals in red indicate alternative effect sizes reported from simplified averaged models.

Invertebrate morphospecies Simpson's diversity

Terrestrial invertebrate morphospecies diversity was negatively associated with the mean Ellenberg Indicator value for light (Figure 3.4a) and with the cover of both INNP (Figures 3.3a and 3.4a). The largest effect sizes were associated with *F.*

japonica and *I. glandulifera* cover, and differed only marginally between the two. Simpson's invertebrate diversity was on average approximately 39% lower at maximum measured invasive cover, compared to uninvaded sites. There was no evidence of any temporal dependency in the response.

Total invertebrate abundance

Total abundance of terrestrial invertebrates was negatively associated with the mean Ellenberg Indicator value for light (Figure 3.4b) and with the cover of both INNP (Figures 3.3b and 3.4b). *Impatiens glandulifera* cover had the largest effect size (-18.36), marginally exceeding that of *F. japonica*. Total invertebrate abundance was on average approximately 57% lower at maximum measured invasive cover, compared to uninvaded sites. There was no evidence of any temporal dependency in the response.

Invertebrate spatial dissimilarity

Terrestrial invertebrate spatial dissimilarity between samples at a site was positively associated with the mean Ellenberg Indicator value for light (Figure 3.4c) and with the cover of both INNP (Figures 3.3c and 3.4c). *Fallopia japonica* cover had the strongest overall effect (0.02). Invertebrate samples were on average approximately 26% more similar at maximum measured *F. japonica* cover, and approximately 18% more similar at maximum measured *I. glandulifera* cover, compared to uninvaded sites. There was no evidence of any temporal dependency in the response.

Invertebrate morphospecies gamma diversity

Overall, gamma diversity of terrestrial invertebrates was positively associated with soil organic content and the mean Ellenberg Indicator value for moisture (Figure 3.4d) and negatively associated with *I. glandulifera* cover (Figures 3.3d and 3.4d). *Impatiens glandulifera* cover had the greatest overall effect (-0.07), followed by the mean Ellenberg Indicator value for moisture (0.05). Gamma diversity of terrestrial invertebrates was on average approximately 21% lower at maximum measured *I. glandulifera* cover, compared to uninvaded sites. *Fallopia japonica* had no detectable effect (Figures 3.3d and 3.4d) and there was no evidence of any temporal dependency in the response.

Indicator species

A larger number of terrestrial invertebrate morphospecies were significantly associated with uninvaded sites compared to invaded sites (Table 3.2). Twenty invertebrate morphospecies were significantly associated with uninvaded sites, compared to eight at invaded sites. The strongest indicators of sites invaded by both *I. glandulifera* and *F. japonica* were morphospecies belonging to the Acari. Uninvaded sites were strongly characterised by members of the Coleoptera and Diptera, alongside other morphospecies of the Acari subclass.

Site type	**Morphospecies**	**Observed Indicator Value**
Invaded by *I. glandulifera*	Acari B**	31.7
	Oligochaeta**	16.7
	Coleoptera (l) K*	6.8
	Chilopoda**	4.6
	Diptera (l) E*	4.6
	Gastropoda C*	2.7
Invaded by *F. japonica*	Acari E***	40.2
	Diptera (l) G*	5.8
Uninvaded	Collembola***	38.2
	Diptera C***	38.2
	Coleoptera A***	35.9
	Acari D*	25.5
	Opiliones**	24.5
	Araneae A*	24.3
	Coleoptera E**	23.6
	Coleoptera (l) G***	21.1
	Acari A**	20.4
	Coleoptera F***	20.1
	Hymenoptera D*	14.7
	Acari C*	14.5
	Isopoda*	11.2
	Coleoptera B**	11.0
	Coleoptera S*	8.9
	Hymenoptera E**	8.2
	Acari G*	6.9
	Diptera Q**	5.9
	Hemiptera C*	5.0
	Diptera D*	2.9

Table 3.2 Significant indicator morphospecies ((l) indicates a larval stage) for invaded and uninvaded sites (invaded sites split by *Impatiens glandulifera* and *Fallopia japonica*). Observed Indicator Value shows the indicator value for each species (0 = no fidelity or specificity; 100 = complete fidelity and specificity). Asterisks indicate the probability of that Indicator Value occurring by chance based on permutation tests (*** <0.001, ** <0.01, * <0.05).

3.4 Discussion

Invertebrate morphospecies Simpson's diversity and abundance

These results indicate that INNP alter the structure and function of riparian vegetation at heavily invaded sites to such a degree that their capacity for supporting high diversity and abundance of terrestrial invertebrates is compromised. The majority of studies focusing on arthropods report a reduction in abundance and taxonomic richness in response to INNP (Litt et al. 2014). In this study, both *F. japonica* cover and *I. glandulifera* cover showed strong negative associations with Simpson's invertebrate diversity and total invertebrate abundance compared to other environmental variables, in both sampling periods. This reflects the ability of INNP to impose strong structural changes on riparian habitats during their period of peak vegetative biomass, as well as during the preceding months when INNP stands are developing.

In the absence of significant relationships between environmental predictors and terrestrial invertebrates, it is likely that the main factors driving invertebrate diversity and abundance are indeed reductions in habitat complexity and resource availability, caused by either *F. japonica* or *I. glandulifera*.

Invasions by INNP can disrupt linkages between above and below-ground communities via changes to soil chemistry (Weidenhamer and Callaway 2010) and to resources entering the soil (Tanner et al. 2013). Lower community functional diversity and redundancy associated with INNP (Kominoski et al. 2013) can alter both the chemical composition and range of degradability of leaf litter, eliciting negative responses in both above and below-ground invertebrate communities through poorer microhabitat structure and persistence (Scherber et al. 2010; Lecerf et al. 2011). Loss of plant species from invaded sites may also deplete invertebrate assemblages that specialise on those plants or their architectural properties, causing an overall reduction in the diversity and abundance of invertebrate morphospecies (Reid and Hochuli 2007).

Both invertebrate morphospecies diversity and abundance were negatively associated with Ell-L, implying either that plants preferring higher light levels support a smaller number of fewer invertebrate morphospecies, or that invertebrates generally prefer more shaded conditions. High light availability would indicate a relatively open canopy, offering relatively little shelter for invertebrates that favour a dense, structurally complex habitat (Warfe and Barmuta 2004). Increased light levels are also associated with reduced terrestrial invertebrate diversity (Meyer and Sullivan 2013) and may also reduce the abundance of terrestrial arthropods that favour shaded habitats (Greenberg et al. 2000).

Invertebrate spatial dissimilarity

Terrestrial invertebrate community composition was more dissimilar at heavily invaded sites for both *F. japonica* and *I. glandulifera*, suggesting that more heterogeneous invertebrate communities are associated with high levels of invasive cover. It is possible that INNP will benefit some invertebrate consumers, as some non-native invasive plants may have higher nitrogen and phosphorus concentrations, as well as larger leaf area ratios, offering higher quality litter and greater microhabitat surface area than their native counterparts (Wardle et al. 2011). However, the negative associations between INNP cover and invertebrate diversity and abundance suggest that although both *F. japonica* cover and *I. glandulifera* were associated with a more heterogeneous fauna, this is at the expense of invertebrate diversity and abundance overall.

Spatial dissimilarity within biological assemblages is often considered a desirable attribute (Swan and Brown 2017). However, such dissimilarity can also be an artefact of reduced morphospecies abundance and diversity. For example, if those invertebrates remaining in heavily invaded areas are patchily distributed, this will generate spatially heterogeneous but impoverished communities. This suggests that some rarer morphospecies may be absent from samples collected at heavily invaded sites, where a reduction in abundance would remove a rarely-occurring individual from the sample altogether, consequently reducing diversity. This loss of rare species may explain the observed increase in heterogeneity between individual traps, but demonstrates that this is actually a negative outcome for terrestrial invertebrate communities.

Invertebrate community composition was also more dissimilar at sites with plant communities associated with higher light levels. Given that higher densities and diversity of invertebrates were associated with more shaded conditions, it is likely that the increased heterogeneity of assemblages in well-lit environments is also an artefact of the reduced richness and abundance of invertebrates, suggesting that sites with lower Ell-L values support shade-tolerant plant species, which may offer invertebrates better quality habitat and resources.

Invertebrate morphospecies gamma diversity

Impatiens glandulifera cover showed a strong negative association with site level gamma diversity of terrestrial invertebrates. By contrast, the effect of *F. japonica* cover was not significant. There were positive associations between Ell-F and soil organic content and invertebrate gamma diversity, but the large negative effect size of *I. glandulifera* outweighed any positive effects of environmental variables at the site scale.

INNP can alter ecosystem structure and functioning through changes to the local microclimate, resulting in changes to food chain resources and the structure of terrestrial invertebrate communities (Kappes et al. 2007). This would be reflected by an overall change in diversity at the site level, as a heavily invaded riparian zone would likely support a greatly altered terrestrial invertebrate community (Pysek et al. 2012). This is evidenced by the reduced number of indicator morphospecies associated with both *I. glandulifera* and *F. japonica* invaded sites, compared to uninvaded sites. More morphospecies were indicative of sites invaded by *I. glandulifera* than *F. japonica*, suggesting that environmental conditions at *F. japonica* sites are more prohibitive to invertebrates. The morphospecies most indicative of uninvaded sites included Collembola and taxa from the Phoridae and Staphylinidae families of Coleoptera. Since the latter two favour decaying organic matter, this supports the theory that increased litter diversity fosters invertebrate diversity (Scherber et al. 2010; Lecerf et al. 2011). Acari were most strongly indicative of sites invaded by either *F. japonica* or *I. glandulifera*, which is unsurprising given their generalist tendencies and reputation for colonising most aquatic and terrestrial habitats by exploiting a wide range of resources (Vacante 2016).

Whilst the use of morphospecies in place of species level identification is well reported and defended (Oliver and Beattie 1996; Krell 2004), it would be valuable to incorporate measures of resource utilisation, foraging styles and microhabitat use (Ramey and Richardson 2017) into future studies to better understand the interactions between invertebrate taxa in riparian systems and to identify why some taxa are more sensitive to invasion. For example, taxon-specific reactions have been demonstrated in response to *I. glandulifera* invasion, which is able to modify the local microclimate, increasing local soil moisture and temperature, thereby promoting an increase in the abundance and diversity of gastropods (Ruckli et al. 2013) and Acari (Rusterholz et al. 2014).

As expected, there were positive associations found between Ell-F, soil organic content and invertebrate gamma diversity. Members of the Collembola, Oligochaeta and Diptera have all been shown to decline in abundance with reduced soil moisture (Hodkinson and Jackson 2005), while Santorufo *et al.* (2012) found that invertebrates were more abundant and diverse in soils with higher organic content and moisture.

3.5 Conclusions

Overall, INNP were associated with reduced terrestrial invertebrate morphospecies abundance and both alpha (sample level) and gamma (site level) diversity. This indicates that their association with increased spatial dissimilarity in assemblages is unlikely to be beneficial, as the increased heterogeneity between traps arises from losing morphospecies, rather than gaining them. INNP species had the greatest effect on terrestrial invertebrate communities, regardless of local environmental conditions, demonstrating their ability to influence the ecosystems which they invade, with impacts extending beyond the immediate plant community. It is evident that INNP have measurable and significant impacts on these communities, which may ultimately affect energy transfer and other linkages between terrestrial and aquatic systems across a range of trophic levels.

Chapter 4: The impact of invasive riparian plants on the dietary selections of juvenile salmonid fish

Stop net in place on the Pow burn, river South Esk, August 2015.

4.1 Introduction

Riparian zones provide an ecologically important link between the terrestrial and aquatic food webs in rivers (Sievers et al. 2017). These biologically rich systems are multifunctional, supporting a wide range of species (Fraaije et al. 2015), offering protection from anthropological stressors (Feld et al. 2018), and connecting habitats at physical and temporal scales (Greenberg and Calles 2010). The modulation of ecosystem processes such as organic matter decomposition and oxygen production (Giller et al. 2004) is important to a number of groups of organisms, but riparian influences on water quality, habitat quality and trophic dynamics (Pusey and Arthington 2003) are particularly important for fish. Inputs of sulphur and nitrogen that reach high enough levels to cause ecological damage are also strong determinants of salmonid population sizes (Harriman et al. 1995; Bridcut et al. 2004).

Fish communities in general are the focus of many aquatic studies, largely due to their economical, societal and ecological importance (Jackson et al. 2001). They can be ecosystem engineers: salmonids exert hydromorphological effects on river systems through the disturbance of substrate, and the magnitude of this effect is greater with increasing fish size (DeVries 2012). There is also increasing evidence that nutrients from adult salmon carcasses directly affect their offspring. Auer *et al*. (2018) showed that this nutrient influx enhances survival chances of eggs and juvenile fish, mitigating the advantage of larger egg size and faster juvenile growth rates observed in streams lacking the adult carcass input. Similarly, Williams et al. (2009) demonstrated a positive relationship between an increasing adult carcass nutrient supplement and the biomass of juvenile *S. salar* in upland streams. Some keystone fish species are able to exert disproportionately large effects (via trophic cascades) on aquatic communities. The bullhead (*Cottus gobio*) is able to suppress grazing by *Gammarus pulex* through its sheer abundance and predatory nature (Woodward et al. 2008), whilst species such as the roach (*Hesperoleucus symmetricus*) and the steelhead trout (*Oncorhynchus mykiss*) can exert cascading top-down pressures on freshwater macroinvertebrate communities, releasing algivorous chironomids from predation by suppressing larger predatory invertebrates (Power 1992).

The brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) are two commercially valuable and recreationally important salmonid species (Pennell and Prouzet 2009), the latter of which is a protected species under European regulation

(HMSO 1994). Both species contribute significantly to the Scottish economy (Butler et al. 2009), and are able to engineer trophic cascades within freshwater food webs through fluctuations in their population size and structure (Simon and Townsend 2003).

Salmonids rely on low order tributary streams as both spawning and nursery grounds (Ryan and Kelly-Quinn 2015). Habitat selection in juvenile *S. trutta* and *S. salar* is influenced by a variety of variables. Although general availability of habitat is likely to most strongly determine distribution of a salmonid population (Armstrong et al. 2003), substrate composition (Heggenes et al. 2013), environmental temperature (Kanno et al. 2015) and water velocity (Millidine et al. 2018) are also important factors. Habitat selection and utilisation also shows a clear seasonal dependence (Heggenes 2002). *Salmo salar* show preference for shelter during the winter, switching to nocturnal activity and seeking refuge during the day – likely to avoid diurnal predators (Valdimarsson and Metcalfe 1998). Similarly, *S. trutta* show a similar avoidance/refuge-seeking behaviour during the day and become active between dusk and dawn (Armstrong et al. 2003). Biotic influences such as the availability of woody debris may function both as a source of refuge (Cramer and Ackerman 2009) and to provide allochthonous dietary inputs in the form of terrestrial invertebrates (Gustafsson et al. 2014).

The sensitivity of *S. trutta* and *S. salar* to local environmental changes within their habitats (Pehlivanov et al. 2012) suggests that the introduction and proliferation of INNP could directly affect salmonid populations. For example, Himalayan balsam (*Impatiens glandulifera*) has been shown to promote soil erosion and thus increase sedimentation rates along riparian zones (Greenwood and Kuhn 2014), whilst increased sedimentation rates negatively affect feeding behaviour, species richness and spawning success (Chapman et al. 2014). Fine sediment accumulation following the winter die-back can inhibit egg incubation success through reduced permeability of gravel and reduced local oxygen concentrations (Greig et al. 2005). Pulses of sediment during the summer may alter the timing and availability of aquatic macroinvertebrate food sources for salmonids, as fine sediment is shown to reduce the abundance of Ephemeroptera, Plecoptera and Trichoptera taxa, and increase the rate of drift in these taxa (Beermann et al. 2018). The riparian canopy offers a vital allochthonous invertebrate subsidy to salmonid fish (Baxter et al. 2005), which may vary in diversity and abundance depending on the availability of appropriate leaf litter entering the stream (Leroy and Marks 2006), and may even exceed autochthonous production (Ryan and Kelly-Quinn 2015).

4.1.1 Limitations on feeding

Salmonids are generally regarded as opportunistic predators, able to shift their diet in response to variations in both the quantity and quality of both terrestrial and aquatic prey resources (Syrjänen et al. 2011; Evangelista et al. 2014). Prey consumption in juvenile salmonids is limited by gape size (Keeley and Grant 2001), which is linked to body size and governs the trophic level at which an organism is able to feed within a community (Nilsson and Bronmark 2000). In addition, selectivity/avoidance behaviour has also been demonstrated in farmed fish in response to the size and shape of food items, with *S. salar* actively favouring longer and softer pellets over those with a more rounded shape (Stradmeyer et al. 1988).

The impact of predators on lower trophic levels is influenced by dietary preferences (Bruno and O'Connor 2005), and is therefore linked to body size. For example, the presence of a high abundance of small predatory species is likely to have a smaller top-down impact on the food web than the presence of a small abundance of comparatively larger predatory species, which in the case of large piscivorous fish, would be able to consume a larger variety and number of prey species, due to a larger gape size (Woodward et al. 2010). This is important when considering the impacts of fish as keystone predators within freshwater ecosystems (Woodward et al. 2008), as the degree to which a population is able to persist and recruit new individuals could affect the trophic dynamics of the system in which they occur.

This relationship between body size and gape size directly affects the type and size of invertebrate prey that juvenile *S. trutta* can select from, and their range of consumable prey increases from insect larvae such as chironomids to larger aquatic invertebrate taxa as well as surface arthropods (Klemetsen et al. 2003), as their own body size increases. A similar relationship between gape size and prey size is apparent in juvenile *S. salar* and their use of invertebrate drift (Piccolo et al. 2014), but they are also observed to focus more on novel prey items as experience is gained (Johansen et al. 2011).

4.1.2 Competition for resources

Although *S. trutta* and *S. salar* display overlaps between life strategies and survival tactics (Klemetsen et al. 2003), the two species also demonstrate variation in their use of certain ecological resources. Whilst the habitat requirements of juvenile *S. trutta* and *S. salar* overlap, possibly generating inter-specific competition (Fausch 1984), *S. trutta* demonstrate more aggressive behaviour and are dominant in their preferred habitat over *S. salar* parr of a similar size (Höjesjö et al. 2010), suggesting that space limitations may be more detrimental to *S. salar*. Conversely, the presence of large woody debris within a stream may reduce competition and risk of predation by increasing visual isolation and providing low-velocity feeding positions next to high-velocity patches (Deschênes and Rodríguez 2007).

Both conspecific and intraspecific competition may arise where resources are limited, particularly during the winter months when conditions are less favourable. For example, both levels of competition have been demonstrated in semi-natural channels during the winter, where both *S. trutta* and *S. salar* showed increased levels of aggression when defending shelters (Harwood et al. 2002b). Behavioural changes observed under sympatric conditions may exist to achieve social dominance to the benefit of an individual species, which differs to the size-based feeding hierarchy observed for both *S. trutta* and *S. salar* in allopatry (Harwood et al. 2002a). Adopting alternative strategies such as hyperphagia (Bull and Metcalfe 1997) may be critically important during the winter months, where the ability to feed and survive during the over-wintering period is highly influential to the short- and long-term growth and survival of *S. salar* (Orpwood et al. 2010).

During the winter months, where unfavourable conditions promote competition, salmonids have been observed to adopt multiple feeding strategies, thought to be caused by more dominant individuals holding optimal positions for feeding, and thus restricting feeding strategies available to subordinate members of the same population (Nislow et al. 2010). The autumnal shift in spatial distribution and habitat use of salmonids is likely in response to either a “biological clock” or other external stimuli (Huusko et al. 2007), such as lower temperature and increased discharge. Such shifts in behaviour are thought to be in response to the relative availability of resources and the subsequent allocation of these resources to growth and restoration of energy reserves (Metcalfe et al. 2002). This period of time represents a trade-off between allocating adequate time to prey acquisition whilst avoiding predation and maintaining optimal energy efficiency by adopting in-stream positions in areas of relatively low flow (Valdimarsson and Metcalfe 1998).

