

Stream invertebrate diversity reduces with invasion of river banks by non-native plants

Running head: Invertebrate response to invasive plants

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Keywords: diversity, *Fallopia japonica*, *Impatiens glandulifera*, invasive species, macroinvertebrates

Summary

1. Invasion of riparian zones by non-native plants is a global issue and commonly perceived as a challenge for river and fishery managers, but the type and extent of ecological changes induced by such invasions remain poorly understood. Established effects on sediment delivery, allochthonous inputs and channel shading could potentially alter aquatic macroinvertebrate assemblages, with implications for in-stream ecological quality.

2. We assessed responses in the diversity, quality and heterogeneity of stream macroinvertebrate communities to riparian invasion by non-native plants. Macroinvertebrates were collected from 24 sites on low order streams in central and southern Scotland during spring and autumn. The effect of invasive non-native plants (INNP) on macroinvertebrates was assessed relative to that of local physical and chemical factors.

3. INNP cover was associated with stronger effects than other factors on local diversity of macroinvertebrates (33% reduction at the highest INNP cover) but also increased macroinvertebrate abundance across sites. Invaded sites were also associated with lower macroinvertebrate biomonitoring scores. Community composition differed between invaded and uninvaded sites in autumn, but not in spring. However, INNP influence on macroinvertebrate composition was generally secondary to that of physicochemical variables (e.g. channel shade, substrate diversity).

4. We demonstrate that the influence of INNP extends beyond well-known impacts on plant communities to reductions mainly in stream macroinvertebrate diversity. Combined with the negative impact on pollution-sensitive macroinvertebrate taxa this raises concerns over the ecological health of streams with heavily invaded riparian zones. Our findings suggest that efforts to improve low order streams by actively managing severe riparian invasions are merited, but the size and uncertainty of the likely ecological gains must also be evaluated against the effort involved.

Introduction

Riparian zones are diverse, complex habitats that provide an ecologically important buffer between land and water, regulating the health and quality of the watercourses 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 & Rees, 2017) and promote long-term changes in macroinvertebrate community structure (Becker & Robson, 2009; Roon et al., 2014). 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 should 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 account of 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 & 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 (Laguerre 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. We hypothesised that changes to riparian vegetation caused by INNP would affect the composition of aquatic macroinvertebrate communities through changes to allochthonous inputs and by modifying local environmental conditions. We predicted that aquatic macroinvertebrate communities at sites with higher INNP cover would exhibit reduced diversity as a result of these physical and chemical changes.

Methods

Study sites

Sites were located on six low (1st to 4th) order streams (Strahler, 1957) in catchments across central and southern Scotland (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. There were 24 study sites in total (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.

