



Leaf breakdown rates as a functional indicator were influenced by an invasive non-native invertebrate in urban ponds

Ian Thornhill^{a,b,*}, Nikolai Friberg^{c,d,e}, Lesley Batty^a, Victoria Thamia^a, Mark E. Ledger^a

^a School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, West Midlands B15 2TT, United Kingdom

^b School of Sciences, Bath Spa University, Newton St. Loe, Bath BA2 9BN, United Kingdom

^c Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway

^d water@leeds, School of Geography, University of Leeds, Leeds LS2 9JT, United Kingdom

^e Freshwater Biological Section, University of Copenhagen, DK-2100 Copenhagen, Denmark

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ABSTRACT

Impacts on biodiversity and the functioning of ecosystems are often overlooked in small waterbodies as they are not regularly monitored as part of the Water Framework Directive (WFD). These small systems are, however, often essential for freshwater biodiversity and are frequently characterized by high beta-diversity. In this study we examined shredder diversity and ecosystem functioning (leaf litter breakdown) as indicators of environmental stress along a gradient of urbanisation. The native isopod *Asellus aquaticus* and the non-native shrimp *Crangonyx pseudogracilis* (Amphipoda) were dominant species of the shredder communities in 26 study ponds. Variation in shredder community composition among ponds was explained by pond surface area ($P < 0.05$) and the coverage of impermeable surface within 500 m ($P < 0.05$), indicative of urban impact, which was strongly, and negatively correlated with shredder richness. Site mean total leaf breakdown was 0.0020 k d^{-1} (range $0.0003 - 0.0053$), whilst breakdown rates owing to microbial and fungal activity were lower and averaged 0.0010 k d^{-1} (range $6.72 \times 10^{-5} - 0.0036$). Both total and microbial activity driven breakdown rates showed relatively weak relationships with the environmental gradient reflecting degrees of urbanization. A model-averaging procedure suggested that total litter breakdown rates could be attributed to activity of shredders with *A. aquaticus* and *C. pseudogracilis* contributing most, explaining 65% of the variance ($R^2 = 0.65$, $F = 13.7$, $P < 0.001$), which both significantly and similarly predicted total leaf breakdown rates ($P < 0.05$). Total leaf breakdown rates were significantly correlated with the densities of both *C. pseudogracilis* ($P < 0.001$) and *A. aquaticus* ($P < 0.001$), however partial correlations indicated that the former showed the strongest association.

The process of urbanisation can have significant, and negative impacts upon freshwater ecosystems, including small water bodies such as ponds both regarding biodiversity and ecosystem functioning. The findings of the current study suggest that ecosystem functioning indicators such as leaf litter decomposition should be paired with structural measures. This is because function sustained by tolerant invading species would not otherwise be detected, and their presence is increasingly likely due to climate change and urbanization.

1. Introduction

Freshwater ecosystems are amongst the most vulnerable, experiencing biodiversity losses above those recorded in terrestrial systems (Sala et al., 2000; Vörösmarty et al., 2010). Concern for the degradation of freshwater systems has been recognised at an international policy level, such as through the adoption of resolution 58/217 'Water for Life' between 2005 and 2015 by the UN (United Nations, 2003) and implementation of the Water Framework Directive (European Commission,

2000); although the latter only affords protection to larger still waters (lakes greater than 50 ha). A key contributing factor to these losses in biodiversity is the process of urbanisation and previous research indicates that high levels of urbanization can reduce macroinvertebrate and macrophyte diversity due to a cocktail of local and landscape-scale factors (Oertli and Parris, 2019; Walsh et al., 2005). Similarly, urbanisation represents a threat to key ecosystem services provided by these freshwater ecosystems, such as freshwater supply, flood mitigation, carbon storage, and soil fertility (Eigenbrod et al., 2011). Such impacts

* Corresponding author at: School of Sciences, Bath Spa University, Newton St. Loe, Bath BA2 9BN, United Kingdom.

E-mail address: i.thornhill@bathspa.ac.uk (I. Thornhill).