4.1.3 Potential effects of INNP on juvenile salmonids

INNP are able to exert controlling effects on hydrological processes, especially where invasion leads to the establishment of dense, monospecific stands (Tickner et al. 2001), as seen with both *I. glandulifera* (Hejda and Pyšek 2006) and Japanese knotweed (*Fallopia japonica*) (Braatne et al. 2007). A key issue concerning the formation of dense, monospecific invasive stands is their tendency to rapidly die back and collapse during the first frosts of the year, particularly in the case of *I. glandulifera* (Greenwood and Kuhn 2014). This increases exposure of the bank to surface water flow, which coupled with decreased bank stability results in increased sedimentation (Pollen and Simon 2005), having potentially deleterious influences on water quality (Greenwood and Kuhn 2014). *Fallopia japonica* is also more commonly associated with higher energy streams with larger bed substrates (Dawson and Holland 1999), which may exacerbate sedimentation and siltation rates brought about by changes to bank structure and stability following invasion (Simon and Collison 2002). Increased exposure to suspended solids as a result of this may negatively affect invertebrate population size and species diversity (Bilotta and Brazier 2008), as well as altering foraging activity and avoidance behaviour in *S. salar* and reducing population size in *S. trutta* (Milner et al. 2003).

INNP can change the makeup of allochthonous inputs to streams by displacing native riparian vegetation, which may alter the observed terrestrial and aquatic macroinvertebrate communities. For example, sites invaded by *F. japonica* have been shown to harbour higher relative abundances of large invertebrate shredders, coupled with increased leaf litter breakdown rates (Lecerf et al. 2007). The provision of a riparian subsidy may affect stream food web dynamics, by altering the intensity of fish predation on aquatic prey species (Nakano et al. 1999). Although this allochthonous subsidy depends partly on the composition of riparian vegetation, it is likely to be more abundant and of greater importance during the plant growing season (Wipfli and Baxter 2010). The riparian canopy may benefit *S. trutta* more than *S. salar*, as *S. trutta* have been shown to demonstrate higher vertical positioning and selection of surface-drifting prey (Gustafsson et al. 2010). In comparison, *S. salar* have been shown to alter feeding behaviours under overhead canopy cover by switching to nocturnal foraging patterns (Orpwood et al. 2010).

Salmonids display behavioural changes and utilise alternative feeding strategies on a seasonal basis, which include the use of differing types of cover throughout the day, in order to maximise feeding efficiency and minimise risk of predation (Riley et al. 2006; McCormick and Harrison 2011). Given the seasonal die-back associated with *I. glandulifera* and *F. japonica*, these areas of cover during the winter would be unavailable to salmonids in invaded areas. This may affect the ability of these fish to survive and fulfil their growth requirements during the winter, which may consequently affect survival rates and time taken to reach maturity (Jensen et al. 2012).

4.1.4 Aims

Although the importance of the riparian zone to salmonid fish is well documented (McCormick and Harrison 2011; Ryan and Kelly-Quinn 2015), less is known about specific links between riparian INNP and the population dynamics and feeding preferences of salmonids. It is also becoming increasingly recognised that it is not sufficient to simply assess the “face value” effects of invasion. More obscure (but potentially critical) interactions must be assessed, such as changes in trophic networks and consequent impacts on ecosystem functioning (Simberloff et al. 2013), range expansions due to climate change coupled with riparian invasion (Lawrence et al. 2014), and linkages between invasion success and environmental conditions (Thomsen et al. 2014). More broadly, there is a present need for more cooperative studies, incorporating relevant research and management plans where common species, environments and organisations are involved (Macchi and Vigliano 2014).

4.2 Methods

Study sites

Sites were located on low (1st to 4th) order streams in catchments across central and southern Scotland (Appendix, Figure S1), providing a range of geographically and environmentally varied sampling locations (Appendix, Table S1). Sites were generally selected based on suitability and accessibility for both juvenile and adult salmonid fish, and were chosen in consultation with local fisheries trusts to ensure that a healthy and representative population of juvenile salmonid fish would be present at each location. On each stream, a pair of control sites were located upstream from a pair of invaded sites containing established stands of either *F. japonica* or *I. glandulifera*, the sites in each pair being separated by an average of 0.35km. There were 24 study sites in total. Sites were limited by the size of INNP stands present, and as such were standardised to a 20m length of bank. Invaded sites were chosen according to the criteria that INNP coverage should exceed 50% of the vegetation cover on at least one bank, whilst other characteristics should as far as possible match those of upstream uninvaded sites (Sax et al. 2005).

Electrofishing surveys

Surveys were carried out using an Electracatch electrofisher (single anode bankside kit with variable pulsed output; max output 300v). Sampling sites were accessed from the downstream direction to minimise disturbance to fish. Stop nets were deployed prior to surveying. Juvenile salmonid populations were surveyed using a standard three-pass depletion survey (Riley and Fausch 1992; Pusey et al. 1998). The electrofishing team moved upstream in a zigzag pattern, moving from bank to bank. Target species were *S. trutta* and *S. salar*. Fish were netted as quickly as possible and transferred to holding containers whilst the surveys were completed. Sampling continued until three runs had been completed, at which point all captured *S. trutta* and *S. salar* were anaesthetised using tricaine mesylate (MS-222) to minimise stress whilst fork length (to the nearest mm) and body mass (to the nearest 0.1g) were recorded. The average wetted width across all sites was 4.2 m, giving an approximate area of 84m^2 to fish at each site. This was extended where necessary and where conditions allowed to meet the minimum suggested sampling area of 100m^2 (Kennedy and Strange 1981).

From these surveys, salmonid population data were generated, including estimates of salmonid density and biomass at each site (Appendix, Table S6). In order to estimate the relative abundance of age classes at each site, fork length data was imported into the FAO-ILARM Fish Stock Assessment Tool (FiSAT), and a modal progression analysis was run using Bhattacharya’s method (Bolland et al. 2007). Additionally, the fork length for each fish was used to estimate cohorts of fish based upon the range and frequency of fork lengths across all sites on a particular river. Based on this preliminary cohort assessment, only 0+ and 1+ fish were taken forward for dietary analysis, as these comprised 94% of fish analysed over the two year sampling period.

Salmonid diet

The gastric lavage procedure was chosen to assess the dietary choices of juvenile salmonids (Strange and Kennedy 1981). The gut contents of a number of captured fish (up to a maximum of 10 per species age-class) were removed for analysis. Following anaesthesia, each individual was held lateral side down and with its head inclined downwards over a plastic funnel leading into a sampling bag. A polyethylene tube with an external diameter of 3mm was inserted into the fish's mouth and gently pushed down into the gut. Water was then pumped through the tubing into the gut using an attached 60ml syringe until the contents had been flushed into the funnel. Gut contents were preserved in the field with 70% industrial methylated spirits and subsequently sorted and identified to equivalent levels as the aquatic and terrestrial invertebrate samples analysed in chapters 2 and 3. Partial items were identified where a head capsule was present. The stomach flushing procedure was not carried out on individuals with fork length below 60mm, as this was restricted by the project licence (PPL 70/8673).

Aquatic and terrestrial invertebrate communities that made up the available food source for salmonids were sampled prior to fish sampling using Surber sampling (Chapter 2; methods), pitfall trapping (Chapter 3; methods) and drift netting. Drift nets (40cm wide by 25cm deep; mesh size 500µm) were installed towards the downstream end of each study site, and situated within the thalweg profile of the river (Figure 4.1). Drift nets were left to sample overnight, and the flow, net depth and immersion time were recorded so that invertebrate drift could be standardised (in m^3s^{-1}) and compared between sites. Week-long terrestrial pitfall samples were collected no more than 24 hours prior to electrofishing surveys at each site. Surber samples from surveys carried out in spring 2015 were used as a proxy for the expected aquatic macroinvertebrate communities during the summer at each site. These surveys were carried out in part to assess the health of the respective invertebrate communities, but also to quantify the abundance and diversity of both aquatic and terrestrial invertebrate prey species that would be available to juvenile salmonids at study sites. In addition to the terrestrial component of non-aquatic prey, malaise traps were also set concurrently with pitfall traps to quantify the aerial invertebrates present at sites (Figure 4.1). Malaise traps (120cm tall, 100cm wide and 150cm long) were left to collect for a week at a time, and invertebrates were collected in an attached sampling bottle using antifreeze (approximately 60mm of 25% ethylene glycol) as a killing agent. Malaise trap contents were found to be highly variable between sites, likely due to variation in environmental conditions and sampling dates. For this reason, the contents of these traps were not included in the final assessment of salmonid diet, as the efficacy of the traps was judged to be too inconsistent across study sites.

Figure 4.1 Drift net (left) and malaise trap (right) *in situ*.

Salmonid dietary analysis

In order to assess the feeding strategies employed by salmonids at study sites, an electivity index was used. A common measure to quantify prey selection is Ivlev's electivity index (Ivlev 1961), but the values generated by this index depend on a number of varying factors, such as the relative abundances of different food types in the environment. Furthermore, modelling a variety of selectivity or avoidance responses based on the proportional selection of a large number of different invertebrate taxa posed a problem when considering the best model design to analyse the data. For these reasons, the Manly-Chesson index (Manly 1974; Chesson 1978, 1983) was chosen as the best and most appropriate representation of salmonid dietary preferences for this study. The Manly-Chesson index allows the proportion of a prey item in the gut to be compared to the proportion of that prey item in the fish's environment, and this gut-to-environment ratio is then expressed as a proportion of all prey items available to the fish. The index formula (reproduced from Jarv *et al.*, 2011) is as follows:

$$\alpha_i = \frac{r_i / p_i}{\sum_{i=1}^{m} r_i / p_i}$$

where r_i = the proportion of the prey item “i” in the gut, p_i = the proportion of that prey item in the environment, and m = the number of prey items in the environment. Values for α range from 0 (indicating complete avoidance) to 1 (indicating complete preference). For each prey item, a value of $\alpha \leq 1/m$ indicates avoidance, a value of $\alpha \geq 1/m$ indicates preference, and a value of $\alpha = 1/m$ indicates indifference.

For this study, prey items were categorised into broad taxa groupings (Ephemeroptera, Plecoptera, Trichoptera, Simuliidae, Chironomidae, Gammaridae other aquatic invertebrate taxa, and aerial invertebrate taxa), in order to be able to compare dietary choices and prey availability from both 2015 and 2016 samples. The total number of different taxa consumed by each fish was also assessed, to investigate whether diversity of prey selection was influenced by INNP cover.

Physico-chemical variables

Environmental data were obtained through on-site measurements during summer 2016. The proportion of the channel that was shaded was estimated visually, and the total number of trees in the study reach exceeding 5m in height was recorded as a proxy for the amount of channel shading caused specifically by riparian trees. Sites were surveyed using an electronic distance measuring instrument (Theomat Wild TC1000 electronic total station, Leica Geosystems Ltd, Milton Keynes, UK) to map the thalweg profile at each site and to derive an accurate measure of channel slope (Jones 2010).

To investigate the heterogeneity of the streambed, a Wolman count was carried out in summer 2016 using a gravelometer (Wolman 1954), which categorises particle sizes according to their intermediate axis. Shannon’s diversity index was then calculated for the substrate particle size composition at each site, treating each size class as a ‘species’, using the “diversity” function in vegan (Oksanen et al. 2017). Cross-sectional transects of water velocity and depth were recorded at each site using a flowmeter (SENSA RC2 Water Velocity Meter, Aqua-data Ltd, UK) and metre rule. A bray-curtis dissimilarity index was calculated using these velocity and depth measurements to provide a representation of habitat heterogeneity at each site.

Biotic indices

To quantify INNP cover at each site, vegetation surveys were conducted during August 2016 to coincide with peak growing season. Using three transects running perpendicular to the channel, three 1m^2 quadrats were placed equidistantly on each transect between the foot and top of each bank, giving a total of 18 quadrats per site (where space permitted). The cover of all plants was estimated visually in each quadrat, and the percentage covers of *F. japonica* and *I. glandulifera* in each quadrat were averaged separately over both banks and standardised by the number of quadrats sampled, to provide an estimate of the average cover per transect of both INNP species at each site.

Native plant community richness (excluding *F. japonica* and *I. glandulifera*) was expressed using Shannon's diversity index. Plant cover estimates obtained from vegetation surveys were adjusted based on the number of quadrats sampled at each site, to allow vegetation cover to be comparable between sites.

Statistical analysis

Generalised linear mixed effects models (GLMMs) were used to investigate drivers of variation in salmonid dietary choices. A GLMM poisson model was used to investigate drivers of variation in the number of invertebrate taxa in salmonid gut contents, as this involved the use of count data. Response variables were the Manly-Chesson selectivity index for Ephemeroptera, Plecoptera, Trichoptera, Simuliidae, Chironomidae, Gammaridae, other aquatic invertebrate taxa, aerial invertebrate taxa, and the number of different invertebrate taxa in the gut. The finalised list of predictors was refined based on preliminary analysis – predictors were checked for collinearity after Zuur et al (2010), model responses were assessed for normality, and normality of the model residuals was checked using normal probability plots. Final predictors were salmonid density, channel shade, *F. japonica* cover, *I. glandulifera* cover, native vegetation diversity using Shannon's index, abundance of invertebrates in Surber samples and abundance of invertebrates in drift samples. River identity was treated as a random effect.

To test for an effect of salmonid species, each model was run with species as a fixed effect. If this model output showed evidence of a significant species effect ($p < 0.05$), salmonid species was then included as an interaction term to determine whether predictors had species-dependent effects. Prior to modelling, predictors were scaled to one standard deviation to allow their effect sizes to be directly compared. All possible combinations of predictors were identified using the "dredge" function in MuMIn

(Barton 2017). Models were then ranked by corrected Akaike information criterion (AICc) to account for small sample sizes. To identify the top set of models (Appendix, Table S5), a threshold of ΔAICc < 2 was set (Burnham and Anderson 2002). From this top set, a fully averaged model was chosen for interpretation of coefficients (Barton 2017). To assess variation explained solely by the fixed effects, as well as variation explained by both the fixed and random effects together, both marginal and conditional R^2 values are reported for each model (Nakagawa et al. 2013).

All statistical analyses were conducted using R 3.4.3 (R Core Team 2017), with the following additional packages: dplyr (Wickham et al. 2018), effects (Fox 2003), labdsv (Roberts 2016), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), MuMIn (Barton 2017), r2glmm (Jaeger 2017), reshape2 (Wickham 2007), selectapref (Richardson 2017) and vegan (Oksanen et al. 2017).

4.3 Results

Response	**Model parameters**	**R^2m**	**R^2c**
M-C Ephemeroptera	*I. glandulifera* cover (1) + Surber invertebrate abundance (1) + channel shade (0.61) + native vegetation diversity (0.29) + salmonid density (0.13) + *F. japonica* cover (0.11)	0.25	0.44
M-C Plecoptera	Salmonid density (1) + Surber invertebrate abundance (0.91) + channel shade (0.20) + *I. glandulifera* cover (0.17) + *F. japonica* cover (0.11) + salmonid species (0.09) + native vegetation diversity (0.09) + drift invertebrate abundance (0.09)	0.15	0.20
M-C Trichoptera	Fork length (1) + *F. japonica* cover (0.88) + native vegetation diversity (0.16) + Surber invertebrate abundance (0.12) + *I. glandulifera* cover (0.11) + channel shade (0.11) + salmonid species (0.10)	0.08	0.08
M-C Simuliidae	Channel shade (1) + drift invertebrate abundance (1) + salmonid density (1) + salmonid species (1) + salmonid species*channel shade (0.33) + salmonid species*salmonid density (0.25) + *I. glandulifera* cover (0.13) + native vegetation diversity (0.11)	0.10	0.10

M-C Chironomidae	*I. glandulifera* cover (1) + salmonid species (1) + native vegetation diversity (1) + salmonid species**I. glandulifera* cover (0.59) + *F. japonica* cover (0.37) + channel shade (0.22) + salmonid density (0.19) + salmonid species*native vegetation diversity (0.13) + Surber invertebrate abundance (0.09) + salmonid species*Surber invertebrate abundance (0.05) + drift invertebrate abundance (0.04)	0.18	0.18
M-C Gammaridae	Surber invertebrate abundance (1) + native vegetation diversity (0.86) + salmonid species (0.80) + salmonid density (0.60) + *I. glandulifera* cover (0.18) + channel shade (0.13) + drift invertebrate abundance (0.06) + *F. japonica* cover (0.06)	0.24	0.46
M-C Other (aquatic taxa)	Fork length (1) + salmonid density (0.62) + Surber invertebrate abundance (0.61) + *I. glandulifera* cover (0.29) + salmonid species (0.17) + drift invertebrate abundance (0.09) + channel shade (0.08) + *F. japonica* cover (0.08) + native vegetation diversity (0.04)	0.08	0.08
M-C Aerial (terrestrial taxa)	Fork length (1) + salmonid density (0.98) + salmonid species (1) + drift invertebrate abundance (0.84) + salmonid species*fork length (0.66) + native vegetation diversity (0.53) + salmonid species*native vegetation diversity (0.53) + salmonid species*salmonid density (0.47) + *I. glandulifera* cover (0.42) + *F. japonica* cover (0.13) + salmonid species**F. japonica* cover (0.13) + channel shade (0.07) + Surber invertebrate abundance (0.04)	0.30	0.30
Gut taxa diversity	Drift invertebrate abundance (1) + fork length (1) + *I. glandulifera* cover (1) + salmonid species (1) + salmonid species*drift invertebrate abundance (1) + salmonid species**I. glandulifera* cover (1) + salmonid density (0.92) + channel shade (0.44) + Surber invertebrate abundance (0.29) + *F. japonica* cover (0.25) + salmonid species**F. japonica* cover (0.08) + salmonid species*salmonid density (0.07) + native vegetation diversity (0.07)	0.15	0.15

Table 4.1 The best, fully-averaged models for models with ΔAICc < 2. Responses are Manly-Chesson (M-C) indices for the stated taxa groupings, and gut taxa diversity.

Relative variable importance is given in brackets, followed by marginal (R^2m) and conditional (R^2c) values.

Manly-Chesson selectivity: Ephemeroptera

Selection of Ephemeroptera was positively associated with both *I. glandulifera* cover (Figures 4.2 and 4.3) and the total abundance of invertebrates in surber samples (Figure 4.2), the latter of which also showed the largest effect size (0.84). There was no evidence of any species dependency in the response.

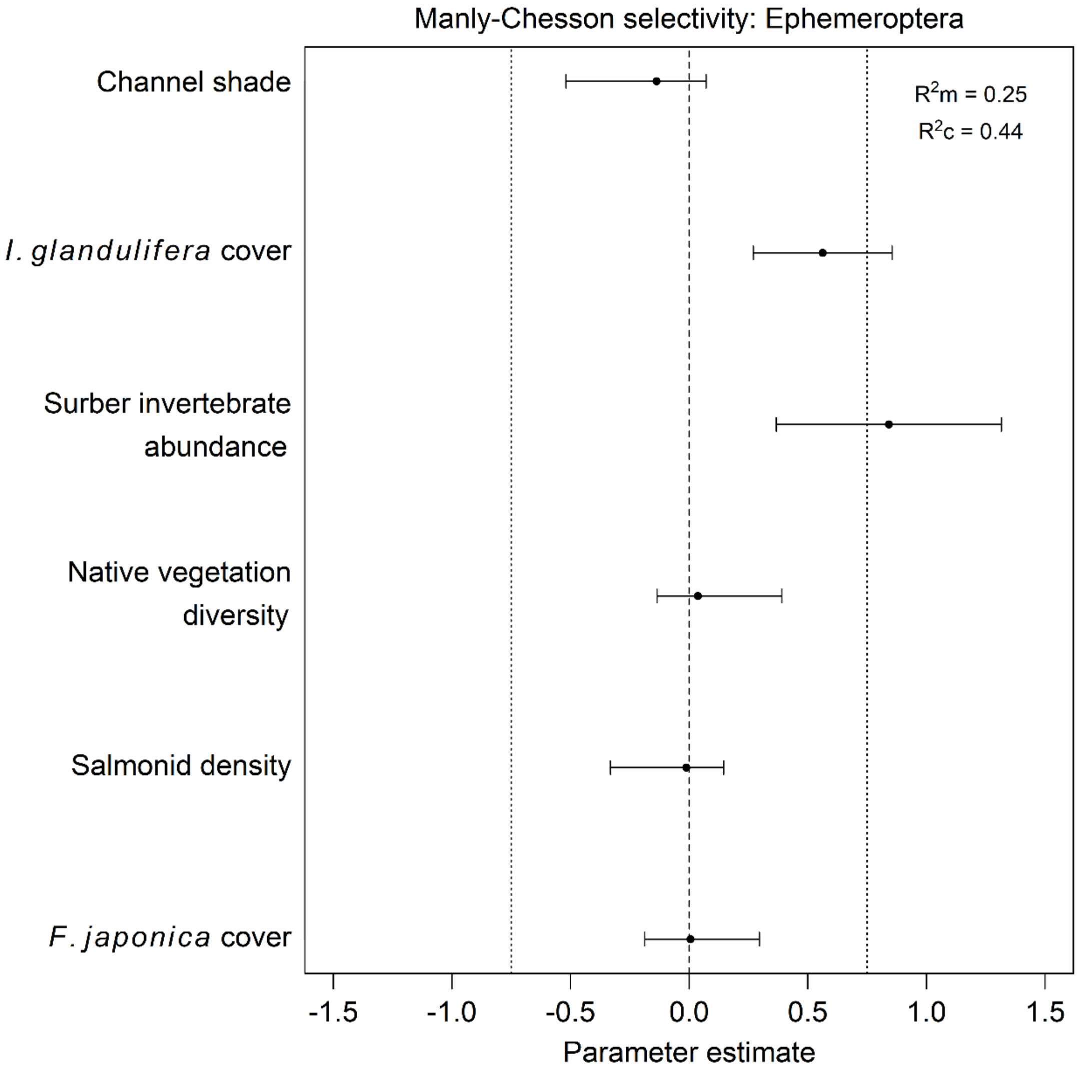

Figure 4.2 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 0.75. Modelled response was Manly-Chesson selectivity for Ephemeroptera. Marginal (R^2m) and conditional (R^2c) values are given.