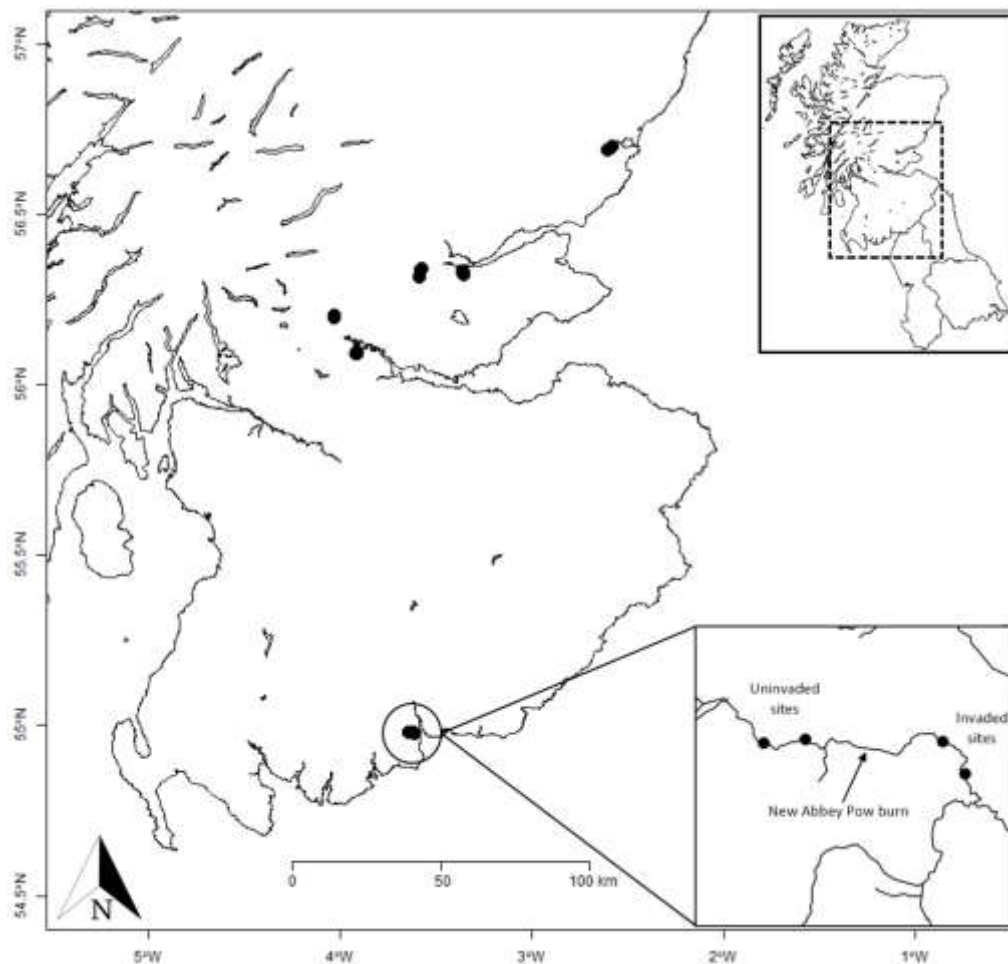


Figure 1. Map of study sites with example for the New Abbey Pow sites inset. Larger inset indicates general location of all study sites across central Scotland.

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 macroinvertebrate 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 macroinvertebrate 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 (Table S3).

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 individual sample 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 1m² 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

We focused on several metrics 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 widely used Biological Monitoring Working Party scoring system, was used to assess water quality. Values for this index range from 10 (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 1st sample to each of the rest, then the 2nd 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. We also considered the total number of individuals per sample as a measure of macroinvertebrate 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 $\Delta\text{AICc} < 2$ was set (Burnham & Anderson, 2002). From this top set (Table S2), 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 a product of the combined specificity and fidelity of aquatic macroinvertebrate species for invaded and uninvaded sites, after Dufrêne & Legendre (1997). 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).

Variation in macroinvertebrate species composition between invaded and uninvaded sites in spring and autumn samples was compared using non-metric multidimensional scaling (NMDS) (Kruskal & 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, we performed a redundancy analysis (RDA) by season, 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 AIC, to adhere to rules of model parsimony. We

also performed a PERMANOVA to assess the relative contribution of individual environmental variables to variance in macroinvertebrate community composition in each season (Table S4 and Table S5).

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).

Results

Response	Model parameters	R ² m	R ² c
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) + n° trees (1) + channel shade*season (1) + conductivity*season (1) + depth*flow B-C (1) + season*substrate diversity (1) + season*n° 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) + n° trees (1) + season (0.78) + conductivity (0.48)	0.19	0.64

Table 1 The best, fully-averaged models for models with $\Delta AICc < 2$. Relative variable importance is given in brackets, followed by marginal (R²m) and conditional (R²c) values.

Simpson's macroinvertebrate diversity

Macroinvertebrate diversity was positively associated with channel slope and negatively associated with habitat heterogeneity (Figure 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 2a and 3a), which had the greatest overall effect size (-0.13), with Simpson's macroinvertebrate diversity being on average 33% ($\pm 5.6\%$) 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 3b) and invasive cover (Figures 2b and 3b). Conductivity (-0.47) and season (0.23) had the greatest overall effects on WHPT score. Macroinvertebrate WHPT score was on average approximately 5% ($\pm 2.4\%$) lower at 60% invasive cover, compared to uninvaded sites. There was a positive interaction between season and conductivity, and season and channel shade. Greater 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 3c) and invasive cover (Figures 2c and 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% ($\pm 3.4\%$) 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 2d and 3d) and negatively associated with channel shade (Figure 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 contained 33% ($\pm 11.0\%$) more macroinvertebrate individuals than uninvaded sites. No other variables were significant and there was no evidence of any seasonal interaction.