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are the result of major changes associated with urbanisation that include greater concentrations and varieties of pollutants in runoff, more extreme hydrology as a result of increased runoff conveyance, increased water temperatures, reduced habitat complexity, restricted interactions between the water bodies and their catchments and the introduction of exotic species (McKinney, 2008; Miguel-Chinchilla et al., 2019; Oertli and Parris, 2019; Paul and Meyer, 2001).

1.1. Leaf breakdown rates as indicators of ecosystem functioning

Understanding the impact of human interventions upon freshwater biodiversity loss and ecosystem functioning has emerged as a pressing concern since the turn of the century (Wenger et al., 2009) and has implications not only for ecosystem functioning, but also the resilience of freshwater ecosystems in the face of global environmental change (Chapin et al., 2000; Gerisch, 2014). Well established structural indices based on biological diversity (Magurran, 2004) or pollution tolerance (Wright et al., 1998) have been used to assess ecosystem health. However, in the past decades, the link between biodiversity and ecosystem functioning (BEF) has been explored along gradients in human degradation in running waters by measuring the key functional process of leaf-litter processing (Chauvet et al., 2011; Imberger et al., 2008; Paul et al., 2006). For many freshwater systems (especially rivers) terrestrial inputs of leaf litter are a critical basal resource (Allan, 1995) and the rate at which leaf litter is broken down has frequently been used to measure ecosystem response to disturbance (Gessner and Chauvet, 2002; Hladysz et al., 2010). However, much less still is known about the breakdown rate of terrestrial litter in lentic (still water) ecosystems along environmental stress gradients.

For small lentic ecosystems (e.g. ponds) leaf decomposition studies are confined to mesocosm experiments (e.g. Brady and Turner 2010), wetland (Tiegs et al., 2013), stormwater (Mackintosh et al., 2016) and woodland (Oertli, 1993) ponds, and the littoral zones of large lakes (Bjelke, 2005; Francis et al., 2007; Pabst et al., 2008). Francis et al. (2007) found that shredders (aquatic invertebrates feeding on leaves; Graça 2001) were typically in higher abundance in undeveloped lake-shores compared to those adjacent to residences suggesting an influence of urbanisation, however land-use impacts are generally unclear (Francis et al., 2007) and differences in decomposition rates may be potentially masked by increase in nutrient (phosphorus) availability resulting in high microbial activity (Tiegs et al., 2013). By contrast, shredder efficiency appears to decrease under low oxygen conditions (Bjelke, 2005; Mackintosh et al., 2016) and increase with pH (Harbourd et al., 2015). Thus, knowledge to this end, particularly from field experiments is severely lacking for still water systems.

Indicators of ecosystem functioning have been shown to be sensitive to a range of stressors across urbanisation gradients including nutrient concentrations, the removal of native vegetation, temperature, flow and stream gradient (Clapcott et al., 2012). Considering leaf breakdown rates, feeding trait detritivore shredders have not been recorded in some urban stream macroinvertebrate (Paul et al., 2006) and populations of other functional groups (e.g. gatherers, scrapers and filterers) can be low (Roy et al., 2003). However, leaf litter processing responses vary across systems. For example, breakdown rates increased with urbanisation in tributaries of the Chattahoochee River (Meyer et al., 2005) and streams in both Melbourne (Imberger et al., 2008) and north-western Portugal (Del Arco et al., 2011). In contrast, Chadwick et al. (2006) found that peak breakdown rates coincided with intermediate levels of urbanisation and several studies found no detectable change across urban gradients (Huryn et al., 2002; Sponseller et al., 2001). A critical factor in these assessments may be the prevalence of multiple species whose function overlaps, thus providing redundancy, which is suggested to be able to retain ecosystem functioning in streams to a certain level of stress, after which function will decline (Woodward et al., 2012).