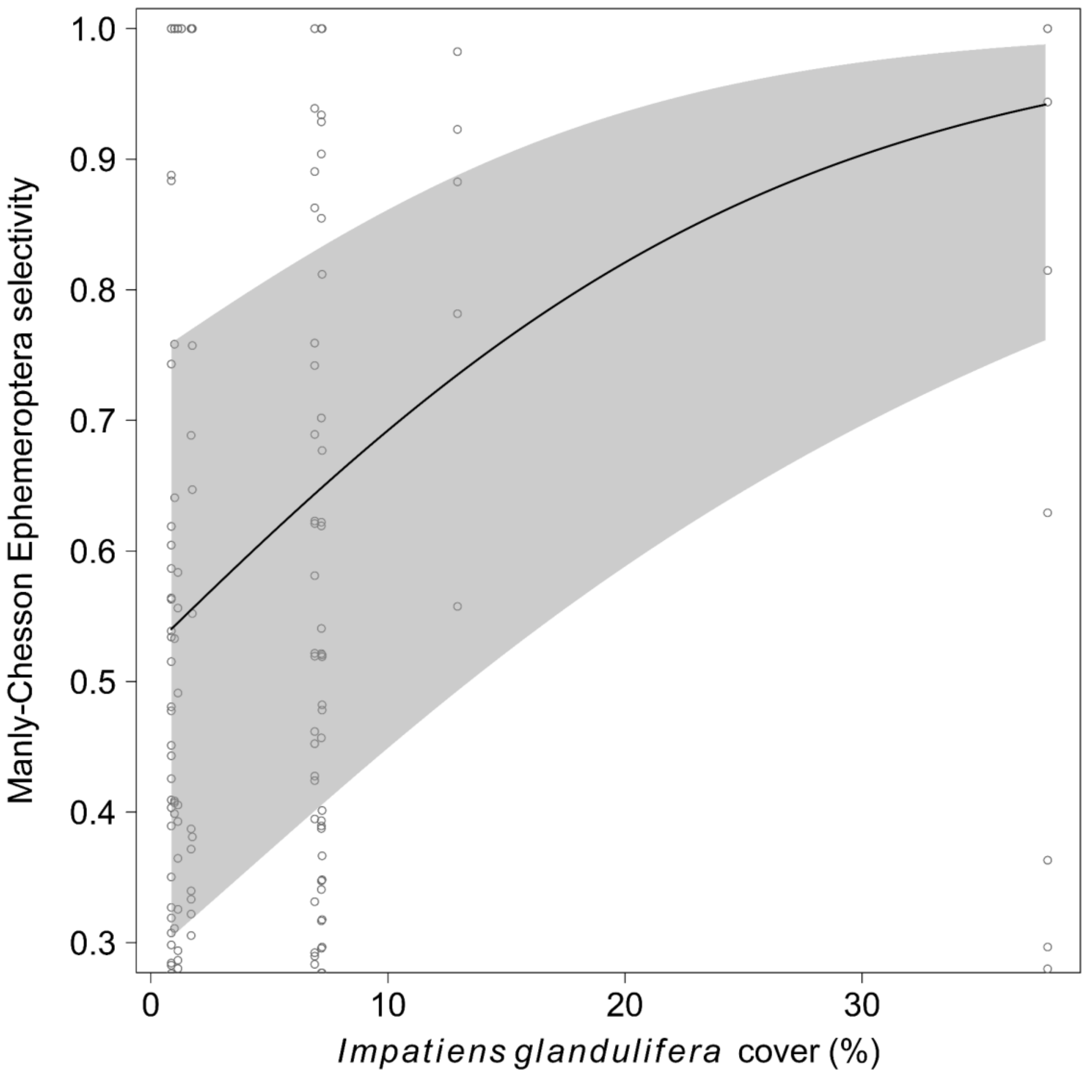

Figure 4.3 Full model predicted values (shaded polygon shows ± 95% confidence intervals) from the GLMM analysis of Manly-Chesson selectivity for Ephemeroptera plotted against *I. glandulifera* cover. Individual points represent raw Manly-Chesson selectivity values. Threshold value not shown (1/*m* = 0.11).

Manly-Chesson selectivity: Plecoptera

Selection of Plecoptera was negatively associated with salmonid density (Figure 4.4). No other variables were significant and there was no evidence of any species dependency in the response. Although selection of Plecoptera appears to be negatively associated with Surber invertebrate abundance, the p-value for this association was greater than 0.05, and as such this was not considered to be significant for the purpose of this study.

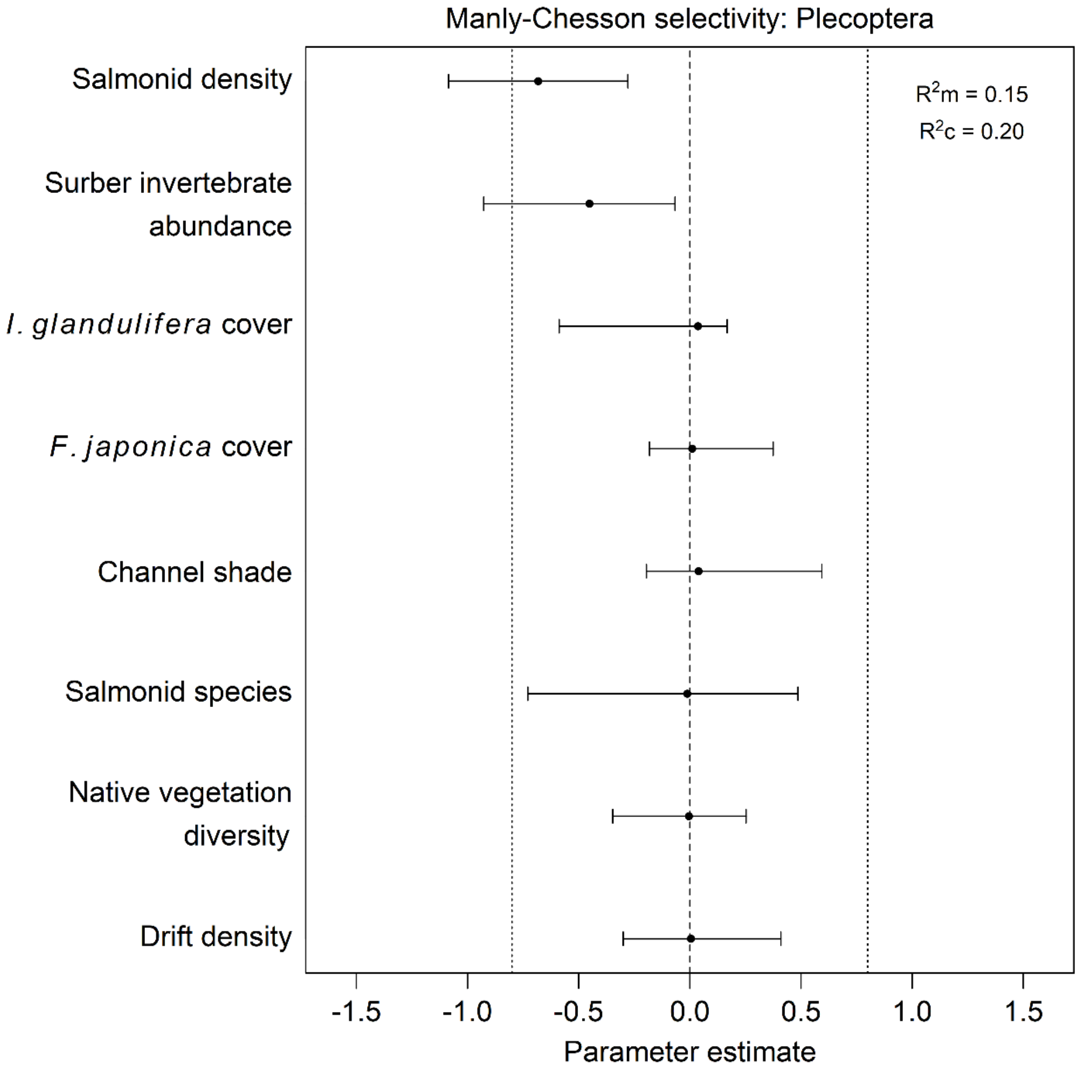

Figure 4.4 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 0.75. Modelled response was Manly-Chesson selectivity for Plecoptera. Marginal (R^2m) and conditional (R^2c) values are given.

Manly-Chesson selectivity: Trichoptera

Selection of Trichoptera was positively associated with salmonid fork length (Figure 4.5). No other variables were significant and there was no evidence of any species dependency in the response.

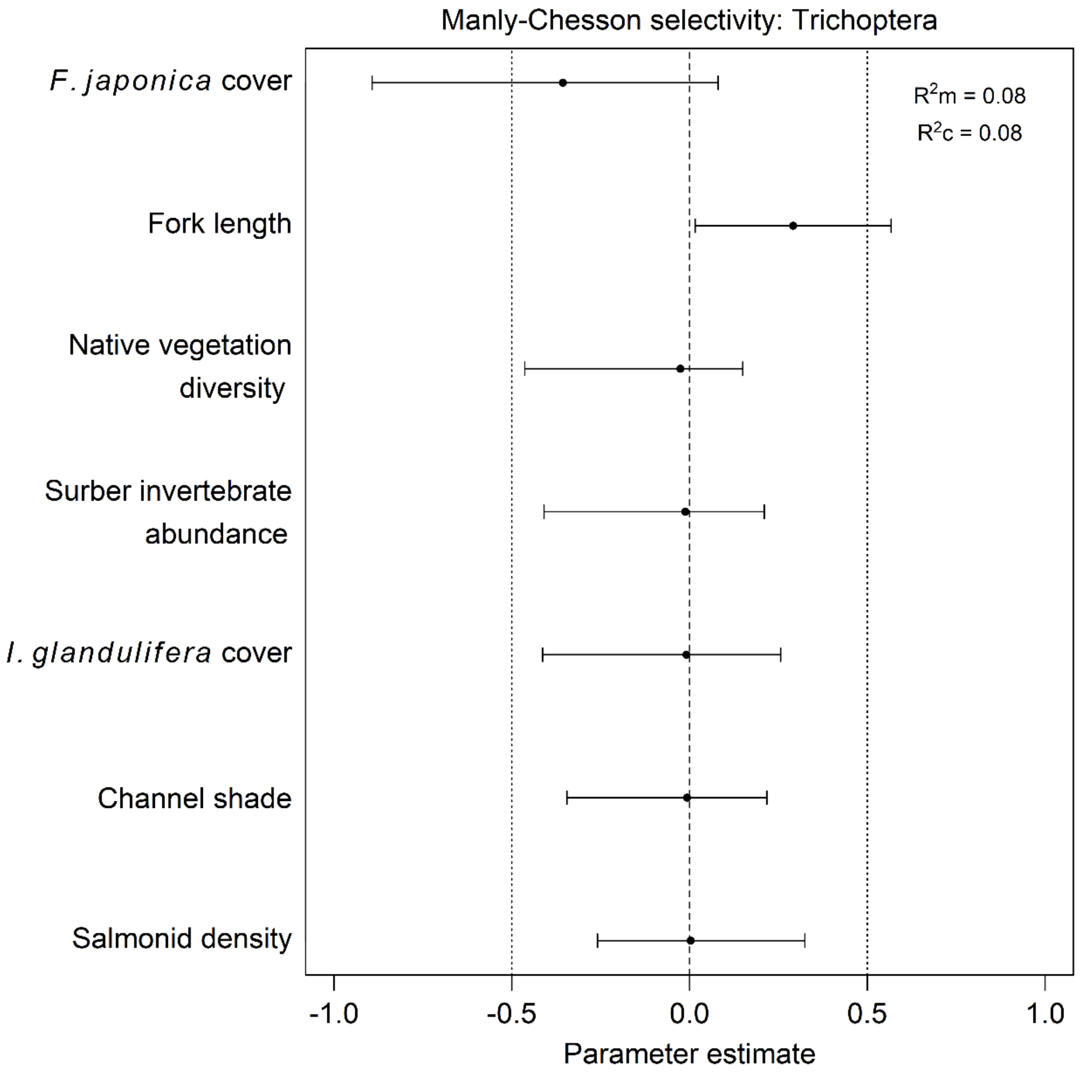

Figure 4.5 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 0.5. Modelled response was Manly-Chesson selectivity for Trichoptera. Marginal (R^2m) and conditional (R^2c) values are given.

Manly-Chesson selectivity: Simuliidae

Selection of Simuliidae was positively associated with the total abundance of invertebrates in the drift and negatively associated with salmonid species (Figure 4.6), the latter of which showed the largest effect size (-0.54). The Simuliidae prey source was utilised more by *S. salar* than *S. trutta*.

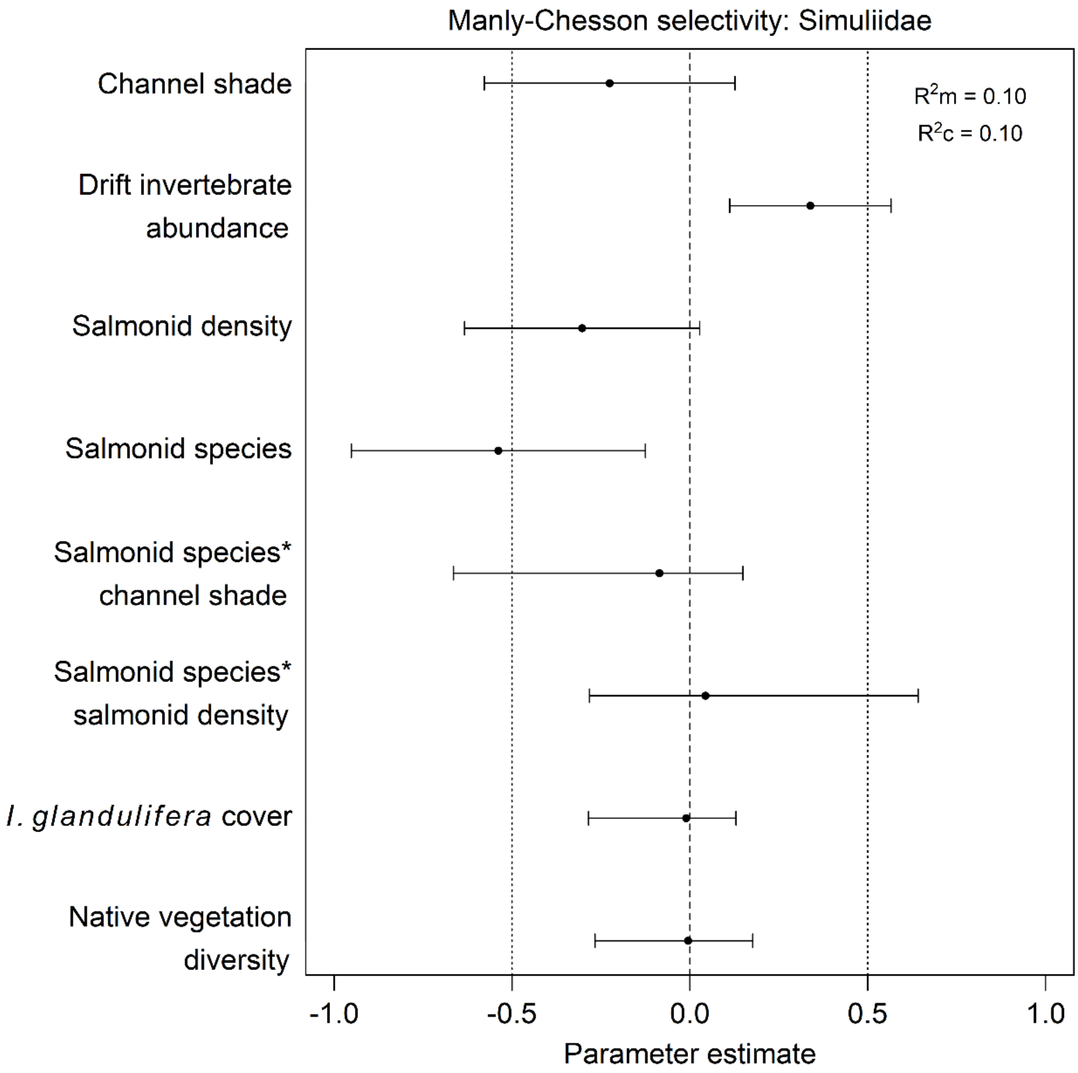

Figure 4.6 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 0.5. Modelled response was Manly-Chesson selectivity for Simuliidae. Marginal (R^2m) and conditional (R^2c) values are given.

Manly-Chesson selectivity: Chironomidae

Selection of Chironomidae was negatively associated with both *I. glandulifera* cover (Figure 4.7 and 4.8) and native vegetation diversity (Figure 4.7), with *I. glandulifera* showing the largest effect size (-0.43). There was no evidence of any species dependency in the response.

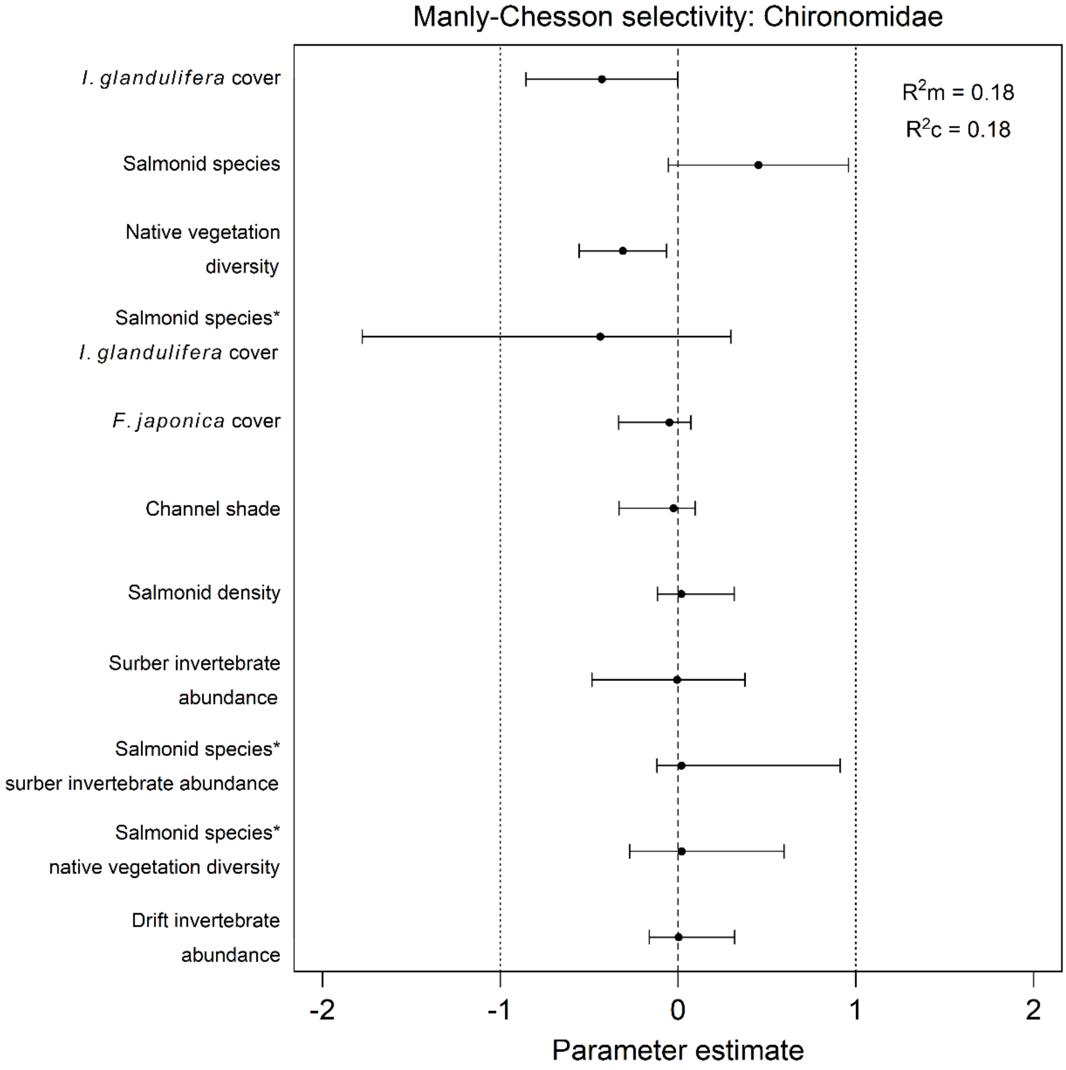

Figure 4.7 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 1. Modelled response was Manly-Chesson selectivity for Chironomidae. Marginal (R^2m) and conditional (R^2c) values are given.