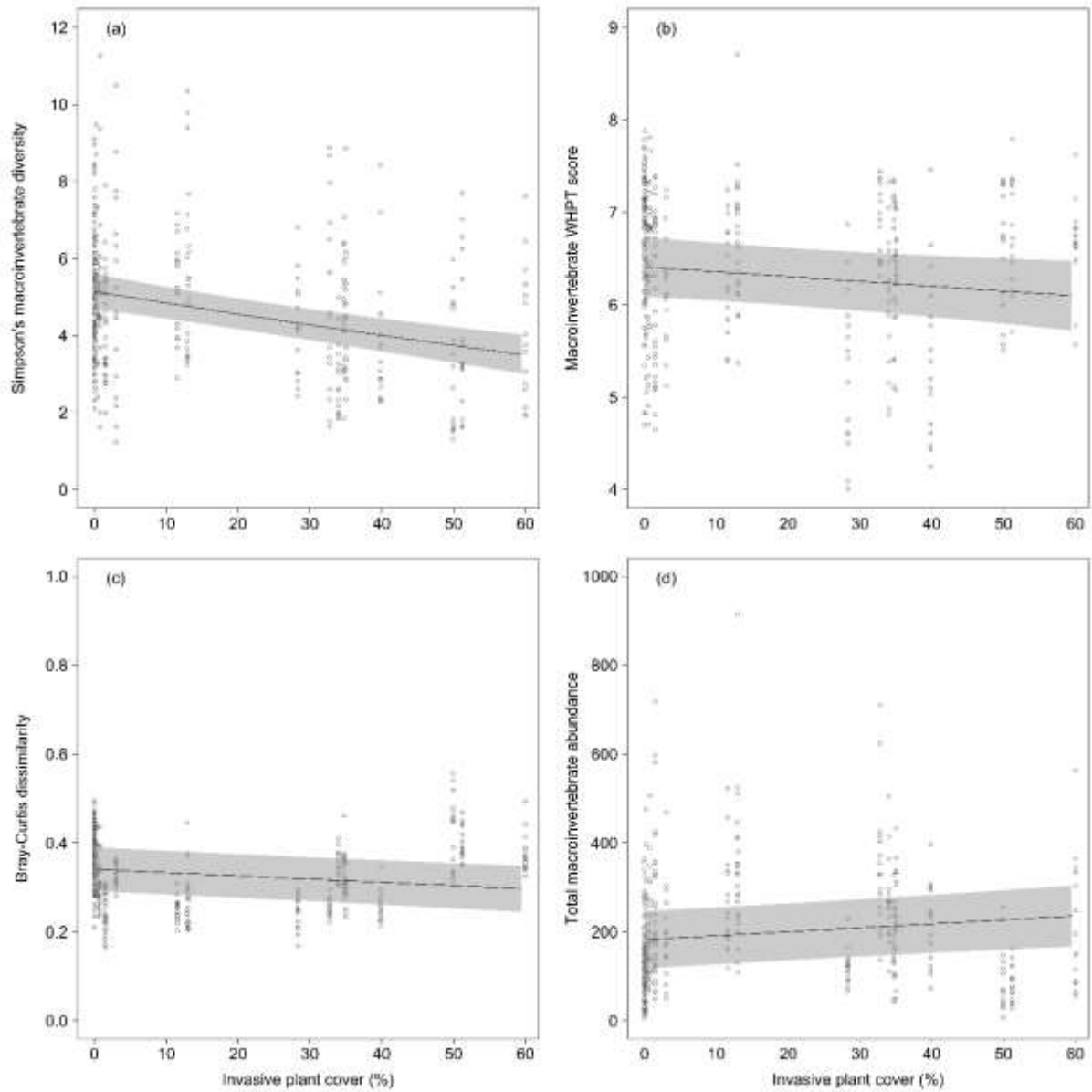


Figure 2. Full model predicted values (shaded polygon shows $\pm 95\%$ confidence intervals) from the LMM analyses of (a) Simpson's macroinvertebrate diversity, (b) macroinvertebrate WHPT score, (c) spatial dissimilarity for individual Surber samples and (d) total macroinvertebrate abundance for individual Surber samples, all plotted against invasive cover.