1.2. The role of invasive species in disturbed environments

Biological invasions are numerous in freshwaters around the world (Strayer, 2010) and with urbanisation comes a high risk of invasion from non-native species whose introduction is facilitated by anthropogenic vectors (Ehrenfeld, 2008; Vermonden et al., 2010). For example, more than 90% of species listed in the Global Invasive Species Database (<http://www.issg.org/database>), are either associated with urban areas, water (e.g. rivers, ponds, lakes) or both (Hassall, 2014). Recently, there is increased interest in the role of non-native species in the context of biodiversity and ecosystem functioning. In freshwaters, Truhlar et al. (2014) suggested that wider temperature tolerances exhibited by the non-native invasive shrimp *Dikerogammarus villosus*, when compared to the native *Gammarus pulex*, could maintain leaf litter breakdown rates during seasonal temperature extremes. Moreover, several studies have identified similar potential for non-native species (Gammaridae and *Crangonyx pseudogracilis*) to exhibit wider physical and chemical tolerance (e.g. salinity and warmer temperature) when compared to native species (MacNeil et al., 1999; Vermonden et al., 2009). Thus, highly tolerant non-native shredder species may be able to persist in degraded systems where native species are absent. Such tolerance is also exhibited by other non-native taxa better able to adapt to stressors associated with urban environments than native counterparts, such as birds and fish (McDonnell and Hahs, 2015), amphibians (Brown and Walls, 2013) and reptiles (Price-Rees et al., 2012).

1.3. Urban ponds as model ecosystems

Ponds in urban areas are hotspots for ecosystem services, providing storm water management and treatment (Briers, 2014; Hill et al., 2016), nutrient cycling (Thornhill et al., 2018), cultural value (Wood and Barker, 2000) and can support biological communities of high conservation value (Hassall, 2014; Thornhill et al., 2017a). Thus, it is imperative that studies are carried out that seek to assess ecosystem responses along a gradient of urbanisation in order to inform ecosystem-based management action (Lapointe et al., 2014) and to suggest appropriate tools to assess these responses to improve ecosystem health.

1.4. Hypotheses

Our overall aim was to understand how the link between biodiversity and ecosystem functioning is impaired in ponds under the combined pressure of urbanization and invasive species. Multiple stressors are the rule rather than the exception in freshwater ecosystems (e.g. Jackson et al., 2016) and provides one of the most important challenges for future biomonitoring. We employed structural and functional indicators within a known pond network across a gradient of anthropogenic stress caused by urbanisation and with the presence of diverse macro-invertebrate assemblages and the non-native amphipod *C. pseudogracilis* (Thornhill et al., 2017a), which is now widespread across Western Europe having first been recorded in England in 1936 (Crawford, 1937). We used diversity of the shredder guild as our structural (diversity) indicator and leaf litter decomposition rates as our functional indicator. We hypothesized that 1) the diversity of the shredding guild would decrease along a gradient of ecosystem disturbance as a result of urbanisation, and that the invasive species *C. pseudogracilis* would be more frequent in the most perturbed ponds, 2) that ecosystem functioning would be reduced in the most impacted ponds because of the loss of species. We based this hypothesis on the findings of Woodward et al. (2012) showing, in streams, that species redundancy can only retain ecosystem functioning (leaf litter decomposition) to a certain level of stress after which function will decline. However, we speculated that the presence of *C. pseudogracilis* could influence breakdown rates along the stress gradient as it is a shredder and potentially more pollution tolerant than native *Gammarus* species (Vermonden et al., 2010).

2. Methods

2.1. Study area

The Birmingham conurbation comprises of Birmingham city, and four boroughs; Wolverhampton, Dudley, Sandwell and Walsall, in the Midlands region of the UK (Fig. 1). The area is dominated by built-up areas and gardens (suburban), dense urban areas and transport infrastructure, improved grassland, including parks and gardens, agricultural land, woodland and other habitats (Owen et al. 2006). Water bodies include ponds, reservoirs, shallow lakes (e.g. Sutton Park), reservoirs, canals, rivers and streams. Ponds are widely dispersed across the region, most of which are artificial and built for ornamental or infrastructure purposes (Thornhill et al., 2017b). Dominant tree species within 10 m of the pond edges were grey (*Salix cinerea*) and crack (*Salix fragilis*) willow, hawthorn (*Crataegus* spp.) and silver birch (*Betula pendula*); beech (*Fagus sylvatica*) typically accounted for <1% of the mature tree community.