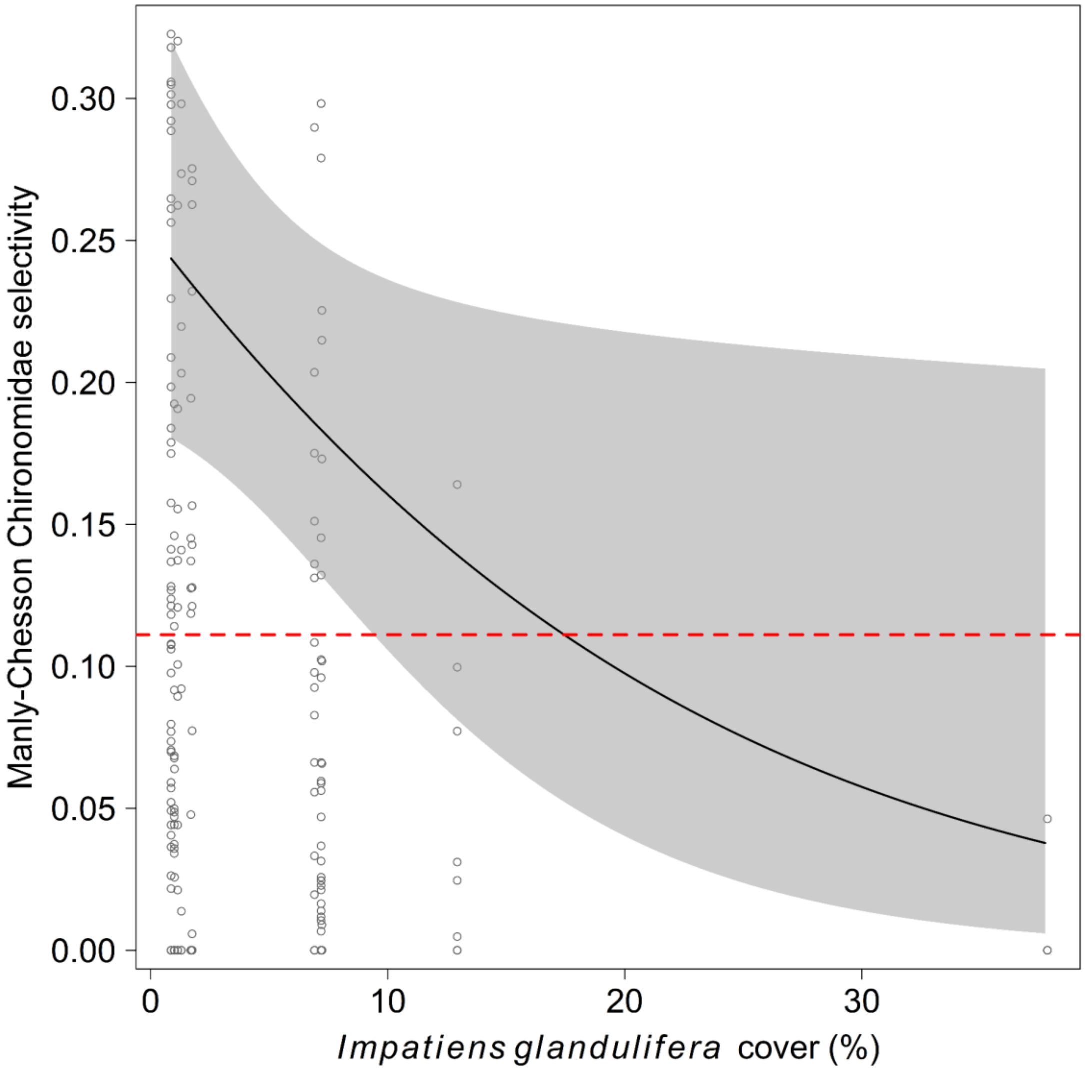

Figure 4.8 Full model predicted values (shaded polygon shows ± 95% confidence intervals) from the GLMM analysis of Manly-Chesson selectivity for Chironomidae plotted against *I. glandulifera* cover. Individual points represent raw Manly-Chesson selectivity values. The red dashed line indicates the 1/*m* threshold: points above this line represent selection; points below this line represent avoidance.

Manly-Chesson selectivity: Gammaridae

None of the modelled predictors showed any significant association with selection of Gammaridae. There was no evidence of any species dependency in the response.

Manly-Chesson selectivity: Other aquatic taxa

Selection of other aquatic invertebrate taxa was positively associated with salmonid fork length (Figure 4.9). No other variables were significant and there was no evidence of any species dependency in the response.

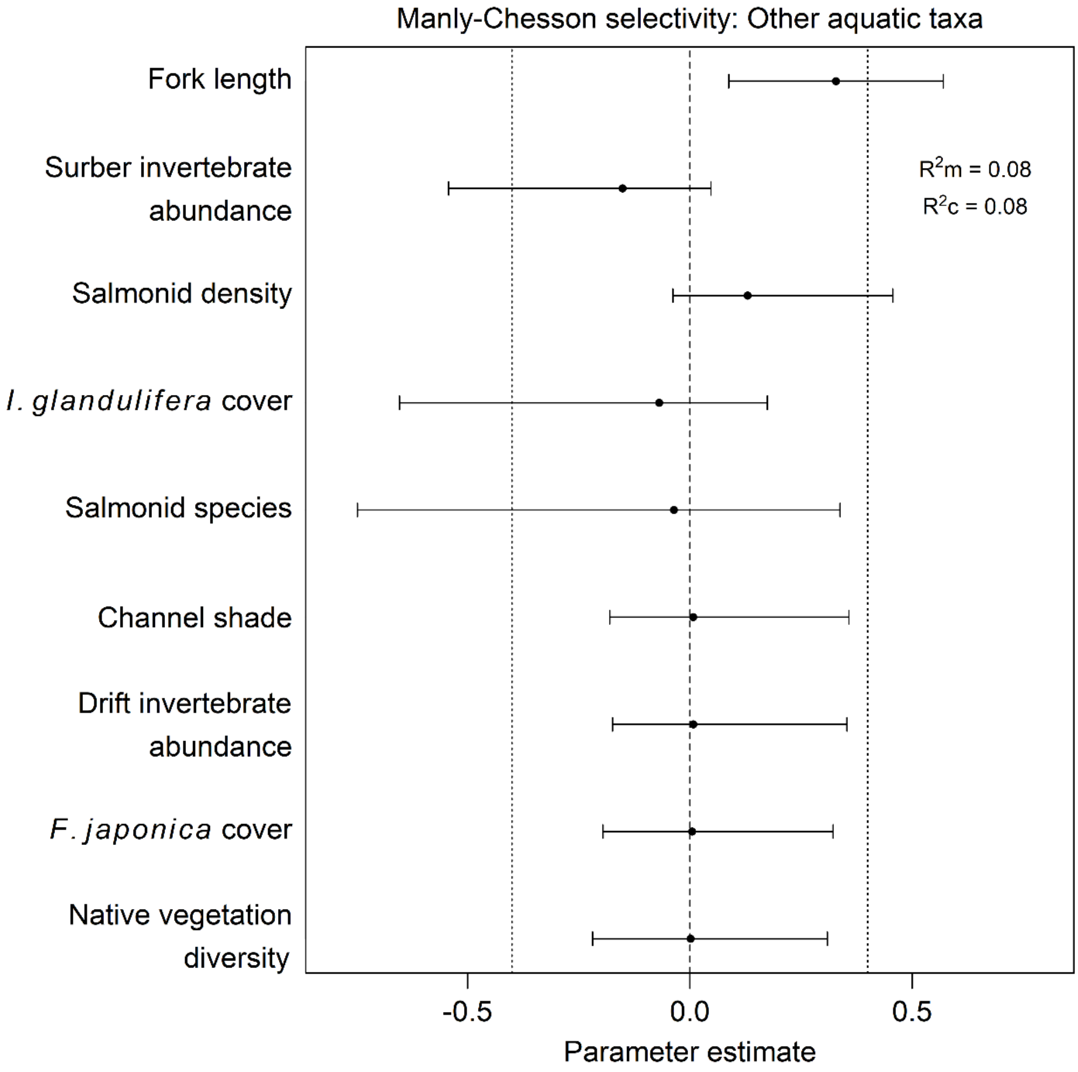

Figure 4.9 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 0.4. Modelled response was Manly-Chesson selectivity for other aquatic invertebrate taxa. Marginal (R^2m) and conditional (R^2c) values are given.

Manly-Chesson selectivity: aerial taxa

Selection of aerial taxa was positively associated with fork length and salmonid species (Figure 4.10), with the latter showing the largest effect size (1.15). The aerial prey source was utilised more by *S. trutta* than *S. salar*. No other variables were significant.

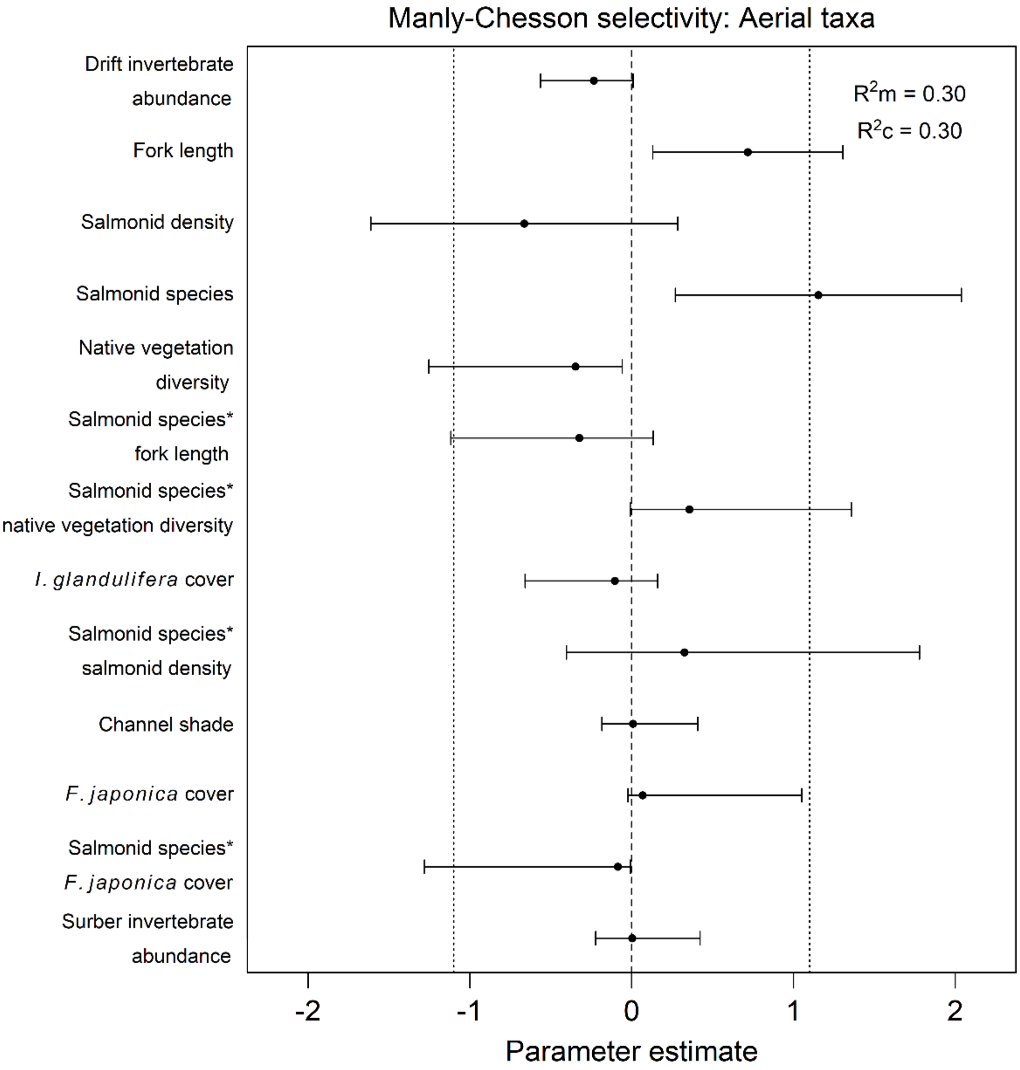

Figure 4.10 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 1.1. Modelled response was Manly-Chesson selectivity for aerial taxa. Marginal (R^2m) and conditional (R^2c) values are given.

Gut taxa diversity

The number of different taxa present in salmonid gut contents was positively associated with the abundance of invertebrates in the drift, fork length and salmonid species (Figure 4.11), the latter of which had the largest overall effect size (0.16). There was a positive interaction between salmonid species and *I. glandulifera* cover, showing that as *I. glandulifera* cover increased, the number of taxa in *S. trutta* gut contents increased at a greater rate compared to *S. salar*. There was a negative interaction between salmonid species and the abundance of invertebrates in the drift, showing that as the abundance of invertebrates in the drift increased, the number of taxa in *S. salar* gut contents increased at a greater rate compared to *S. trutta*.

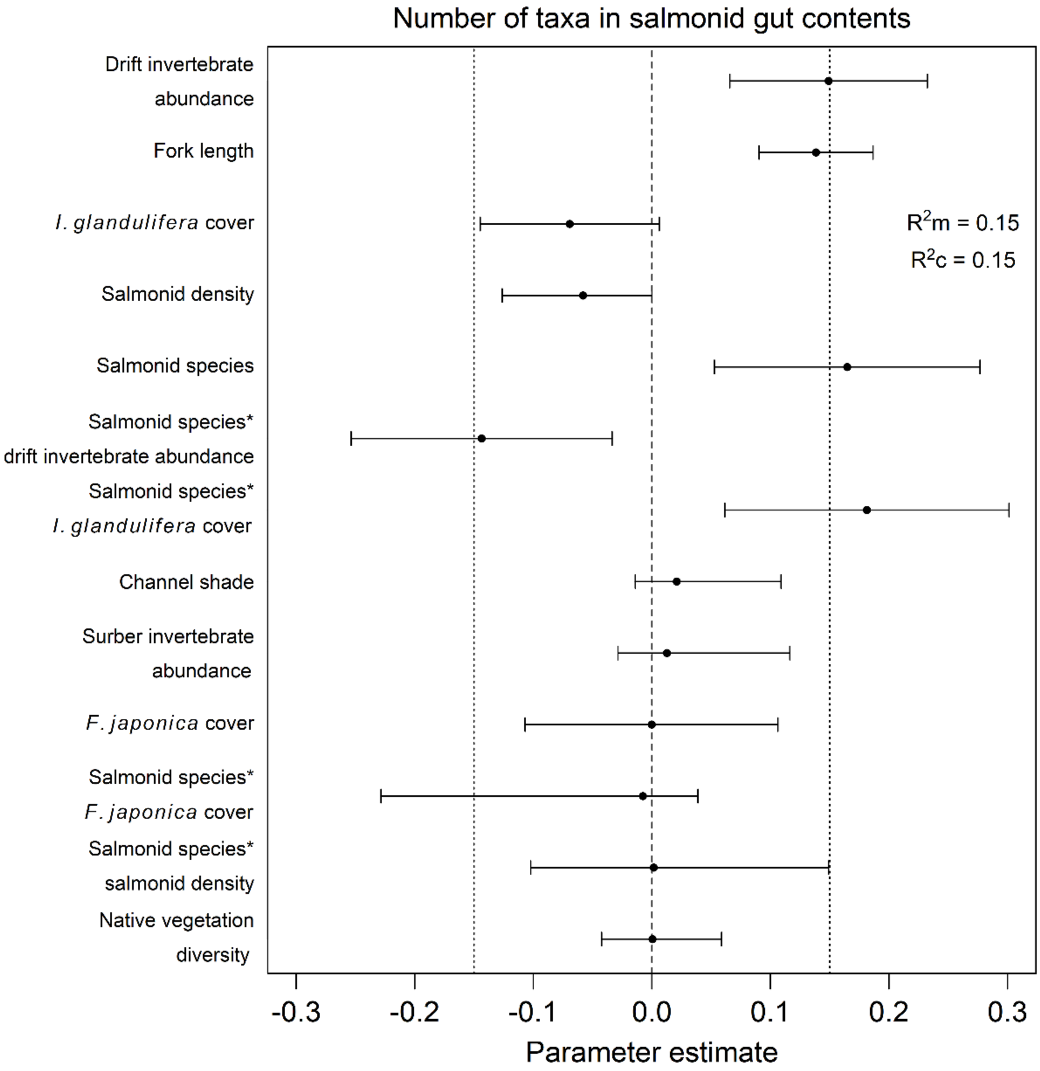

Figure 4.11 Full, model-averaged parameter estimates ± 95% confidence intervals. Dotted lines represent an effect size of 0.15. Modelled response was the number of taxa in salmonid gut contents. Marginal (R^2m) and conditional (R^2c) values are given.

Summary

M-C selectivity	**Significant predictors**	**Effect size**
Ephemeroptera	*I. glandulifera* cover	0.52
	Surber invertebrate abundance	0.84
Plecoptera	Salmonid density	-0.68
Trichoptera	Fork length	0.29
Simuliidae	Drift invertebrate abundance	0.34
	Salmonid species	-0.54
Chironomidae	*I. glandulifera* cover	-0.43
	Native vegetation diversity	-0.31
Gammaridae	NONE	N/A
Other aquatic taxa	Fork length	0.33
Aerial taxa	Fork length	0.72
	Salmonid species	1.15
Gut taxa diversity	Drift invertebrate abundance	0.15
	Fork length	0.14
	Salmonid species	0.13
	Salmonid species*Drift invertebrate abundance	-0.14
	Salmonid species**I. glandulifera* cover	0.18

Table 4.2 Summary of model predictors that were shown to significantly affect salmonid Manly-Chesson (M-C) selectivity of each invertebrate taxa group and overall gut taxa diversity. Predictor effect sizes are also given (as all models were run independently, effect sizes are not comparable between models or taxonomic

groupings). A negative effect of salmonid species indicates greater use of a prey source by *S. salar* compared to *S. trutta*, and vice versa.

4.4 Discussion

INNP species were only observed to have a significant effect on the dietary selection of two (Ephemeroptera and Chironomidae) out of eight main taxa groups (Ephemeroptera, Plecoptera, Trichoptera, Simuliidae, Chironomidae, Gammaridae, other aquatic invertebrate taxa, and aerial invertebrate taxa). This suggests that whilst INNP may affect the dietary choices of juvenile salmonids, these changes in diet appear to be relatively limited and do not apply to the full range of available prey resources. Furthermore, this effect was only observed for *I. glandulifera* and not for *F. japonica*, indicating that the two INNP species examined in this study are likely exerting their effects through different pathways.