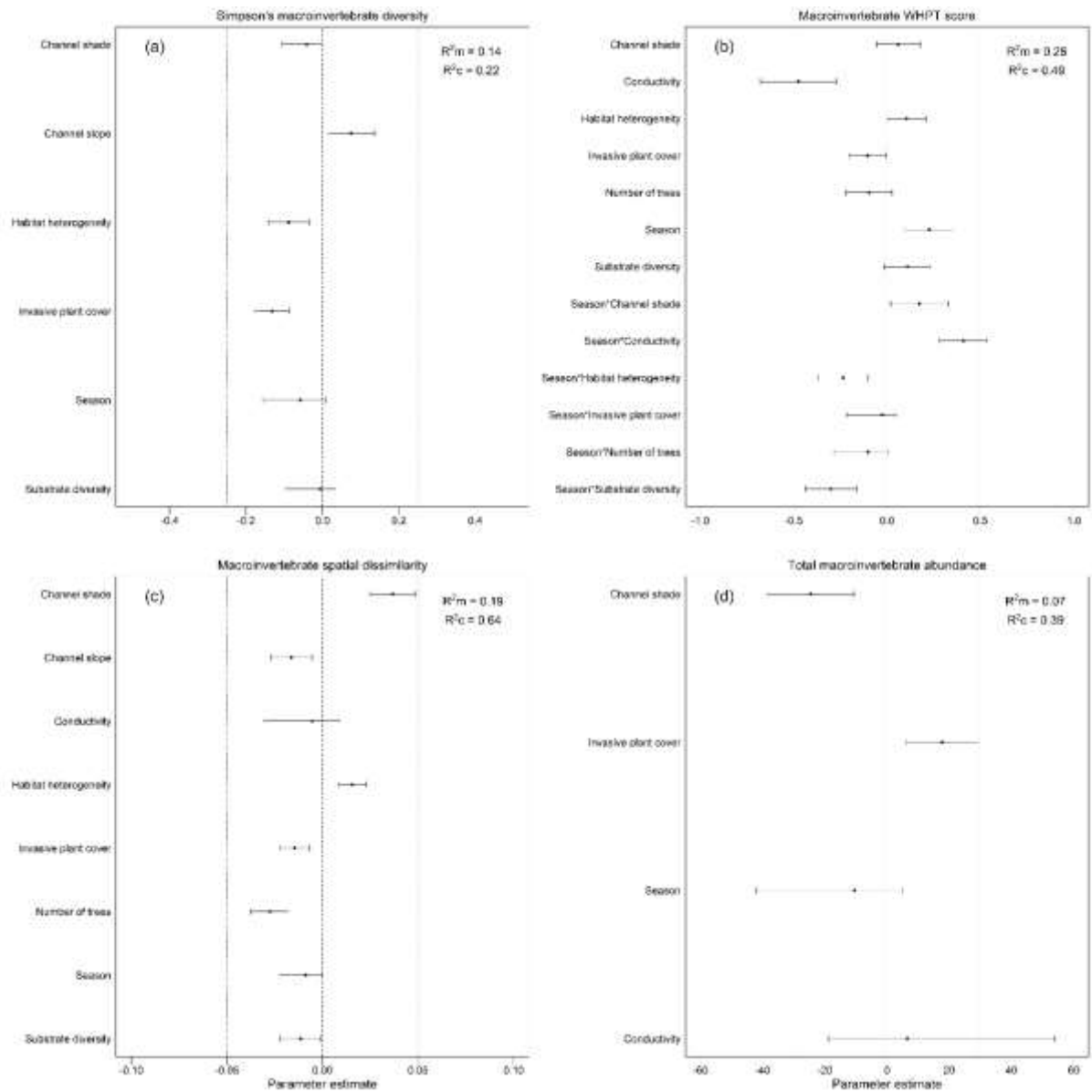


Figure 3. Full, model-averaged parameter estimates \pm 95% confidence intervals. Modelled responses were (a) Simpson's macroinvertebrate diversity, (b) macroinvertebrate WHPT score, (c) spatial dissimilarity for individual Surber samples and (d) total macroinvertebrate abundance. Marginal (R^2_m) and conditional (R^2_c) values are given.