2.2. Study design

Thirty ponds were selected that were known to hold water for at least four consecutive months, and were of a surface area between 2 m² and 20,000 m² (2 ha) (Pond Conservation Group, 1993) (Table 1; Fig. S1). These sites were selected to stratify a gradient of urban land-uses classes after Owen et al. 2006 (see also Thornhill et al., 2017a), from heavily urbanised city centres, to rural villages that were reflective of the Birmingham conurbation. In order to consider potential influences upon differences observed we also recorded a suite of physical characteristics and chemical measures in each pond. The use of fine and coarse mesh

Table 1

Summary of selected physical and chemical variables. For a full list, see [Supplementary Material Table S1](#).

Variable	Mean ± 1SD (min. – max)	Unit
Chemical		
pH	7.72 ± 0.46 (6.71–8.54)	–
Temperature	17.8 ± 1.53 (15.0–21.4)	°C
Dissolved oxygen	47.4 ± 31.6 (10.9–118.5)	%
Nitrate	0.72 ± 1.65 (0.0–6.71)	mg/L
Phosphate	0.54 ± 0.68 (0.02–2.46)	mg/L
Physical		
Shading	33.8 ± 32.1 (0.00–100)	% cover
Fringing vegetation	11.7 ± 13.7 (0.00–41.4)	% cover
Floating vegetation	4.78 ± 10.0 (0.00–47.2)	% cover
Macrophyte richness	7.04 ± 5.58 (0.00–20.0)	n taxa
Water depth fluctuation	388.9 ± 1116 (4.15–4698)	WLF
Fish presence	0.42 ± 0.50 (0–1)	0–1
Surface area	3211 ± 3579 (299–14920)	m ²
Land-use		
IS 100 m	13.3 ± 10.1 (0.0–32.4)	% cover
IS 500 m	26.4 ± 10.8 (3.0–48.2)	% cover
IS 1000 m	29.9 ± 11.3 (7.1–51.9)	% cover

bags allowed separation of microbial and macroinvertebrate driven breakdown with mesh bags being employed in each pond for one 80 days period. Macroinvertebrates were collected only from coarse mesh bags and not from naturally occurring pond habitats. This was done to reduce variability in macroinvertebrate composition that otherwise would be introduced by differences in pond hydromorphology across the sites investigated.