The findings presented in chapters two and three suggested that both aquatic and terrestrial invertebrate communities should be less diverse and (in the case of terrestrial morphospecies) less abundant at sites with greater INNP cover. The absence of a clear and consistent impact of INNP on salmonid dietary choices is perhaps unsurprising, given their opportunistic feeding strategies and ability to adapt to both quantitative and qualitative changes in prey resources. Evangelista *et al.* (2014) demonstrated that changes in riparian land use and cover may direct *S. trutta* towards alternative aquatic prey items, especially when terrestrial prey inputs to streams are lowered.

Dietary choices – invasive cover

Impatiens glandulifera cover was positively associated with selection of Ephemeroptera and negatively associated with selection of Chironomidae. In the absence of any species-specific effects, this suggests that salmonids are actively selecting Ephemeroptera over and above their occurrence in the environment at sites with greater INNP cover, whilst avoiding Chironomidae.

Ephemeroptera are a common freshwater prey item for both *S. salar* (Johansen et al. 2011) and *S. trutta* (Montori et al. 2006). The positive association between Ephemeroptera selection and *I. glandulifera* cover may indicate conditions that promote invertebrate drift. At more invaded sites, the replacement of a riparian tree canopy by a comparatively smaller INNP riparian overhang may increase the overall insolation time of the stream channel, promoting drifting behaviour in Ephemeroptera for extended lengths of time, in a bid to avoid biological damage (Hitchings 2009). This may simultaneously making them more available to foraging salmonids; *S. salar* may feed diurnally when there is a need to do so to maintain growth rate (Orpwood et al. 2006). This would also be supported by the positive association between the abundance of invertebrates in the benthic Surber samples and the overall selection of Ephemeroptera, as the relative abundance of these taxa in the drift is likely to increase as their overall abundance does (Shearer et al. 2003). This relationship was observed between ratios of Ephemeroptera found in the benthos and drift in this study (Appendix, Figure S5).

Chironomidae tend to be deposit feeders (Murphy and Giller 2000) and as such are likely to prefer habitats with reasonable levels of detritus and organic matter entering the stream. Although it is therefore possible that the presence of Chironomidae may be altered in invaded environments due to the presence of alien litter sources, this study did not find evidence to support this, and an NMDS analysis of community composition (chapter 2) demonstrated no strong preference by Chironomidae for either invaded or uninvaded sites. It is likely then that the reduced selection of these taxa by salmonids is due to reduced ease of acquisition – salmonids are visual feeders (Alanärä et al. 2007), and as such may prefer the more easily accessible Ephemeroptera prey source in the drift at invaded sites.

Native vegetation diversity was negatively associated with selection of Chironomidae. Greater riparian vegetation diversity has been shown to increase fungal species richness on leaf litter, subsequently enhancing leaf litter breakdown rate (Lecerf et al. 2005). This may mean that the leaf litter resource at sites with higher native plant diversity has a shorter residence time, providing a less persistent nutrient source for Chironomidae taxa. In contrast, sites with poorer native plant diversity may indicate greater disturbance (potentially due to *I. glandulifera* or *F. japonica* invasion in this study), which would foster a greater abundance of Chironomidae due to their substantial tolerance for disturbance (Paisley et al. 2014).

Dietary choices – competition

Salmonid density was negatively associated with selection of Plecoptera, whilst salmonid species was negatively associated with selection of Simuliidae (indicating greater use by *S. salar*), and positively associated with selection of aerial invertebrate taxa (indicating greater use by *S. trutta*).

The greater use of Simuliidae prey exhibited by *S. salar* may be an artefact of interspecific competition – if *S. trutta* parr are dominant over *S. salar* parr (Höjesjö et al. 2010; Nislow et al. 2010), this may force *S. salar* individuals to choose alternative prey resources. In this case, *S. trutta* may control the drift, at which point *S. salar* may adopt a more benthic-orientated foraging strategy (Johansen et al. 2011), consuming more Simuliidae. The abundance of invertebrates in the drift was also positively associated with selection of Simuliidae. Given that *S. trutta* are likely to dominate feeding niches during the day when in sympatry with *S. salar* (Johansen et al. 2011), it is likely that both species will interact with Simuliidae larvae, which are likely to be anchored to the substrate during the day and exhibit more drifting behaviour after sunset (Adler et al. 1983).

A greater rate of selection of aerial prey sources was demonstrated by *S. trutta* and is again likely in part due to their sympatric dominance. *Salmo trutta* are known to utilise prey from terrestrial sources (Wipfli 1997; Dineen et al. 2007), and prey items from these sources can often be the most important part of their diet (Bridcut and Giller 1995; Bridcut 2000). Studies have demonstrated a negative correlation between fish density and aquatic macroinvertebrate biomass (Hornung and Foote 2005), and it is possible that at sites with higher densities of fish, *S. trutta* are adapting to less readily available aquatic prey sources by switching to a more terrestrially-dominated diet (Ryan and Kelly-Quinn 2015).

Reduced selection of Plecoptera in response to increased salmonid density may be due to behavioural changes in fish which take priority over foraging. Increased density causes an increase in the number of aggressive interactions and level of aggression between fish (Blanchet et al. 2006), with *S. trutta* generally responsible for both intra- and inter-specific attacks (Höjesjö et al. 2010). These interactions within higher density populations may mean that either less time is spent on foraging, or that a greater proportion of foraging attempts are unsuccessful

(Kaspersson et al. 2010). However, total salmonid densities in this study ranged from 0.04-0.85 individuals m^{-2} (Appendix, Table S6), which could be considered relatively low (Grant and Imre 2005).

Although Plecoptera are regular components of drift, they are not often found at the same level of occurrence as Ephemeroptera (Bridcut 2000), and adopt more crepuscular drifting patterns (Rader and McArthur 1995). It may also be the case that higher fish densities cause an overall reduction in the abundance of some aquatic invertebrate taxa, as habitat-specific and taxa-specific reductions in benthic invertebrate abundance have been demonstrated in response to predatory fish (Effenberger et al. 2011; Winkelmann et al. 2011).

Body size limitations

Salmonid fork length was positively associated with selection of aerial taxa, Trichoptera and an assortment of other aquatic taxa (mainly comprising aquatic stages of Diptera larvae outwith the Chironomidae family, Coleoptera and Hemiptera). The relationship between prey length and gape size is well established for fish - use of larger surface-drifting prey with a potentially terrestrial origin has been observed more regularly in larger *S. trutta* compared to their smaller conspecifics (Gustafsson et al. 2010), whilst selection of larger prey items and associated rejection of smaller prey items has been demonstrated by *S. salar* (Wañkowski 1979).

Given that the aerial taxa group is mainly comprised of adults from the Ephemeroptera, Plecoptera, Trichoptera, and some terrestrial orders including Diptera and Hymenoptera, it follows that their consumption appears to be limited by fork length, as fish with a larger body length will have a larger gape relative to smaller conspecifics and will take larger prey (Neveu 1999; Keeley and Grant 2001). Given that these particular prey items are terrestrial in nature and therefore not adapted for an aquatic lifestyle, any individuals from these groups would immediately become much more vulnerable to predation by salmonids upon entering the water column, particularly as they would likely remain in the drift. Furthermore, the drift is likely to be controlled by larger, more dominant fish (McCormick and Harrison 2011), which would be of an adequate size to consume these prey items. Encounter rates between salmonids and some of these taxa are also likely to be less frequent. For example, the larval Trichoptera occurring at sites in this study are likely to move much more slowly than Ephemeroptera, adopting walking, burrowing or semi-sessile mobility strategies (Tachet et al. 2010). Given the nature of *S. trutta* to feed on invertebrates with more vulnerable life history traits (e.g. high tendency to drift or aggregate) (De Crespin De Billy 2002), it is unlikely that Trichoptera would form a substantial proportion of their prey. Additionally, five out of six Trichoptera families recorded in this study represented case-building taxa, which would likely be too large for smaller salmonids to consume.

Considering fork length as a proxy for age, it may be that larger fish have had more time to learn from their previous foraging efforts and are now able to incorporate prey sources that were not previously known to them. Johansen *et al.*, (2011) discuss the ability of juvenile *S. salar* to learn to focus both on common prey items and also novel prey as they gain more experience. The ability to learn and respond to changes in both the abundance and diversity of prey enables these fish to maintain a high foraging efficiency in sub-optimal conditions (Reiriz et al. 1998). Fork length was positively associated with the diversity of prey items found in salmonid stomach contents, and this analysis also demonstrated that *S. salar* consumed a greater diversity of prey items than *S. salar* when the abundance of invertebrates in the drift increased. This indicates a greater familiarity with the drift in *S. salar*, which have been shown to learn to recognise and track profitable foraging areas (Warburton 2003). There was also an overall positive association between gut taxa diversity and the abundance of invertebrates in the drift, which may be driven by increased risk-taking behaviour to achieve satiation in both *S. trutta* (Biro et al. 2005) and *S. salar* (Vehanen 2003).

4.5 Conclusion

The findings of previous chapters have demonstrated that INNP have measureable effects on riparian communities of both aquatic and terrestrial invertebrates. Whilst this suggests that sites with the greatest riparian INNP cover are ecologically poorer in terms of their invertebrate communities compared to their uninvaded counterparts, this diet study suggests that for the most part, juvenile salmonid diet selection is not affected to the same degree. Furthermore, INNP appear to even increase the rate at which both *S. trutta* and *S. salar* are able to consume Ephemeroptera, one of their preferred and commonly selected prey items.

That populations of anadromous salmonids are able to persist in highly dynamic and potentially disturbed environments is not surprising (Reeves et al. 1995), and the adaptability of both species to changes in environmental conditions and the quantity and quality of prey items available to them is well known (Dineen et al. 2007; Johansen et al. 2011).

This study demonstrates that whilst the prey items available to juvenile salmonids may be significantly affected by INNP, the translation of this impact to a significant alteration in the feeding habits of these fish seems to be a relatively infrequent occurrence, particularly compared to factors like fish density and overall abundance of prey items in the drift and benthos.

Previous chapters have already highlighted the potential need for treatment-based management efforts in order to control riparian invasions and more towards restoring the ecological quality of riparian ecosystems. Salmonids are the focus of a wide range of studies examining the impacts of in-stream and riparian restoration efforts on fish populations (many, but see Summers et al. 2005; Saunders & Fausch, 2007; Thomas et al. 2015). Management plans specifically focusing on riparian restoration aim to restore in-stream and riparian habitat through mitigation of harmful pollution and sediment ingress, and introduction of large woody debris and riparian buffers amongst other beneficial impacts (Feld et al. 2018). Although studies show that salmonids utilise riparian-derived prey (Ryan and Kelly-Quinn 2015) to supplement diet and cover afforded by riparian canopy for refugia (McCormick and Harrison 2011), the adaptable and opportunistic nature of salmonids suggests that they may be able to adjust to variations in prey availability and that increasing riparian INNP cover may have little impact on the broad dietary selection of juvenile *S. trutta* and *S. salar*. Studies focusing on the wider effects of INNP invasions on physical and hydrological changes (Louhi et al. 2008) to both riparian and in-stream habitats would be more beneficial in assessing any detrimental effects of riparian INNP invasions on salmonids.

Chapter 5: General discussion

Impatiens glandulifera dominates the bank of the Bannockburn, Forth catchment, July 2016.

5.1 The current state of invasion ecology

The field of invasion ecology has made significant advances since attention was first drawn to plant and animal invasions by Elton in 1958, and IAS are now considered to be one of the greatest threats to global biodiversity (Simberloff et al. 2013). However, significant deficiencies remain, both in research and in understanding. These include the accurate assessment of the threats posed by IAS at an ecosystem (and perhaps species-specific) level, and the incorporation of these assessments into management policies (Sandiford et al. 2015). A review by Hering *et al.* in 2010 concluded that only 4% of classification approaches compliant with the Water Framework Directive focus on IAS as factors causing deterioration in ecological status. Furthermore, there is evidence to suggest that published studies often contradict each other, offering conflicting advice and only serving to muddy the waters in terms of effective management strategies for IAS (Robinson et al. 2017). Moving forward, potential pitfalls in the field of invasion ecology are likely to include the generation of new control methods with potentially unseen consequences and the interactive effects of warming and anthropogenic pressures on ecosystems (Ricciardi et al. 2017).

Rivers, and freshwater ecosystems generally, are unquestionably important and provide an array of social, economic and ecological benefits. In particular, the invertebrate taxa that these systems harbour and sustain are extremely important because of the ecosystem services that they provide (Macadam and Stockan 2015), and due to their incorporation into a variety of indices for monitoring water and habitat quality (Paisley et al. 2014; Brand and Miserendino 2015; Doretto et al. 2018). Rivers are ecologically entwined with riparian zones, which act as vital buffers against terrestrial pressures; so much so that riparian systems are increasingly becoming focal areas for addressing stressors affecting river ecosystems (Feld et al. 2018). Studies that further our understanding of these highly biodiverse habitats provide us with an insight as to how INNP might affect riparian and river ecosystems (O'Toole et al. 2016; Sinnadurai et al. 2016; Turunen et al. 2017). However, there is still a comparative lack of knowledge as to the specific pathways through which riparian invaders exert their effects, and this provides an important niche which should be addressed by future research (Pattison et al. 2017). Of particular concern is the growing link between IAS and freshwater extinctions, and this thesis supports recent suggestions that current and future studies should work on resolving the uncertainty surrounding the detection and prediction of IAS impacts on freshwater systems (Moorhouse and Macdonald 2015).

The research presented in this thesis aimed to tease apart the effects of riparian INNP (Figure 5.1) from the multitude of environmental drivers that affect aquatic and terrestrial invertebrate communities. By doing so, it also aimed to assess how changes to invertebrate communities in response to INNP might ripple through to salmonid populations, examining the dietary choices of two important salmonid species in their juvenile life stages. This thesis also aimed to quantify the effects of riparian INNP cover on a continuous scale, departing from the binary "invaded versus uninvaded" status in favour of addressing subtle changes in composition and salmonid resource usage with incremental increases in riparian INNP cover.

Figure 5.1 Facing downstream on the Dunning burn (Tay catchment), both banks dominated by *Impatiens glandulifera* during the summer months (August 2016).

5.2 Impacts of riparian INNP on invertebrate communities

Chapters 2 and 3 highlighted the ability of riparian INNP to significantly alter the composition of invertebrate assemblages in both aquatic and terrestrial habitats. This association appeared to be more pronounced in terrestrial habitats, where riparian INNP cover showed the strongest effect on all measured community responses. This is in contrast to aquatic macroinvertebrates, which were generally more strongly affected by measured environmental variables. These findings generally support recent studies which demonstrate negative effects of riparian INNP cover on aquatic and terrestrial invertebrate communities (e.g. Tanner et al., 2013; Roon et al., 2014; Custer et al., 2017; McNeish et al., 2017), and which also highlight the potential for significant and positive changes in invertebrate community composition following INNP removal. However, other recent work suggesting that riparian INNP rarely have severe ecological consequences on local ecosystems (Fogelman et al. 2018) or that they may even foster greater invertebrate richness and density under specific conditions (Kuglerová et al. 2017) are not supported by the findings of this thesis.

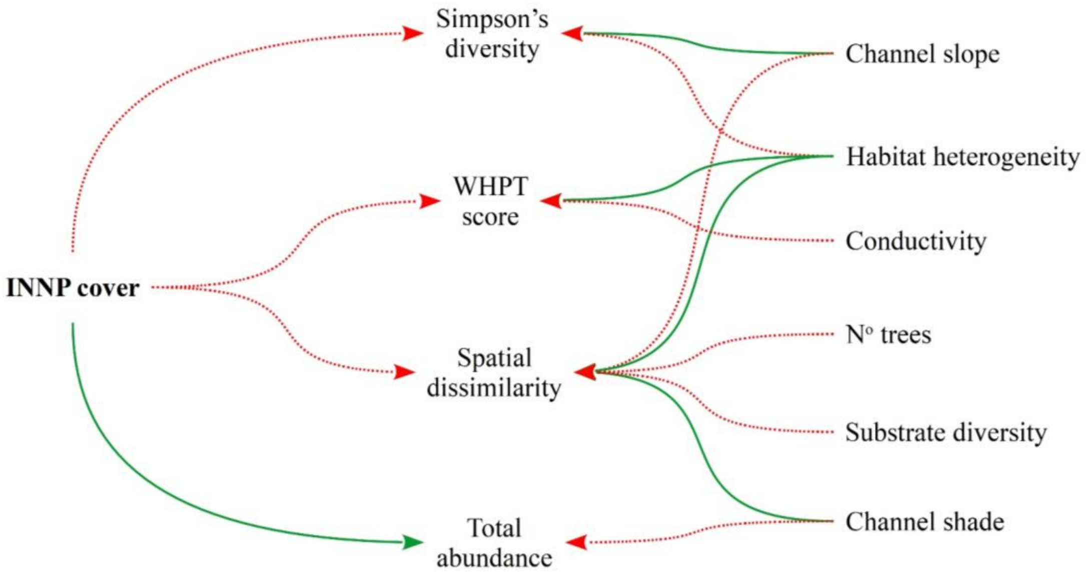

Figure 5.2 The effects of statistically significant environmental predictors on modelled responses of aquatic macroinvertebrate communities. Solid green arrows represent a positive effect; dotted red lines represent a negative effect.

Riparian zones are dynamic environments, and organisms inhabiting these ecosystems are generally adapted to disturbance (Jackson et al. 2015). However, the significantly altered riparian vegetation at invaded sites may remove the buffer between anthropogenic stressors and stream biota (Hunt et al. 2017), resulting in conditions which may exclude more sensitive taxa. In chapter 2, increasing riparian

INNP cover was demonstrated to exert broadly negative effects on the composition and diversity of aquatic macroinvertebrate communities, though these were also influenced by hydrological and physical habitat factors, such as substrate diversity and conductivity. The higher abundance of invertebrates (e.g. *Dicranota* spp., Gammaridae, *Lymnaea* spp.) at more heavily invaded sites was generally an indication of degraded environmental conditions, suggesting a negative association between riparian INNP cover and the quality of connected freshwater habitats.

Although riparian INNP cover was significantly associated with all measures of aquatic invertebrate community composition, it only had the strongest effect size for alpha diversity, suggesting that the localised effect of invasion in low order streams is generally subordinate to other environmental pressures. This is evidenced by the greater effects of environmental stressors such as conductivity, number of riparian trees and habitat heterogeneity on broader scale macroinvertebrate responses such as total abundance and spatial dissimilarity. There may be as yet undescribed interactions between environmental stressors and INNP species, particularly given the ability of invasive species generally to colonise disturbed environments. It is also possible that factors such as habitat heterogeneity and channel slope, which were observed to positively affect invertebrate communities, may mitigate the negative impacts of INNP on freshwater macroinvertebrates, explaining their comparatively lesser influence. Perhaps in this study, it is a case of association rather than causation, whereby INNP are found to colonise disturbed areas of riverbank, but are not themselves the drivers of ecological change (Greenwood et al. 2018).The relatively greater influence of riparian INNP cover on terrestrial invertebrate communities may be due to their more immediate proximity to these plants. Significant pressures arising from land use changes, habitat degradation and loss of ecosystem function negatively affect terrestrial species richness and abundance (Newbold et al. 2015), and changes to the local plant community can depress fungal communities (Dukes and Mooney 2004), altering decomposition rates and modifying the local habitat.