Indicator species

Site type	Species	Observed IV	Biological/ecological trait group	Functional feeding group
Invaded, spring	<i>Serratella ignita</i> ***	0.63	f/C1	Deposit feeder
	Gammaridae***	0.56	b1/C1	Shredder
	<i>Dicranota</i> spp.***	0.50	c1/D1	Predator
	Elminthidae***	0.37	e3/B1	Scraper
	<i>Drusus annulatus</i> ***	0.26	f/A	Shredder
	<i>Ancylus fluviatilis</i> *	0.21	e2/C1	Scraper
	<i>Ecclisopteryx guttulata</i> *	0.13	f/A	Shredder
Uninvaded, spring	<i>Baetis rhodani</i> **	0.47	e2/C1	Scraper
	<i>Rhyacophila dorsalis</i> *	0.40	c1/B2	Predator
	<i>Lepidostoma hirtum</i> ***	0.16	f/C1	Grazer
	<i>Rhyacophila munda</i> *	0.06	c1/B2	Predator
Invaded, autumn	<i>Dicranota</i> spp.**	0.55	c1/D1	Predator
	Gammaridae*	0.46	b1/C1	Shredder
	<i>Silo pallipes</i> ***	0.44	e2/B1	Scraper
	<i>Limnius volckmari</i> ***	0.37	e3/B1	Scraper
	<i>Ecclisopteryx guttulata</i> *	0.36	f/A	Shredder
	<i>Ancylus fluviatilis</i> ***	0.35	e2/C1	Scraper
	<i>Lymnaea</i> spp.*	0.17	c2/F3	Scraper
	<i>Baetis scambus</i> *	0.12	e2/C1	Scraper
	<i>Paraleptophlebia</i> spp.**	0.12	f/C1	Deposit feeder
Uninvaded, autumn	<i>Hydropsyche siltalai</i> *	0.36	e1/C1	Filter feeder
	<i>Protonemura meyeri</i> ***	0.33	f/A	Shredder
	<i>Amphinemura sulcicollis</i> *	0.21	f/A	Shredder
	<i>Capnia bifrons</i> **	0.14	e2/B2	CPOM feeder
	<i>Philopotamus montanus</i> **	0.08	e2/A	Filter feeder

Table 2 Significant indicator species for invaded and uninvaded sites. Observed IV shows the Indicator Value (a product of fidelity and specificity (Dufrêne & Legendre, 1997)) for each species (0 = no fidelity or specificity; 1 = complete fidelity and specificity). Asterisks indicate the probability of that IV 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 & Giller, 2000.

A larger number of macroinvertebrate taxa were significantly associated with invaded sites compared to uninvaded sites in both spring and autumn (Table 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 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.

Macroinvertebrate community composition

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

Our 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 (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. PERMANOVA indicated consistently high relative importance of conductivity and substrate diversity on variance in macroinvertebrate community composition, and these two variables were responsible for more than half of the variance explained by environmental variables in both spring and autumn (Table S4 and S5).

Discussion

Effects on macroinvertebrate metrics

Riparian INNP cover had the strongest association with Simpson's macroinvertebrate diversity compared to other measured environmental variables 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). Additionally, 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 & Brazier, 2008), and homogenising sediments through fine sediment ingress (Burdon et al., 2013). However, our PSI analysis suggested that the

benthic habitat at most sites in this study were minimally or only slightly sedimented, offering no evidence to link macroinvertebrate community response to INNP cover via channel sedimentation. Nevertheless, whilst the actual process of change remains undetermined, our 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 & 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 line 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. We suggest that 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). However, it seems that overall, despite some clearly negative effects on macroinvertebrates, riparian INNP cover explains a relatively small amount of variation in macroinvertebrate community structure and is distinctly secondary to other environmental factors in this regard.

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 reducing 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 & D'Antonio, 2017), and certain treatment or removal approaches may themselves adversely affect native biota (Flory & Clay, 2009; Kettenring & 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

We 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 we cannot exclude the possibility that some other unmeasured but causal pressure covaried closely with INNP cover, the effects we report are consistent with impacts reported 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 our study demonstrates negative associations between INNP cover and macroinvertebrate communities, these effect sizes were often relatively 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.

Authors' Contributions

All authors conceived the ideas and designed the methodology; AS, CB, NW and ZP collected the data; AS and ZP analysed the data; AS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We gratefully acknowledge financial support from Scottish Natural Heritage. Fergus McFarlane and Jack Shelton assisted with the collection and processing of macroinvertebrate samples. The authors declare they have no conflict of interest regarding this manuscript.