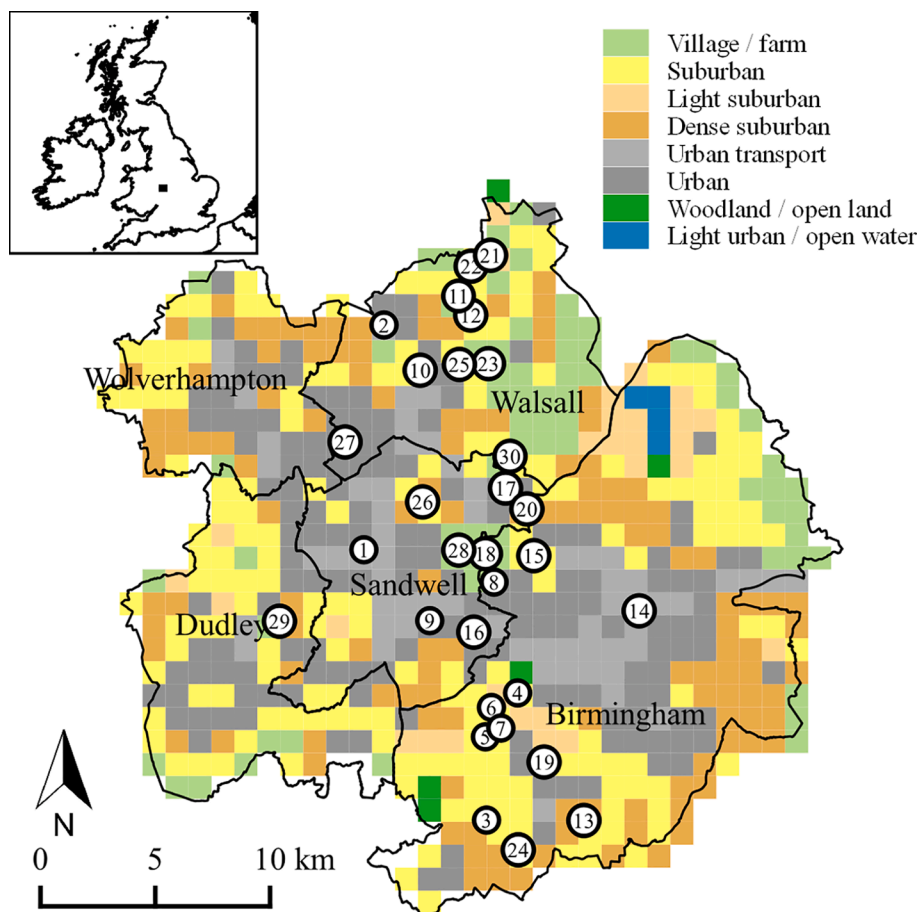


Fig. 1. The West Midlands conurbation (Birmingham, Wolverhampton, Dudley, Sandwell and Walsall) (study extent) with land-use classes after Owen et al. (2006) and sites displayed, and United Kingdom context (inset).

2.3. Leaf decomposition

A leaf litter breakdown experiment was carried out in late summer 2010 between July – October (four months) to encompass natural fall periods. On 11th December 2009, abscised beech (*F. sylvatica*) leaves were sourced from Winterbourne Botanical Gardens, Edgbaston, Birmingham to be used as an assay for the experiment. The leaves were air-dried in laboratory conditions on the same day of collection. Beech was selected as a native tree to temperate northern Europe.

To consider the relative contribution of microbial and macroinvertebrate activity to leaf breakdown rates, leaf packs (15 cm × 15 cm) of differing size plastic mesh were constructed to exclude or include macroinvertebrates (Boulton and Boon, 1991). To this end, fine and coarse leaf packs had 0.25 mm and 5 mm mesh respectively, each containing 5 g (±0.05 g) of beech leaves. Three replicate pairs (one fine and one coarse bag in each pair) of leaf packs were attached to a small brick weight, and attached to the bank side by a peg and fishing line if necessary. Bags were placed on top of pond sediments and at similar depths (~0.5 m) in all sites. Macroinvertebrates were removed upon retrieval and the remaining leaves were gently cleaned and dried to constant mass at 105 °C in an oven, and weighed to the nearest 0.001 g.

2.3.1. Leaf mass loss corrections

First, to correct for moisture content in air-dried leaves, the oven-dry weight (105 °C, 48 h) of 10 g of non-experimental beech leaves was recorded. A conversion factor (*m*) was then calculated by dividing the oven-dry mass by the air-dry mass and applied to the initial air-dried mass of all experimental leaf packs (*d_i*). Second, to correct for leaching losses (the loss of soluble organic and inorganic compounds) 10 g of non-experimental leaves were submersed in deionised water for 72 h and the oven-dry (105 °C, 48 h) weight recorded. This conversion factor (*l*) was then calculated from the non-experimental packs as: post-leaching oven-dry mass / (air-dry mass × *m*) and applied to *d_i*. Third, to correct for the non-organic, ash component of leaves, one conversion factor was calculated and applied to the initial air-dry leaf mass (*d_i*), and one to the oven-dry leaf mass remaining after submersion (*d_r*). The first (*a₁*) corresponds to the mean remaining weight of 5 × 0.5 g (±0.025 g) samples of non-experimental leaf reduced in a muffle-furnace at 550 °C for two hours. The second (*a₂*) used the same method for *a₁* but using a subsample of 0.5 g (±0.025 g) of remaining leaf litter from each experimental leaf pack post-submersion. The post furnace ash mass was then divided by the oven dried mass in both instances and applied as conversion factors (*a₁*, *a₂*). Leaf breakdown rates were thus corrected for ash content, leaching processes and initial moisture content.