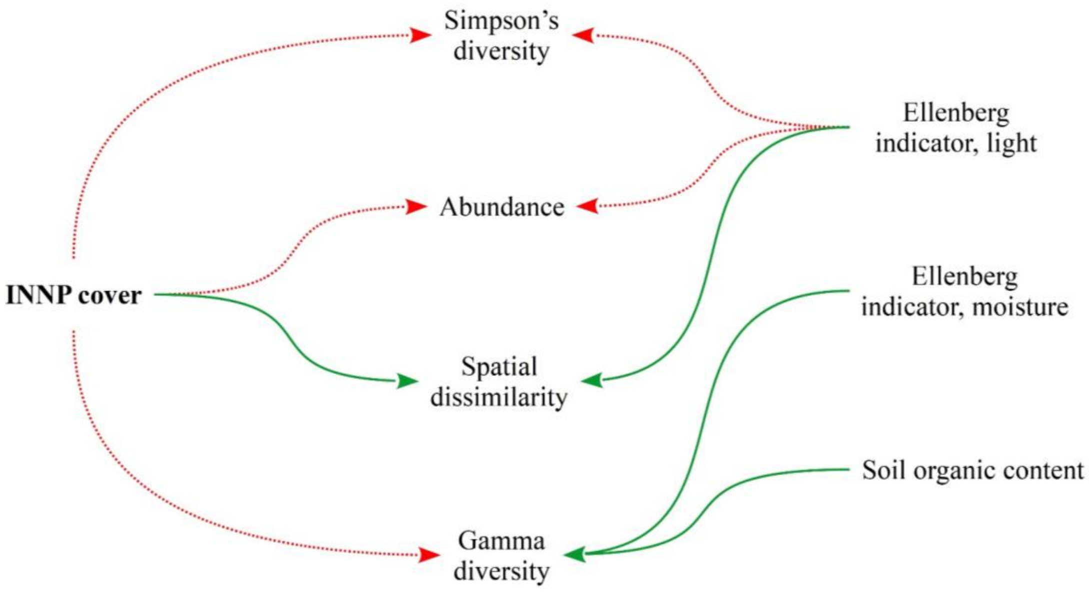

Figure 5.3 The effects of statistically significant environmental predictors on modelled responses of terrestrial invertebrate morphospecies. Solid green arrows represent a positive effect; dotted red lines represent a negative effect.

The establishment of INNP may significantly alter soil fertility, litter quality and quantity, and introduce novel disturbances such as an altered fire regime (Wardle and Peltzer 2017), which can be expected to affect a range of organisms that depend on the plant community (such as invertebrate, vertebrate and fungal groups). Possible changes in environmental conditions at more heavily invaded sites were supported by the association of more generalist terrestrial Acari taxa, compared to the more sensitive Coleoptera and Diptera taxa associated with uninvaded sites. It may be the case that ecosystem engineers such as *I. glandulifera* and *F. japonica* cause such significant changes in the local habitat and environmental conditions that associated terrestrial invertebrate communities are themselves significantly altered. The reduced diversity and abundance of terrestrial invertebrates at invaded sites observed in chapter 3 seems to support this, and there is also evidence of significant reductions in terrestrial invertebrate diversity and abundance in plant communities which favour well-lit conditions. The negative association between the Ellenberg vegetation indicator for light and terrestrial invertebrate abundance and diversity may indicate an INNP effect – *I. glandulifera* has a light index of 5, and measured *Fallopia* species have values of 6-7 (Ellenberg 1986), indicating preferences for moderately to well-lit conditions.

Whilst the rivers studied in this thesis were relatively small, there are thus clear effects of riparian INNP cover on both aquatic and terrestrial invertebrates. The findings from these two chapters offer evidence to support negative associations between riparian INNP and invertebrate habitat quality, and studies such as this at a relatively small scale may be used as indicators of larger-scale change (Woodward et al. 2010; Sigurdsson et al. 2016).

5.3 Do juvenile salmonids feel the effects of riparian INNP invasions?

Chapter 4 showed that despite community-level changes in both aquatic and terrestrial invertebrate communities at heavily invaded sites, the dietary choices of juvenile salmonids are relatively unchanged in direct response to riparian INNP invasions. Significant variations in selection of invertebrate prey as a result of INNP cover were only observed for two out of eight taxa groups tested, namely Ephemeroptera and Chironomidae. Furthermore, these INNP effects were matched or surpassed by other factors, suggesting that even when there are significant impacts of riparian INNP on salmonid dietary choices, they are not the only source of variation (e.g. a lower effect size of 0.52 for the relationship between *I. glandulifera* and Ephemeroptera selection compared to 0.84 for the relationship between Surber invertebrate abundance and Ephemeroptera selection). Broadly, the drivers of dietary variation were community-level variables such as salmonid species and density, or measures of the overall available prey source (e.g. abundance of invertebrate prey in the drift and benthos). These findings are in agreement with studies that demonstrate the effects of inter- and intraspecific competition on foraging behaviour in fish populations (Evangelista et al. 2014; Houde et al. 2015). Whilst invasions can alter food web structure (David et al. 2017), higher trophic consumers that are able to either adopt a generalist approach to prey acquisition and/or adapt their behaviour in response to changing environmental conditions may be less affected by changes at lower trophic levels. Such a response conforms with studies suggesting that even when faced with a reduced terrestrial subsidy, salmonids are able to maintain a high rate of prey consumption (Roon et al. 2016). This elastic behaviour may help to mitigate some of the negative changes to invertebrate communities as a results of riparian INNP, and suggests that the more concerning impacts of invasions may be the hydrological and morphological changes that occur at heavily invaded sites, as suggested by Kováč (2015).

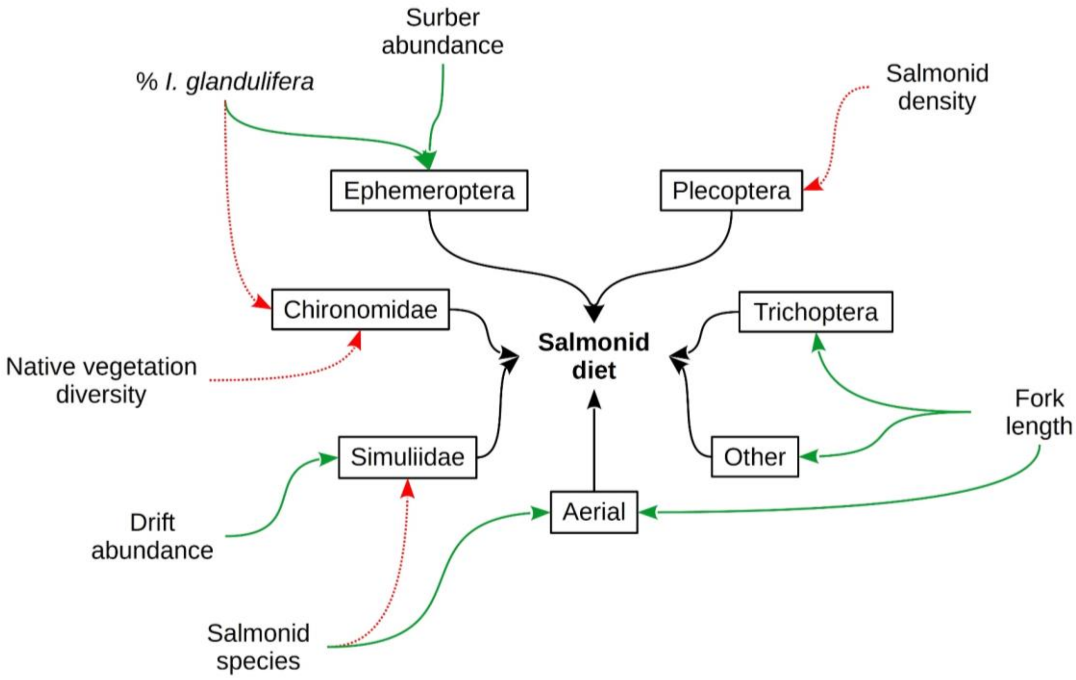

Figure 5.4 The effects of significant modelled predictors on the dietary selection of invertebrates. Solid green arrows represent a positive effect; dotted red lines represent a negative effect. Ephemeroptera, Plecoptera, Trichoptera, Chironomidae and Simuliidae refer to larval stages of aquatic invertebrate taxa; “Other” refers to both larval and adult stages of remaining aquatic invertebrate taxa; “Aerial” refers to adult stages of both aquatic and terrestrial invertebrate taxa.

Reductions in the abundance and diversity of aquatic invertebrates highlighted in chapter 2 were broadly associated with hydromorphological features such as substrate diversity and habitat heterogeneity, suggesting that unfavourable benthic conditions may reduce the overall availability of prey items for fish. This is supported by altered selection of Ephemeroptera and Simuliidae taxa in response to changes in their abundance in surber and drift samples respectively. Although these changes in habitat quality and structure were not directly linked to INNP in this thesis, links between INNP and stressors such as sedimentation (Bilotta and Brazier 2008; Jones et al. 2015) and physical habitat alteration (Jackson et al. 2017) are well-recognised and as such, it is possible that riparian INNP may alter invertebrate availability to fish indirectly through habitat modification.

Nevertheless, there is evidence of significant interactions between IAS and salmonid diet in the wider literature. Rush et al. (2012) showed that the replacement of a native salmonid prey fish species by the invasive round goby (*Neogobius melanostomus*) reduced the overall ability of the offshore food web to support populations of lake trout (*Salvelinus namaycush*), forcing an increased reliance on alternative energy pathways. Schultz and Dibble (2012) found that invasive macrophytes may reduce the abundance of native fish through changes to habitat, hypoxic conditions and poor food quality, but that the mechanisms underlying these changes were not significantly different from native macrophytes. Interactions with IAS may also occur at different life stages; Taylor and Dunn (2016) demonstrated in a laboratory study that invasive killer shrimp (*Dikerogammarus villosus*) may predate upon fish eggs, potentially reducing recruitment. However, this effect was minor in *S. trutta*, and appeared more pronounced in the cyprinid ghost carp (*Cyprinus carpio*).

It is possible that whilst riparian INNP invasions have potentially serious and damaging consequences for local ecosystems (Schirmel et al. 2016), they may still facilitate recruitment and persistence of juvenile salmonids populations, providing any hydromorphological changes are not prohibitive to them. INNP with dense canopies such as *F. japonica* offer shading, a dense overhang with a large litter input and the potential for an invertebrate subsidy to supplement the aquatic invertebrate diet. There is also evidence of differing effects for different INNP species – whilst *I. glandulifera* cover significantly altered the selection of Ephemeroptera and Chironomidae taxa, there was no evidence of any effect of *F. japonica* cover, suggesting that salmonid prey selection may be affected to varying degrees depending on the INNP in question. Whilst terrestrial invertebrate abundance dropped by approximately 57% at maximum INNP cover, aquatic invertebrate abundance increased by approximately 25%. Given the generalist feeding nature of salmonids, reductions in invertebrate diversity and abundance may not have a significant impact if they are not limiting (Albertson et al. 2018). However, a change in the composition of the invertebrate prey resource may influence salmonid foraging behaviour and timing, with implications for factors such as spatial distribution, productivity and predation risk.

5.4 Management implications

Freshwater fish and invertebrates from both freshwater and terrestrial environments help to form both conceptual and ecological links between riparian and freshwater ecosystems, and as such are critically important in assessing the health of rivers, and designing suitable management strategies. Studies focusing on restorative and management efforts have demonstrated a number of important drivers that elicit positive responses from fish populations. The inclusion of woody debris may foster a larger trout population (Sievers et al. 2017), whilst terrestrial and aquatic habitat improvements, such as the exclusion of cattle and introduction of more heterogeneous substrate (Turunen et al. 2017) may foster increased abundance and diversity of invertebrates, providing a more reliable prey source whilst simultaneously improving the ecological quality of their respective habitats.

Invasions by alien species are a widespread issue, and this promotes a global network of studies assessing the impacts of invasion, management approaches to restore native biota, and the short- to long-term effects of IAS removal. The process of controlling established IAS is often reliant on significant investment of resources and time, with an end result that is only temporary, requiring repeated efforts to reach a more permanent solution (Haight et al. 2017). However, the promise of ecological gains following IAS removal often necessitates management action, particularly from an ecological point of view. Clearing of a number of invasive alien trees from riparian systems may improve functional diversity of invertebrate assemblages (Modiba et al. 2017), removal of Chinese privet (*Lingustrum sinense*) enables the recovery of native plant communities (Hudson et al. 2014; Barnett et al. 2016), and use of a biocontrol agent in the treatment of saltcedar (*Tamarix* spp.) promoted increased herpetofauna abundance due to more favourable canopy and surface conditions (Mosher and Bateman 2016).

However, focusing on specific interactions between small numbers of species may not result in the durable ecological gain that would be anticipated after sometimes very significant financial investment. Without understanding the ecosystem functions and ecological processes that are affected by IAS, it is likely that restoration efforts will be unsuccessful, as they may lead to surprising and unpredictable results (Jackson et al. 2016; Jackson et al. 2017). Removal of *Tamarix* spp. has been shown to promote secondary invasions in riparian systems (González et al. 2017), and removal of Amur honeysuckle (*Lonicera maackii*) may cause a shift in the plant community of restored areas (Hopfensperger et al. 2017). Treated areas may also be more prone to invasion in the long-term, particularly if funding and associated management efforts cease (Fill et al. 2017).

Given that the focus of IAS removal is generally to increase the ecological "value" of an ecosystem, it is worth noting that some IAS may provide benefits to other biota and as such, it is important to consider invasions on a case-by-case basis, rather than in a binary "invaded or native" manner. Thus, for example, the larvae of the endangered island marble butterfly (*Euchloe ausonides insulanus*) feed on two non-native plants – field mustard (*Brassica rapa*) and tumble mustard (*Sisymbrium altissimum*), whilst *Tamarix* spp. provide habitat for the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (Dunwiddie and Rogers 2017). It may also be beneficial to design management strategies that introduce more gradual changes over a longer period of time, rather than aiming to quickly eradicate IAS (Lampert et al. 2014). However, this is still a far cry from literature which suggests that IAS will ultimately be the ecological "salvation" that enables restoration of our imperilled ecosystems (Pearce 2015). The findings of this thesis broadly agree with studies that promote the careful and considered treatment of riparian INNP (Urgenson et al. 2014), but concede that in some scenarios, there may be ecological benefits attributable to some IAS that should not be overlooked (Schlaepfer 2018).

Taking pre-emptive measures to prevent invasion is often preferable and cheaper than designing and implementing management plans (Mack et al. 2000), but moving forwards, this will require a detailed understanding of the pathways through which IAS become established and subsequently exert their effects on native biota (Faulkner et al. 2015). A species and pathway based approach that also considers the sensitivity and susceptibility of ecosystems to invasion on a site-specific basis is likely to provide the best synthesis for predicting invasion (McGeoch et al. 2016). This approach has also fostered the recent development of metrics designed to predict the size of impact of an IAS (Dick et al. 2017), and calls to classify alien species based on the size of their environmental impacts (Davis et al. 2011; Blackburn et al. 2014), enabling management plans to be more specifically targeted. It is also important to consider that whilst INNP management at the local scale may yield relatively small improvements, these may be essential in a bid to prevent larger regional-scale invasions which may have far more significant and devastating impacts on our freshwater and riparian ecosystems. Expanding transportation networks throughout and between landscapes are increasing the number of routes through which invasive species may spread, and resistance to invasive species control in the form of stakeholder conflicts, misconceptions surrounding management tools and the increasing rise of invasive species denialism threaten to allow invasive species to spread relatively uncontested (Ricciardi et al. 2017). Studies show the potential for economically and ecologically significant impacts of a single species invasion (Walsh et al. 2016), perhaps owing in part to their ability to modify local habitat, creating more favourable conditions for themselves whilst subsequently impacting native communities (Ricciardi et al. 2013). Documented improvements following invasive species management and removal suggest that this should be the preferred choice, even at a small scale. Glen et al. (2013) discuss the conservation and restorative benefits to island biodiversity following invasive species management, whilst other studies suggest that conflict surrounding the management of invasive tree species may ultimately increase treatment costs (Dickie et al. 2013) and that control efforts should focus on preventing further spread into cleared or uninvaded areas (Wise et al. 2012).

Whilst this thesis does not examine recovery following INNP removal, it does quantify the ecological impact of two prominent, widespread and often managed INNP species on riparian ecosystems. Maximum INNP cover was associated with reductions in the diversity (-33%), WHPT score (-5%) and dissimilarity (-12%) of aquatic macroinvertebrate communities, fostering an increased abundance (+25%) of tolerant taxa. Similarly, maximum INNP cover was associated with reductions in sample (-39%) and site level (-21%, *I. glandulifera* only) diversity and abundance (-57%) of terrestrial invertebrate morphospecies, and although this fostered more spatially heterogeneous assemblages (+26%, *F. japonica*; +18%, *I. glandulifera*), this was as a result of morphospecies extirpation. These findings offer support for the management of riparian INNP species, as heavily invaded riparian sites are clearly of a lower quality than their uninvaded counterparts. However, given the relatively low number of taxa groups that are predated upon in significantly different proportions by juvenile salmonids at invaded sites, it is unlikely that these improvements will be felt by resident *S. salar* and *S. trutta* populations at invaded sites. It is possible that ecological improvements may be seen instead through in-stream and bankside morphological improvements following IAS removal and the re-establishment of native vegetation, but these pathways were not extensively tested in this thesis, and this area is therefore highlighted for consideration in future studies.

5.5 Outstanding questions/study limitations

The research presented within this thesis has provided evidence that riparian INNP do have a measurable and significantly negative impact on the invertebrate (both aquatic and riparian) and salmonid fauna associated with stream ecosystems. It has also highlighted the way in which this effect may vary between different groups of taxa with a range of sensitivities to disturbance and as such, emphasises the need for a more holistic understanding of the subtle interactions between riparian and freshwater biota and IAS. Chapter 2 demonstrated a small amount of community variation as a result of riparian INNP cover, but was unable to isolate the ecological pathways through which this change was directed. Examining the change in community composition and associated variations in environmental parameters at more regular intervals (e.g. monthly) may help to better demonstrate how these plants exert their effects. For example, assessing the aquatic and terrestrial invertebrate community structure immediately prior to the commencement of riparian INNP growth (April to May), and taking monthly samples as the growth increases throughout the summer and subsequently dies back in the autumn, would allow more subtle changes in response to an increasing INNP pressure to be evaluated.

In chapter 2, the impacts of riparian INNP on freshwater macroinvertebrates were assessed by combining *I. glandulifera* and *F. japonica* cover into a single measure of invasive cover. This is in contrast to chapters 3 and 4, where the invasive cover of each INNP species was quantified separately. The focus of chapter 2 was on the overall effects of invasion-related disturbances rather than differences between similar INNP species, but given the species-specific relationships demonstrated in chapters 3 and 4, it is possible that similar variations in the effects of the study INNP on freshwater macroinvertebrates may also be present. Species-specific analysis in chapter 3 demonstrated small variations in the effect sizes of *I. glandulifera* and *F. japonica* (where these effects were significant), but did not show differences in the direction of these effects. It is therefore unlikely that collectively assessing these two species in chapter 2 is masking any significantly different relationships between INNP and freshwater macroinvertebrates.

Chapter 4 assessed the response of juvenile salmonids to increasing riparian INNP cover, and demonstrated that whilst their selection of two invertebrate taxa groups was significantly altered at heavily invaded sites, they broadly responded to community and environmental stressors. To improve upon these links, it would be interesting to incorporate the use of stable isotope analysis, not only to further elucidate changes in the feeding habits of salmonids along an increasing gradient of riparian INNP cover, but also to allow the resolution of site-specific invertebrate functional feeding groups, which would allow for the construction of individual food webs, each under a differing degree of INNP pressure. This would be particularly instructive when considering the possibility of altered litter breakdown rates at heavily invaded sites, and the potential for variations in associated invertebrate community structure (Fogelman et al. 2018). Recent studies have highlighted variation in the functional composition of invertebrate communities in response to inter-habitat variation (Mendes et al. 2017), as well as using stable isotope analysis to provide a more robust assessment of the origin of allochthonous and autochthonous energy sources (Collins et al. 2016). This could also be combined with a volumetric assessment of stomach contents (Janjua and Gerdeaux 2011), which may allow for an estimate of satiation to be calculated and related to fish length or age.

Model averaging was employed as a technique to provide the best possible approximation of the impacts of INNP and a variety of environmental predictors on freshwater and terrestrial invertebrates, and salmonid fish. There is concern that the model averaging approach may not always be the most suitable for ecological data (Richards et al. 2010) and as such, the validity of this approach was tested via comparison with a standard model simplification approach using stepwise AIC comparison (Burnham and Anderson 2002; Burnham et al. 2010). The results of this comparison (Figure 3.4) show that there is negligible variation in effect sizes between the two statistical approaches, and there is therefore little evidence to suggest that effects reported in this thesis have been either misinterpreted or over/under-represented.

5.6 Conclusions

In 1958, Charles S. Elton concluded his seminal publication with the following advice:

“*From now on, it is vital that everyone who feels inclined to change or cut away or drain or spray or plant any strip or corner of the land should ask themselves three questions: what animals and plants live in it, what beauty and interest may be lost, and what extra risk changing it will add to the accumulating instability of communities*”.