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Appendices

Table S1. Study site characteristics

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

Table S2. Model selection summary for models with $\Delta AIC_c < 2$, 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 + n° trees + channel shade*season + conductivity*season + depth*flow B-C*season + season*substrate diversity + season*n° trees	-346.63	674.41	0.00	0.43
	Channel shade + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + n° trees + channel shade*season + conductivity*season + depth*flow B-C*season + invasive cover*season + season*substrate diversity + season*n° trees	-347.67	675.06	0.65	0.31
	Channel shade + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + n° 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 + n° trees	532.47	-1113.96	0.00	0.52
	Channel shade + channel slope + conductivity + depth*flow B-C + invasive cover + season + substrate diversity + n° trees	529.02	-1112.41	1.44	0.25
	Channel shade + channel slope + conductivity + depth*flow B-C + invasive cover + substrate diversity + n° trees	531.93	-1112.14	1.72	0.22

Table S3. Taxon list

<i>Agapetus delicatulus</i>	<i>Drusus annulatus</i>
<i>Agapetus fuscipes</i>	Dryopidae
<i>Allogamus auricollis</i>	Dytiscidae
<i>Amphinemura sulcicollis</i>	<i>Ecclisopteryx guttulata</i>
<i>Ancylus fluviatilis</i>	<i>Ecdyonurus dispar</i>
Annelida	<i>Ecdyonurus insignis</i>
<i>Antocha</i> spp.	<i>Ecdyonurus torrentis</i>
<i>Aphelocheiridae</i>	<i>Ecdyonurus venosus</i>
<i>Asellus aquaticus</i>	<i>Electrogena lateralis</i>
<i>Athripsodes</i> spp.	Elmidae
<i>Baetis fuscatus</i>	Elminthidae
<i>Baetis muticus</i>	<i>Elmis aenea</i>
<i>Baetis niger</i>	<i>Elodes</i> spp.
<i>Baetis rhodani</i>	Empididae
<i>Baetis scambus</i>	<i>Ephemera danica</i>
<i>Baetis vernus</i>	<i>Ephemerella notata</i>
<i>Bathyomphalus contortus</i>	Ephydriidae
<i>Beraeodes minutus</i>	Erpobdellidae
<i>Berosus</i> spp.	<i>Esolus parallelepipedus</i>
<i>Brachyptera risi</i>	Forcipomyinae
<i>Caenis rivulorum</i>	Gammaridae
<i>Capnia atra</i>	Glossiphoniidae
<i>Capnia bifrons</i>	<i>Glossosoma</i> spp.
<i>Capnia vidua</i>	<i>Goera pilosa</i>
Ceratopogoninae	<i>Gyraulus albus</i>
<i>Chaetopteryx villosa</i>	Gyrinidae
Chironomidae	<i>Habrophlebia fusca</i>
<i>Chloroperla torrentium</i>	<i>Halesus digitatus</i>
<i>Chloroperla tripunctata</i>	<i>Halesus radiatus</i>
Clinocerinae	Hebridae
Collembola	<i>Helophorus</i> spp.
<i>Cordulegaster boltonii</i>	Hydrachnidae
Corixidae	<i>Hydraena</i> spp.
Curculionidae	Hydraenidae
<i>Dasyhelea</i> spp.	Hydrophilidae
<i>Dicranota</i> spp.	Hydroporinae
<i>Dinocras cephalotes</i>	<i>Hydropsyche angustipennis</i>
<i>Diura bicaudata</i>	<i>Hydropsyche instabilis</i>
Dixidae	<i>Hydropsyche pellucidula</i>

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

Mesovelica 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 oblitterata

Scirtidae

Sericostoma personatum

Serratella ignita

Sialidae

Silo pallipes

Simuliidae

Siphonuridae

Sphaeriidae

Taeniopterygidae

Theodoxus fluviatilis

Tipulidae

Velia spp.

Wormaldia spp.

Table S4. Relative contribution of environmental predictors to variance in spring macroinvertebrate community composition.

Environmental variable	Variance explained (%)
Conductivity	10.7***
Substrate diversity	9.7***
Depth*flow B-C	2.8***
Channel shade	2.7***
Invasive cover	2.5***
Number of trees	2.1***
Channel slope	1.3**

Table S5. Relative contribution of environmental predictors to variance in autumn macroinvertebrate community composition.