2.3.2. Calculation of leaf processing rate

The exponential decay coefficient *-k* (Petersen and Cummins, 1974) was used to calculate processing rates for each leaf bag. This standard measure of decomposition rate assumes that there is a constant fractional loss of material at any given time, therefore allowing processing rates to be comparable among different aquatic systems. As a single extraction experiment, we assumed that leaf decomposition rates would accord to logarithmic regression (i.e. rapid initial loss of mass, which slows over time), as is frequently observed in freshwater environments (e.g. Hladysz et al., 2010). *-k* was calculated following the formula.

$$-k = \frac{\ln\left(\frac{d_r \times a_2}{d_i \times a_1}\right)}{d} \quad (1)$$

Alternatively as:

$$-k = \frac{\ln(AFDM_r / AFDM_i)}{d} \quad (2)$$

where in Eq. 1, *d_r* is the mass remaining in grams of the leaf pack once removed from the pond and *d_i* is the initial mass in the leaf pack in grams prior to submersion. Time (*d*) was expressed as the number of days submersed. In Eq. 2, *AFDM_r* is the ash-free dry mass of the leaf litter

remaining post-experiment and *AFDM_i* is the ash-free dry mass prior to submersion. Breakdown rates were calculated for total breakdown (macroinvertebrate and microbial breakdown) in the coarse bags (*k_{total}*) and microbial only breakdown in the fine mesh bags (*k_{micro}*). For simplicity, *-k* rates are expressed positively hereafter.

2.4. Macroinvertebrate processing

Four of the 30 sites did not return any leaf packs and were assumed discarded or removed by passers-by or fauna, thus 26 sites remained studied. All recovered leaf packs were collected after a mean of 80 days submersion, transferred to plastic bags, and stored at -15 °C. In the laboratory, leaves were removed from each pack and rinsed over a 0.5 mm sieve, and any macroinvertebrates sorted from leaf debris identified and counted. Macroinvertebrates were identified to the lowest practicable taxonomic unit (Table S2), counted and classified to functional feeding groups (FFG) after Tachet et al. (2010). Macroinvertebrates may be classified to several FFGs using Tachet et al. (2010), however, the FFG to which the taxa had highest affinity i.e. highest rank, was selected. All taxa with at least some shredding capacity were included in the analyses.

2.5. Explanatory variables

The concentration of major ions and trace metals was determined from 50 ml water samples collected from each pond in June and August 2010 from just below the water's surface at the inflow, outflow and midpoint on each sampling occasion. This allowed for an overall, and comparable, characterisation of physical-chemical conditions. These conditions were assumed to be representative for the pond and hence to location of leaf bags. Samples were filtered (1.2 µm Whatman GF/C) and stored at -20 °C with samples for trace metals acidified to pH 2 using nitric acid. Anions were measured using a Dionex ICS2000 (Cl, NO₃, PO₄³⁻, SO₃) and cations measured with a Dionex DX500 (Dionex Corporation, CA, USA) (Na, NH₃, K, Mg, Ca). Titration (to pH 4.5) was used to determine alkalinity (HACH, Dusseldorf, Germany). Trace metals (Mg, Zn, Mn, Fe) were quantified using a Perkin Elmer AA300 (Perkin Elmer, MA, USA).

A separate 5L water sample was also collected for determination of suspended solids and chlorophyll *a*. Suspended solids were determined as the freeze-dried mass (mg) of material filtered (Whatman GF/C, 1.2 µm pore size) from each sample. Chlorophyll *a* (mg/L) was determined using spectrophotometry using standard methods (Jeffrey & Humphrey, 1975). Dissolved oxygen (% saturation), pH and electrical conductivity (µS/cm) were also measured in the field commensurate to water sampling using a YSI 556 handheld multi-probe meter (YSI, OH, USA).