This advice holds true today, and recent studies stress the need to take carefully consider the ecological consequences of IAS removal (Wohl et al. 2015; Hopfensperger et al. 2017; Schlaepfer 2018). Riparian ecosystems are dynamic, diverse environments that facilitate change, and the removal of a particular riparian invader will not necessarily result in the restoration of pristine, “native” conditions. This thesis offers support for the careful and considered management of riparian INNP, particularly in areas where these plants are drivers of change. It also provides evidence of the range of responses of different riparian organisms to environmental and invasion pressures, and demonstrates that the severity of riparian INNP must be assessed relative to other (and perhaps more dominant) environmental and anthropogenic stressors. In particular, there is a need to assess species-level responses when planning management and restorative efforts, particularly when the organisms in questions may be able to adapt to the pressures that IAS exert.

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Supporting Information

Table S1 Study site characteristics.

Catchment	Catchment area (km²)	Study river	Site	Grid ref	Stream order	Invasive species	Invasive cover (%)	Distance from source (km)	Dominant 50m land use
Forth	1029	Argaty	1 – Native	NN 73986 03332	1st	None	0	2.5	Mixed woodland/Improved grass
			2 – Native	NN 73965 03257	1st	None	0	2.4	Improved grass
			3 – Invasive	NN 73974 03201	1st	*F. japonica*	60	2.3	Mixed woodland/Improved grass
			4 - Invasive	NN 74125 02505	1st	*F. japonica*	35	1.5	Mixed woodland
		Bannockburn	1 – Native	NS 80780 90449	3rd	None	0	8.7	Improved grass
			2 – Native	NS 80993 90508	3rd	None	3	8.5	Improved grass
			3 – Invasive	NS 81141 90715	3rd	*F. japonica*	35	8.2	Suburban
			4 - Invasive	NS 81245 91140	3rd	*I. glandulifera*	34	7.8	Suburban
Tay	4990	Dunning	1 – Native	NO 02050 14918	2nd	None	2	3.3	Tilled land
			2 – Native	NO 02035 15075	2nd	None	1	3.1	Tilled land
			3 – Invasive	NO 02552 17372	3rd	*I. glandulifera*	13	0.5	Tilled land
			4 - Invasive	NO 02586 17625	3rd	*I. glandulifera*	33	0.2	Tilled land
		Farg	1 – Native	NO 16284 15553	2nd	None	0	3.4	Improved grass
			2 – Native	NO 16168 15830	2nd	None	0	3.0	Tilled land
			3 – Invasive	NO 15972 16240	2nd	*I. glandulifera*	13	2.6	Scrub/Tall herbs/Tilled land
			4 - Invasive	NO 15772 16504	2nd	*I. glandulifera*	12	2.2	Suburban/Rough pasture
Nith	1230	New Abbey Pow	1 – Native	NX 95086 66385	3rd	None	0	6.6	Improved grass
			2 – Native	NX 95461 66419	3rd	None	0	6.2	Improved grass
			3 – Invasive	NX 96699 66398	3rd	*F. japonica*	50	4.7	Improved grass
			4 - Invasive	NX 96901 66109	3rd	*F. japonica*	51	4.1	Tilled land
South Esk	3350	Pow	1 – Native	NO 62889 55530	3rd	None	0	4.3	Tilled land
			2 – Native	NO 63026 55535	3rd	None	2	4.1	Tilled land
			3 – Invasive	NO 64303 56472	4th	*I. glandulifera*	40	2.4	Tilled land
			4 - Invasive	NO 64404 56531	4th	*I. glandulifera*	28	2.2	Tilled land

Table S2. Taxon list for freshwater macroinvertebrates, chapter 2.

Agapetus delicatulus

Agapetus fuscipes

Allogamus auricollis

Amphinemura sulcicollis

Ancylus fluviatilis

Annelida

Antocha spp.

Aphelocheiridae

Asellus aquaticus

Athripsodes spp.

Baetis fuscatus

Baetis muticus

Baetis niger

Baetis rhodani

Baetis scambus

Baetis vernus

Bathyomphalus contortus

Beraeodes minutus

Berosus spp.

Brachyptera risi

Caenis rivulorum

Capnia atra

Capnia bifrons

Capnia vidua

Ceratopogoninae

Chaetopteryx villosa

Chironomidae

Chloroperla torrentium

Chloroperla tripunctata

Clinocerinae

Collembola

Cordulegaster boltonii

Corixidae

Curculionidae

Dasyhelea spp.

Dicranota spp.

Dinocras cephalotes

Diura bicaudata

Dixidae

Drusus annulatus

Dryopidae

Dytiscidae

Ecclisopteryx guttulata

Ecdyonurus dispar

Ecdyonurus insignis

Ecdyonurus torrentis

Ecdyonurus venosus

Electrogena lateralis

Elmidae

Elminthidae

Elmis aenea

Elodes spp.

Empididae

Ephemera danica

Ephemerella notata

Ephydridae

Erpobdellidae

Esolus parallelepipedus

Forcipomyinae

Gammaridae

Glossiphoniidae

Glossosoma spp.

Goera pilosa

Gyraulus albus

Gyrinidae

Habrophlebia fusca

Halesus digitatus

Halesus radiatus

Hebridae

Helophorus spp.

Hydrachnidae

Hydraena spp.

Hydraenidae

Hydrophilidae

Hydroporinae

Hydropsyche angustipennis

Hydropsyche instabilis

Hydropsyche pellucidula

Hydropsyche siltalai

Hydroptilidae

Isoperla grammatica

Lepidostoma hirtum

Leuctra fusca

Leuctra inermis

Leuctra hippopus/moselyi

Limnebius spp.

Limnius volckmari

Limnophora spp.

Limoniinae

Lymnaea spp.

Mesophylax impunctatus

Mesovelia furcata

Nemoura cambrica

Nemoura cinerea

Neureclipsis bimaculata

Noteridae

Odontocerum albicorne

Oligochaeta

Oulimnius spp.

Paraleptophlebia spp.

Pedicia spp.

Perlodes mortoni

Philopotamus montanus

Piscicola geometra

Planariidae

Planorbis corneus

Platambus spp.

Plectrocnemia conspersa

Polycelis spp.

Polycentropus flavomaculatus

Potamophylax latipennis

Proasellus meridianus

Protonemura meyeri

Protonemura praecox

Psychodidae

Psychomyia pusilla

Rhabdiopteryx acuminata

Rhithrogena semicolorata

Rhyacophila dorsalis

Rhyacophila munda

Rhyacophila obliterata

Scirtidae

Sericostoma personatum

Serratella ignita

Sialidae

Silo pallipes

Simuliidae

Siphlonuridae

Sphaeriidae

Taeniopterygidae

Theodoxus fluviatilis

Tipulidae

Velia spp.

Wormaldia spp.

Table S3 Model selection summary for models with ΔAICc < 2, for each response variable. Models are ranked in order of decreasing AICc weight (W_i); models with a higher weighting carry more support. Log-likelihood ratios are also given

Response	Model parameters	logLik	AIC_c	Δ_i	W_i
Simpson's diversity	Channel shade + channel slope + depth*flow B-C + invasive cover + season	-203.94	392.92	0.00	0.38
	Channel slope + depth*flow B-C + invasive cover + season	-203.01	393.97	1.05	0.23
	Channel shade + channel slope + depth*flow B-C + invasive cover	-203.24	394.07	1.15	0.21
	Channel shade + channel slope + depth*flow B-C + invasive cover + season + substrate diversity	-206.20	394.42	1.50	0.18
WHPT	Channel shade + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + nº trees + channel shade*season + conductivity*season + depth*flow B-C*season + season*substrate diversity + season*nº trees	-346.63	674.41	0.00	0.43
	Channel shade + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + nº trees + channel shade*season + conductivity*season + depth*flow B-C*season + invasive cover*season + season*substrate diversity + season*nº trees	-347.67	675.06	0.65	0.31
	Channel shade + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + nº trees + channel shade*season + conductivity*season + depth*flow B-C*season + season*substrate diversity	-346.45	675.45	1.04	0.26
Abundance	Channel shade + invasive cover + season	-2286.02	4610.72	0.00	0.32
	Channel shade + invasive cover	-2290.37	4610.73	0.01	0.31
	Channel shade + conductivity + invasive cover + season	-2281.44	4611.24	0.53	0.24
	Channel shade + conductivity + invasive cover	-2286.53	4612.53	1.81	0.13
Spatial dissimilarity	Channel shade + channel slope + depth*flow B-C + invasive cover + season + substrate diversity + nº trees	532.47	-1113.96	0.00	0.52
	Channel shade + channel slope + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + nº trees	529.02	-1112.41	1.44	0.25
	Channel shade + channel slope + conductivity + depth*flow B-C + invasive cover + substrate diversity + nº trees	531.93	-1112.14	1.72	0.22

Table S4 Model selection summary for models with ΔAICc < 2, for each response variable. Models are ranked in order of decreasing AICc weight (W_i); models with a higher weighting carry more support. Log-likelihood ratios are also given.

Response	**Model parameters**	**logLik**	**AIC_c**	**Δ_i**	**W_i**
Simpson's diversity	*I. glandulifera* cover + *F. japonica* cover + Ell-Moisture + Ell-Light	-934.89	1877.77	0.00	0.52
	I. glandulifera cover + *F. japonica* cover + Ell-Light	-935.09	1878.94	1.18	0.29
	I. glandulifera cover + *F. japonica* cover + Ell-Moisture + Ell-Light + soil organic content	-935.58	1879.74	1.98	0.19
Total abundance	*I. glandulifera* cover + *F. japonica* cover + Ell-Light	2393.73	4821.71	0.00	0.29
	I. glandulifera cover + *F. japonica* cover + Ell-Moisture + Ell-Light	2390.74	4822.22	0.51	0.22
	I. glandulifera cover + *F. japonica* cover + Ell-Light + month	2390.53	4822.44	0.73	0.20
	I. glandulifera cover + *F. japonica* cover + Ell-Moisture + Ell-Light + month	2387.48	4822.64	0.94	0.18
	I. glandulifera cover + *F. japonica* cover + Ell-Light + natural land use at 50m	2391.10	4283.51	1.81	0.12
Spatial dissimilarity	*I. glandulifera* cover + *F. japonica* cover + Ell-Light + month	620.10	-1266.86	0.00	0.38
	I. glandulifera cover + *F. japonica* cover + site elevation + Ell-Light + month	616.06	-1265.28	1.59	0.17
	I. glandulifera cover + *F. japonica* cover + Ell-Light + month + tree density	615.97	-1265.04	1.82	0.15
	I. glandulifera cover + *F. japonica* cover + Ell-Moisture + Ell-Light + month	615.83	-1264.98	1.88	0.15
	I. glandulifera cover + *F. japonica* cover + Ell-Light + month + soil organic content	615.93	-1264.97	1.90	0.15
Gamma diversity	*I. glandulifera* cover + Ell-Moisture + soil organic content	16.55	-38.54	0.00	0.44
	I. glandulifera cover + *F. japonica* cover + Ell-Moisture + soil organic content	14.24	-37.19	1.35	0.22
	I. glandulifera cover + Ell-Moisture + soil organic content + tree density	14.22	-36.76	1.78	0.18
	I. glandulifera cover + Ell-Moisture	17.31	-36.55	2.00	0.16

Table S5 Model selection summary for models with ΔAICc < 2, for each response variable. Models are ranked in order of decreasing AICc weight (W_i); models with a higher weighting carry more support. Log-likelihood ratios are also given.

Response	**Model parameters**	**logLik**	**AIC_c**	**Δ_i**	**W_i**
M-C Ephemeroptera	Channel shade + *I. glandulifera* cover + Surber invertebrate abundance	-296.02	602.16	0.00	0.27
	I. glandulifera cover + Surber invertebrate abundance	-297.26	602.60	0.44	0.21
	I. glandulifera cover + Surber invertebrate abundance + native vegetation diversity	-296.45	603.01	0.85	0.17
	Channel shade + *I. glandulifera* cover + salmonid density + Surber invertebrate abundance	-295.73	603.62	1.46	0.13
	Channel shade + *I. glandulifera* cover + Surber invertebrate abundance + native vegetation diversity	-295.84	603.84	1.68	0.11
	Channel shade + *F. japonica* cover + *I. glandulifera* cover + Surber invertebrate abundance	-295.92	604.02	1.85	0.11
M-C Plecoptera	Salmonid density + Surber invertebrate abundance	-181.83	371.73	0.00	0.24
	I. glandulifera cover + salmonid density + Surber invertebrate abundance	-181.12	372.40	0.67	0.17
	F. japonica cover + salmonid density + Surber invertebrate abundance	-181.60	373.32	1.59	0.11
	Channel shade + salmonid density + Surber invertebrate abundance	-181.64	373.40	1.66	0.11
	Salmonid density + salmonid species + Surber invertebrate abundance	-181.75	373.62	1.89	0.09
	Salmonid density + Surber invertebrate abundance + native vegetation diversity	-181.87	373.68	1.95	0.09
	Drift invertebrate abundance + salmonid density + Surber invertebrate abundance	-181.78	373.68	1.95	0.09
	Channel shade + salmonid density	-182.81	373.69	1.96	0.09
M-C Trichoptera	*F. japonica* cover + fork length	-162.58	333.24	0.00	0.27
	F. japonica cover + fork length + native vegetation diversity	-162.07	334.27	1.03	0.16
	Fork length	-164.40	334.84	1.60	0.12
	F. japonica cover + fork length + Surber invertebrate abundance	-162.38	334.88	1.64	0.12
	F. japonica cover + fork length + *I. glandulifera* cover	-162.47	335.05	1.81	0.11

	Channel shade + *F. japonica* cover + fork length	-162.48	335.08	1.84	0.11
	F. japonica cover + fork length + salmonid density	-162.56	335.23	1.99	0.10
M-C Simuliidae	Channel shade + drift invertebrate abundance + salmonid density + salmonid species	-324.08	660.32	0.00	0.28
	Channel shade + drift invertebrate abundance + salmonid density + salmonid species + salmonid species*channel shade	-323.28	660.78	0.46	0.23
	Channel shade + drift invertebrate abundance + salmonid density + salmonid species + salmonid species*salmonid density	-323.76	661.74	1.42	0.14
	Channel shade + drift invertebrate abundance + *I. glandulifera* cover + salmonid density + salmonid species	-323.80	661.83	1.51	0.13
	Channel shade + drift invertebrate abundance + salmonid density + salmonid species + native vegetation diversity	-324.00	662.22	1.90	0.11
	Channel shade + drift invertebrate abundance + salmonid density + salmonid species + salmonid species*channel shade + salmonid species*salmonid density	-323.01	662.31	1.99	0.11
M-C Chironomidae	*I. glandulifera* cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-282.56	577.30	0.00	0.10
	I. glandulifera cover + salmonid species + native vegetation diversity	-283.61	577.35	0.05	0.09
	F. japonica cover + *I. glandulifera* cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-281.75	577.72	0.41	0.08
	F. japonica cover + *I. glandulifera* cover + salmonid species + native vegetation diversity	-282.96	578.09	0.79	0.07
	Channel shade + *I. glandulifera* cover + salmonid species + native vegetation diversity	-282.98	578.13	0.83	0.06
	Channel shade + *I. glandulifera* cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-282.10	578.43	1.13	0.06
	I. glandulifera cover + salmonid density + salmonid species + native vegetation diversity	-283.21	578.59	1.29	0.05

	Channel shade + *F. japonica* cover + *I. glandulifera* cover + salmonid species + native vegetation diversity	-282.22	578.66	1.36	0.05
	Channel shade + *F. japonica* cover + *I. glandulifera* cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-281.19	578.66	1.36	0.05
	I. glandulifera cover + salmonid species + Surber invertebrate abundance + native vegetation diversity + salmonid species**I. glandulifera* cover + salmonid species*Surber invertebrate abundance	-281.19	578.66	1.37	0.05
	I. glandulifera cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover + salmonid species*native vegetation diversity	-282.24	578.72	1.42	0.05
	F. japonica cover + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-281.26	578.82	1.52	0.05
	I. glandulifera cover + salmonid density + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-282.31	578.84	1.54	0.04
	F. japonica cover + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity	-282.32	578.86	1.56	0.04
	Drift invertebrate abundance + *I. glandulifera* cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover	-282.34	578.90	1.60	0.04
	I. glandulifera cover + salmonid species + Surber invertebrate abundance + native vegetation diversity + salmonid species**I. glandulifera* cover	-282.37	578.96	1.66	0.04
	I. glandulifera cover + salmonid species + native vegetation diversity + salmonid species*native vegetation diversity	-282.43	579.02	1.72	0.04
	F. japonica cover + *I. glandulifera* cover + salmonid species + native vegetation diversity + salmonid species**I. glandulifera* cover + salmonid species*native vegetation diversity	-281.43	579.15	1.85	0.04

M-C Gammaridae	Salmonid density + salmonid species + Surber invertebrate abundance + native vegetation diversity	-90.11	192.39	0.00	0.15
	Salmonid species + Surber invertebrate abundance + native vegetation diversity	-91.25	192.62	0.24	0.13
	Salmonid species + Surber invertebrate abundance	-92.79	193.65	1.27	0.08
	Salmonid density + Surber invertebrate abundance + native vegetation diversity	-91.78	193.67	1.29	0.08
	I. glandulifera cover + salmonid density + salmonid species + Surber invertebrate abundance + native vegetation diversity	-89.76	193.74	1.36	0.07
	Surber invertebrate abundance + native vegetation diversity	-92.84	193.75	1.37	0.07
	Channel shade + salmonid density + salmonid species + Surber invertebrate abundance + native vegetation diversity	-89.86	193.95	1.56	0.07
	Channel shade + salmonid species + Surber invertebrate abundance + native vegetation diversity	-90.90	193.98	1.59	0.07
	Drift invertebrate abundance + salmonid density + salmonid species + Surber invertebrate abundance + native vegetation diversity	-89.93	194.08	1.70	0.06
	Salmonid density + salmonid species + Surber invertebrate abundance	-92.00	194.11	1.72	0.06
	F. japonica cover + salmonid density + salmonid species + Surber invertebrate abundance + native vegetation diversity	-89.94	194.12	1.73	0.06
	I. glandulifera cover + salmonid density + Surber invertebrate abundance + native vegetation diversity	-91.89	194.34	1.95	0.05
	I. glandulifera cover + salmonid species + Surber invertebrate abundance + native vegetation diversity	-91.10	194.37	1.98	0.05
M-C Other	Fork length + Surber invertebrate abundance	-202.06	412.20	0.00	0.10
	Fork length + salmonid density + Surber invertebrate abundance	-201.09	412.30	0.10	0.09
	Fork length + salmonid density	-202.14	412.36	0.15	0.09
	Fork length + *I. glandulifera* cover + salmonid density	-201.28	412.68	0.48	0.08
	Fork length + *I. glandulifera* cover + Surber invertebrate abundance	-201.45	413.02	0.81	0.07

	Fork length + *I. glandulifera* cover + salmonid density + Surber invertebrate abundance	-200.64	413.45	1.25	0.05
	Fork length + salmonid density + salmonid species + Surber invertebrate abundance	-200.67	413.51	1.31	0.05
	Fork length + *I. glandulifera* cover	-202.75	413.59	1.39	0.05
	Channel shade + fork length + salmonid density	-201.78	413.69	1.48	0.05
	Drift invertebrate abundance + fork length + salmonid density	-200.81	413.78	1.58	0.05
	Fork length + salmonid species + Surber invertebrate abundance	-201.86	413.84	1.64	0.04
	Drift invertebrate abundance + fork length + Surber invertebrate abundance	-201.89	413.90	1.70	0.04
	F. japonica cover + fork length + salmonid density	-201.91	413.94	1.74	0.04
	Fork length + *I. glandulifera* cover + salmonid density + salmonid species	-200.93	414.03	1.83	0.04
	Fork length + salmonid density + salmonid species	-201.98	414.08	1.87	0.04
	Fork length + Surber invertebrate abundance + native vegetation diversity	-202.00	414.13	1.93	0.04
	F. japonica + fork length + Surber invertebrate abundance	-202.02	414.17	1.97	0.04
	Channel shade + fork length + salmonid density + Surber invertebrate abundance	-201.01	414.20	2.00	0.04
M-C Aerial	Drift invertebrate abundance + fork length + salmonid density + salmonid species + native vegetation diversity + salmonid species*fork length + salmonid species*native vegetation diversity	-179.70	377.76	0.00	0.08
	Drift invertebrate abundance + fork length + salmonid density + salmonid species + native vegetation diversity + salmonid species*native vegetation diversity	-180.85	377.99	0.23	0.07
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity + salmonid species*native vegetation diversity	-180.06	378.49	0.73	0.06
	Drift invertebrate abundance + fork length + salmonid density + salmonid species + native vegetation diversity + salmonid species*fork length + salmonid species*salmonid density + salmonid species*native vegetation diversity	-179.15	378.76	1.00	0.05
	Drift invertebrate abundance + fork length + salmonid density + salmonid species + salmonid species*fork length	-182.29	378.81	1.05	0.05