Environmental variable	Variance explained (%)
Conductivity	10.1***
Depth*flow B-C	8.7***
Substrate diversity	5.0***
Channel shade	3.1***
Invasive cover	2.7***
Number of trees	1.8***
Channel slope	1.3***

Figure S1. 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)

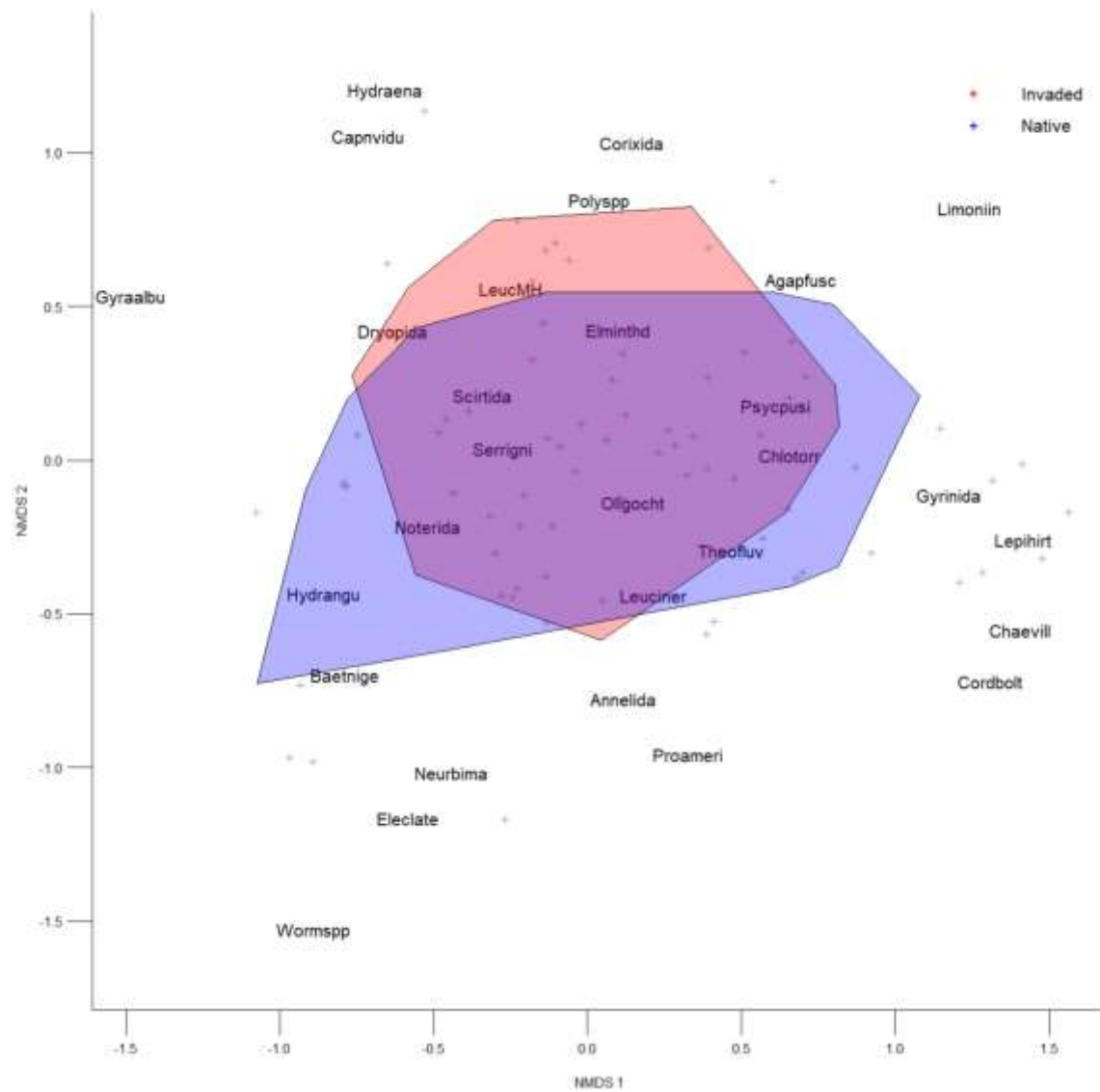


Figure S2. Non-metric multidimensional scaling ordination (NMDS) plot of macroinvertebrate species composition, comparing invaded (red polygon) and uninvaded (blue polygon) sites in autumn across 24 riparian sites (stress=0.22)

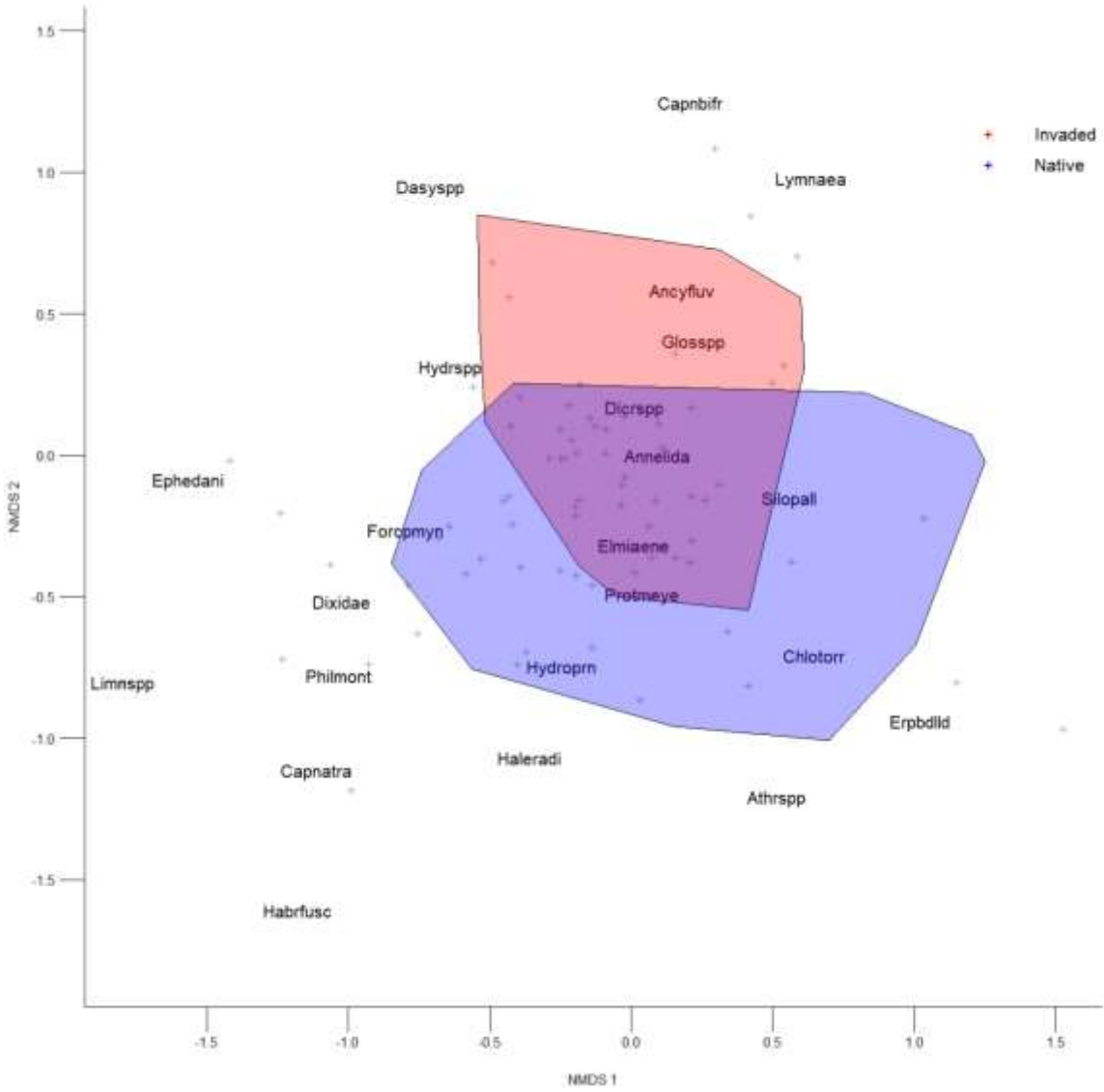


Figure S3. Redundancy analysis (RDA) ordination of macroinvertebrate communities in autumn.
Environmental variables include conductivity (S/m) and invasive non-native plant cover (%)