	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity + salmonid species*fork length + salmonid species*native vegetation diversity	-179.18	378.82	1.06	0.05
	Drift invertebrate abundance + fork length + salmonid density + salmonid species + salmonid species*fork length + salmonid species*salmonid density	-181.33	378.95	1.19	0.05
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*fork length + salmonid species*salmonid density	-180.37	379.11	1.35	0.04
	Drift invertebrate abundance + fork length + salmonid density + salmonid species + native vegetation diversity + salmonid species*salmonid density + salmonid species*native vegetation diversity	-180.40	379.18	1.42	0.04
	Channel shade + drift invertebrate abundance + fork length + salmonid density + salmonid species + native vegetation diversity + salmonid species*fork length + salmonid species*native vegetation diversity	-179.42	379.29	1.53	0.04
	Drift invertebrate abundance + *F. japonica* cover + fork length + salmonid density + salmonid species + salmonid species**F. japonica* cover + salmonid species*fork length	-180.48	379.33	1.57	0.04
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*salmonid density	-181.52	379.34	1.58	0.04
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*fork length	-181.53	379.35	1.59	0.04
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity + salmonid species*salmonid density + salmonid species*native vegetation diversity	-179.47	379.39	1.63	0.04

	Drift invertebrate abundance + fork length + salmonid density + salmonid species + Surber invertebrate abundance + native vegetation diversity + salmonid species*fork length + salmonid species*native vegetation diversity	-179.51	379.47	1.71	0.04
	Channel shade + drift invertebrate abundance + fork length + salmonid density + salmonid species + native vegetation diversity + salmonid species*native vegetation diversity	-180.58	379.52	1.76	0.03
	Fork length + salmonid density + salmonid species + salmonid species*fork length + salmonid species*salmonid density	-182.68	379.59	1.83	0.03
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity + salmonid species*fork length + salmonid species*salmonid density + salmonid species*native vegetation diversity	-178.54	379.59	1.86	0.03
	F. japonica cover + fork length + salmonid density + salmonid species + salmonid species**F. japonica* cover + salmonid species*fork length + salmonid species*salmonid density	-180.63	379.62	1.86	0.03
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species	-182.70	379.62	1.87	0.03
	Drift invertebrate abundance + *F. japonica* cover + fork length + salmonid density + salmonid species + salmonid species**F. japonica* cover + salmonid species*fork length + salmonid species*salmonid density	-179.62	379.63	1.93	0.03
	Fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*salmonid density	-182.74	379.69	1.94	0.03
	Fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*fork length + salmonid species*salmonid density	-181.71	379.72	1.96	0.03
	F. japonica cover + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species**F. japonica* cover + salmonid species*fork length + salmonid species*salmonid density	-179.64	379.74	1.98	0.03

Gut taxa diversity	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-989.30	1996.97	0.00	0.18
	Channel shade + drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-988.45	1997.34	0.37	0.15
	Channel shade + drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + Surber invertebrate abundance + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-987.50	1997.55	0.58	0.13
	Drift invertebrate abundance + *F. japonica* cover + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-988.96	1998.38	1.41	0.09
	Channel shade + drift invertebrate abundance + *F. japonica* cover + fork length + *I. glandulifera* + salmonid density + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-988.01	1998.56	1.60	0.08
	Channel shade + drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-989.07	1998.59	1.62	0.08
	Drift invertebrate abundance + *F. japonica* cover + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**F. japonica* cover + salmonid species**I. glandulifera* cover	-988.03	1998.60	1.63	0.08
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + Surber invertebrate abundance + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-989.11	1998.67	1.70	0.08

	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover + salmonid species*salmonid density	-989.23	1998.91	1.95	0.07
	Drift invertebrate abundance + fork length + *I. glandulifera* cover + salmonid density + salmonid species + native vegetation diversity + salmonid species*drift invertebrate abundance + salmonid species**I. glandulifera* cover	-989.25	1998.95	1.98	0.07

Table S6 Salmonid densities recorded during electrofishing surveys, August 2016.

Catchment	**River**	**Site**	***S. salar* density (per m^2)**	***S. trutta* density (per m^2)**	**Total salmonid density (per m^2)**
Forth	Argaty	1 – Native	0.00	0.79	0.79
		2 – Native	0.00	0.48	0.48
		3 – Invasive	0.00	0.77	0.77
		4 - Invasive	0.00	0.85	0.85
	Bannockburn	1 – Native	0.09	0.05	0.14
		2 – Native	0.22	0.10	0.32
		3 – Invasive	0.34	0.19	0.53
		4 - Invasive	0.18	0.11	0.29
Tay	Dunning	1 – Native	0.09	0.23	0.32
		2 – Native	0.10	0.34	0.44
		3 – Invasive	0.12	0.01	0.13
		4 - Invasive	0.08	0.02	0.09
	Farg	1 – Native	0.18	0.13	0.31
		2 – Native	0.33	0.23	0.56
		3 – Invasive	0.13	0.23	0.36
		4 - Invasive	0.15	0.32	0.47
Nith	New Abbey Pow	1 – Native	0.08	0.08	0.16
		2 – Native	0.18	0.06	0.23
		3 – Invasive	0.08	0.08	0.15
		4 - Invasive	0.10	0.10	0.19
South Esk	Pow	1 – Native	0.16	0.16	0.32
		2 – Native	0.00	0.02	0.02
		3 – Invasive	0.00	0.05	0.05
		4 - Invasive	0.01	0.02	0.04

Figure S1 Map of study sites with example for the New Abbey Pow sites inset.

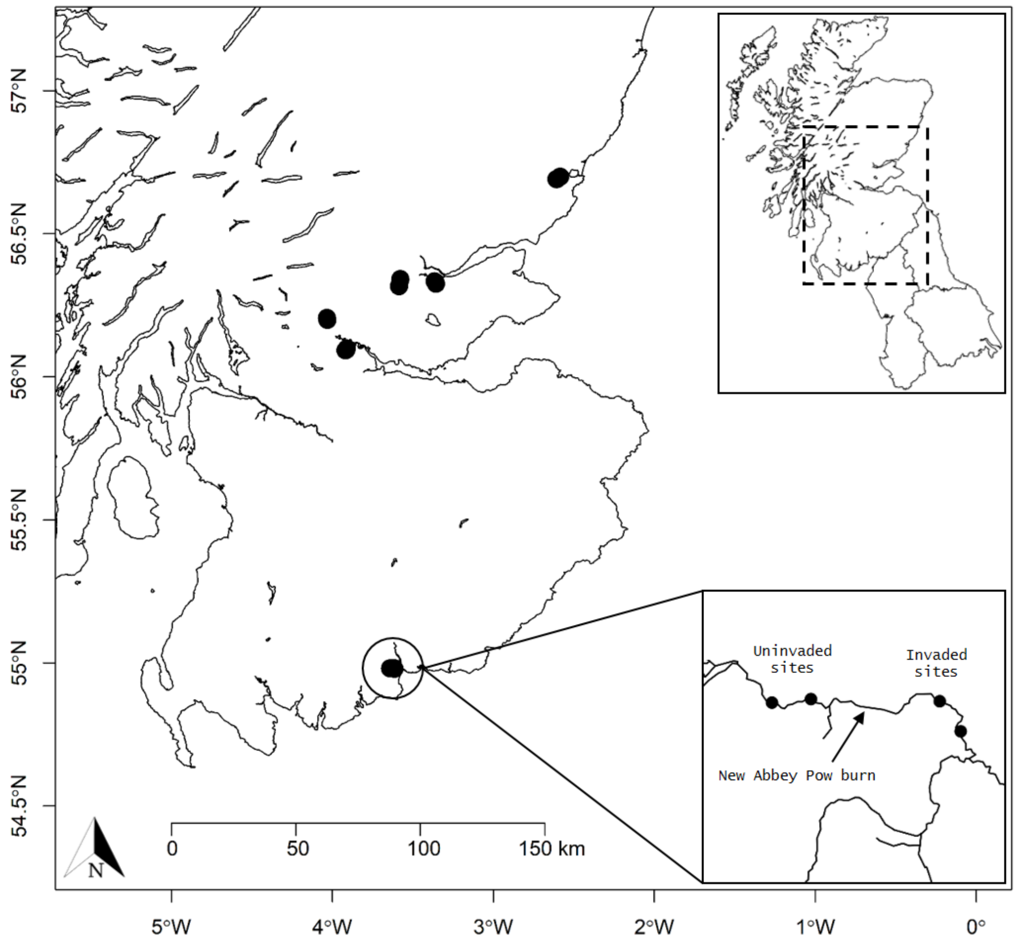

Figure S2 Non-metric multidimensional scaling ordination (NMDS) plot of macroinvertebrate species composition, comparing invaded (red polygon) and uninvaded (blue polygon) sites in spring across 24 riparian sites (stress=0.22).

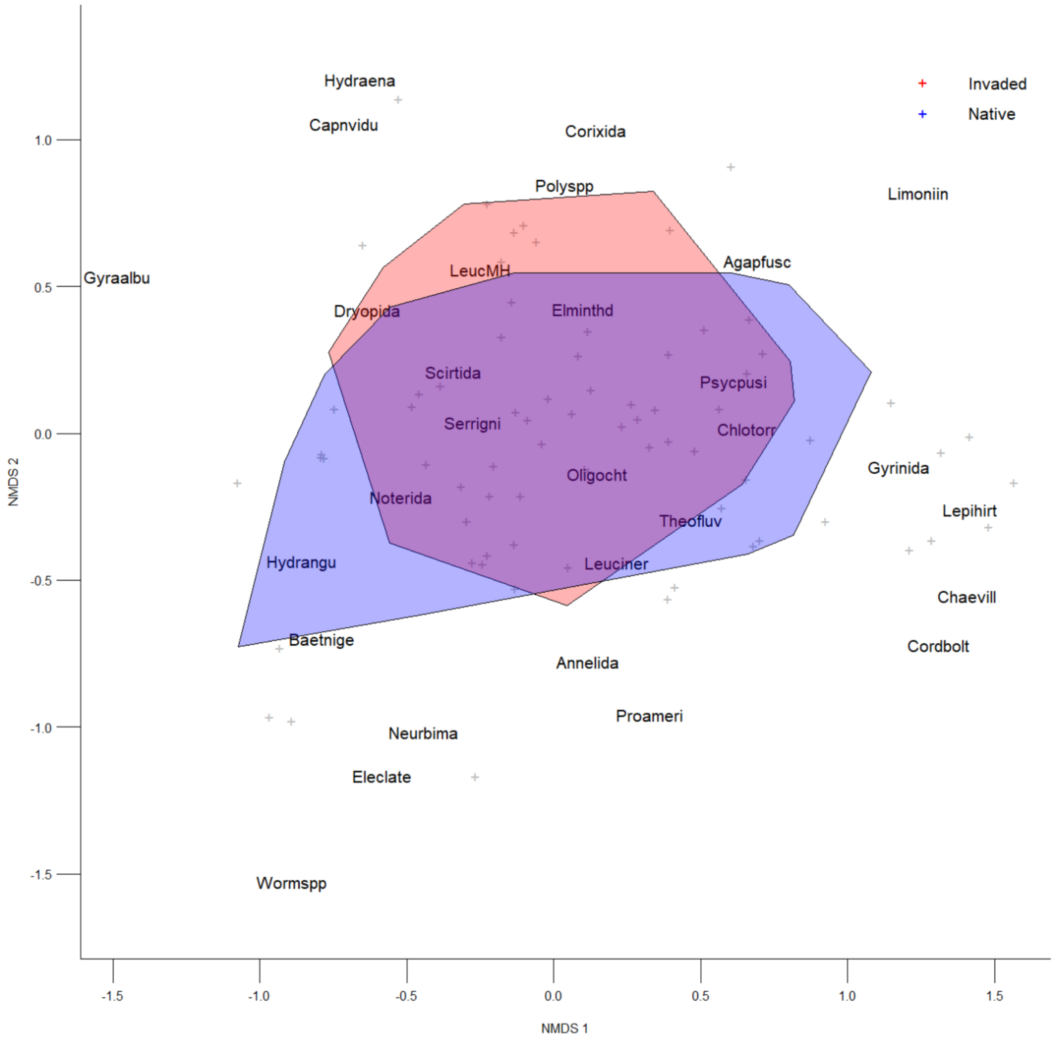

Figure S3 Non-metric multidimensional scaling ordination (NMDS) plot of macroinvertebrate species composition, comparing invaded (red polygon) and uninvaded (blue polygon) sites in autumn across 24 riparian sites (stress=0.22).

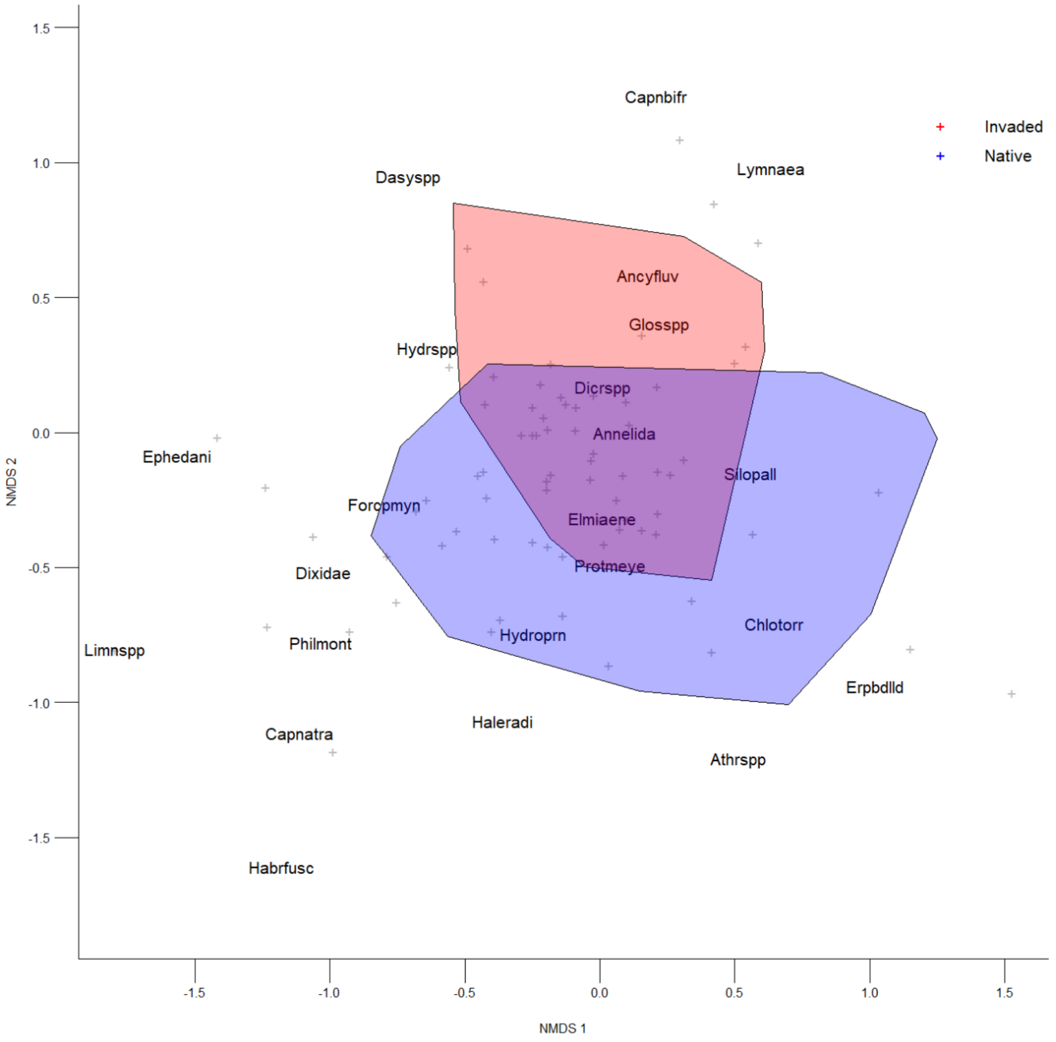

Figure S4 Redundancy analysis (RDA) ordination of macroinvertebrate communities in autumn. Environmental variables include conductivity (S/m) and invasive non-native species abundance (%).

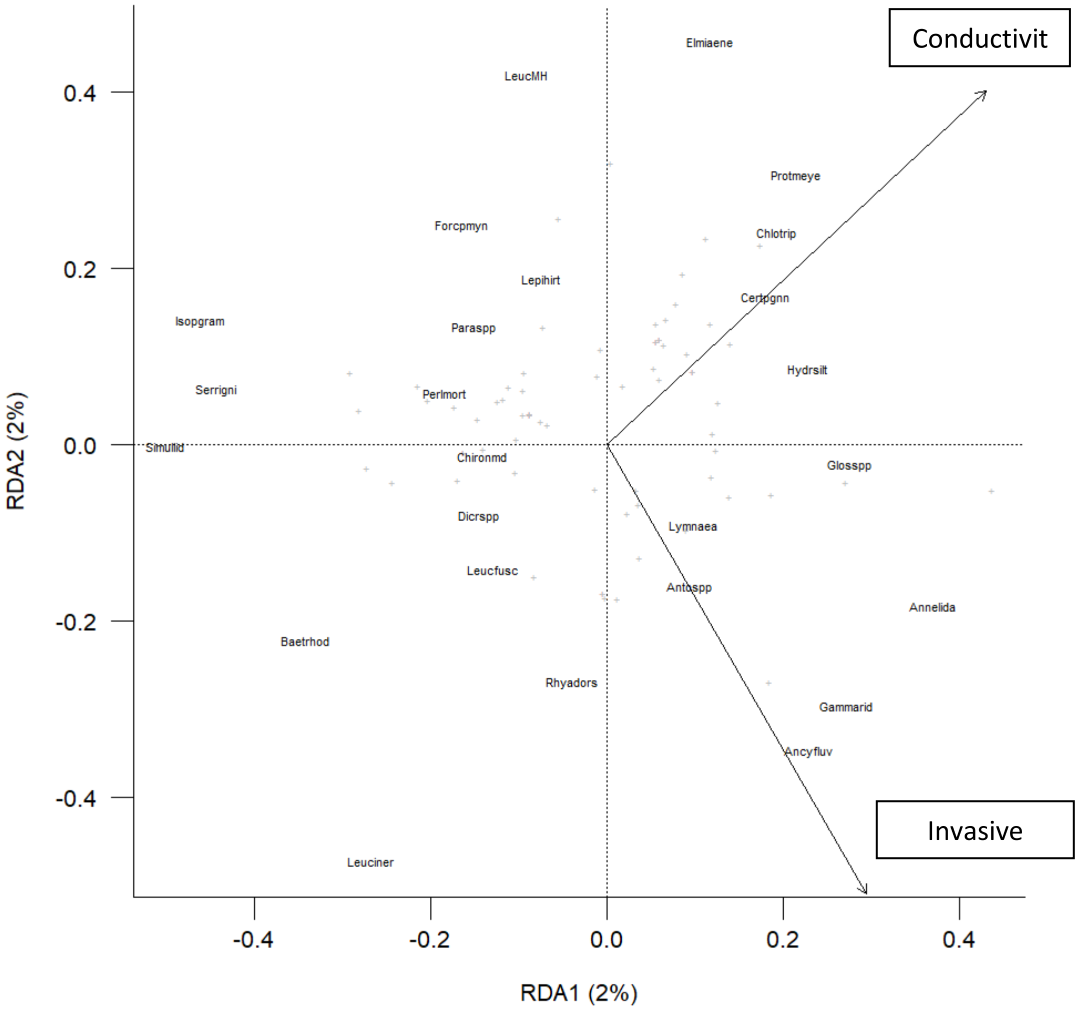

Figure S5 Spearman correlation analysis between the percentage of Ephemeroptera found in benthic Surber samples and the percentage of Ephemeroptera found in drift samples across study sites (shaded polygon shows ± 95% confidence intervals). R = 0.8, $p < 0.001$