Additional physical parameters were recorded from a combination of aerial imagery in an ArcGIS 9.3 Geographical Information System (ESRI, Redlands California), and field notes. These were pond surface area (ha) and the percentage of area classified as having fringing (e.g. *Typha* spp.) or floating vegetation (e.g. *Nymphaea* spp.), was shaded or open water, and percentage of hard-engineered pond bank (e.g. sheet piling). Stakeholder consultations and site investigations determined the presence or absence of fish. Indicative rates of water level fluctuation (WLF) were calculated as the standard deviation of water depth at fixed points sampled during spring, summer and autumn of 2010. Total macrophyte richness was determined as a count of plant taxa within mesohabitats (Biggs et al., 1998). Macrophytes (free floating, submerged, emergent or floating) were usually identified to species level (Haslam et al., 1995).

A number of previous pond studies have identified a distance of 100 m (Declerck et al., 2006; Thornhill et al., 2017a; Williams et al., 2010), 500 m (Williams et al., 1998) and 1 km (Hill et al., 2016) from the pond edge as being most correlated with both water quality and macroinvertebrate assemblages. Therefore the extent of urbanisation was characterised within each of these distances (100 m, 500 m 1 km) by calculating the percentage cover of impermeable surface (roads,

pavements, buildings and other hardstandings) using OS Mastermap (OS, 2008) and ArcGIS 9.3 which has previously been found to strongly correlate with other commonly used urbanisation indicators (Hahs and McDonnell, 2006).

2.6. Statistical methods

The relationship between the shredder assemblage and environmental variables was examined using redundancy analysis (RDA) in the package 'vegan' (Oksanen et al., 2018). A forward and backward stepwise selection procedure was used to select the best model and environmental variables that significantly ($P < 0.05$) explained the variance in the relative abundance of taxa within the shredder assemblage using the 'ordistep' function in vegan, which uses permutation-based significance tests (999 permutations). We also characterized beta-diversity of the shredder assemblage using the package 'betapart' (Baselga et al., 2018) to divide the overall Sorensen beta-diversity into nested and turnover components.

Multiple linear regression was used to establish which members of the shredding invertebrate community were associated with k_{total} . Leaf breakdown rates were square-root transformed and shredder counts (averaged across leaf packs) were logged to fit model assumptions (see Table S1). A model-averaging approach was used to establish the most important predictors of leaf breakdown rate using the package 'MuMin' (Barton, 2018). Model combinations within a dredge procedure were restricted to three predictors in order to retain statistical power. The three most important members of the shredder community as identified by the model averaging procedure within the 95th percentile confidence interval model set (after Burnham and Anderson, 2002) were then validated in a separate multiple linear regression model and the residuals checked for model validity. Linear regression was carried out in R Statistical Software (R Core Team, 2019), for partial Pearson correlations to control for the influence of one or more other variables, the package 'ppcor' was used (Kim, 2015).

3. Results

3.1. Leaf breakdown rates

Microbial and fungal activity typically contributed $\sim 50\%$ (min. 5.6%, max 100%) to k_{total} . Site mean total leaf breakdown rates (coarse mesh) were $0.0020 k$ (range 0.0003–0.0053), whilst breakdown rates owing to microbial and fungal activity (fine mesh) averaged $0.0010 k$ (range 6.72×10^{-5} –0.0036). Thus, mean total mass loss due to the action of both macroinvertebrates and microbes was 14.1% (range 2.0%–30.5%) and per day 0.18% (range 0.007%–0.601%). Mean mass loss due to the action of microbes only was 7.7% (range 0.4%–24.8%) and per day 0.10% (range 0.006%–0.292%). There was no association between the extent of urbanisation and leaf breakdown rate (Fig. S1).

3.2. Shredder community composition

A total of 64 taxa were identified within retrieved leaf packs with Gastropoda (13 species) and Trichoptera (12 species) the most diverse groups represented. Scrapers and shredders were the most abundant FFGs comprising on average 33% and 29% of the macroinvertebrate assemblages recorded. Thirteen macroinvertebrate taxa were identified from within the coarse mesh leaf packs with known shredding traits, of which ten had a higher affinity for shredding than for other feeding habits. Total beta-diversity (Sorensen) was 0.88, comprised of a large species turnover component (0.59) and less nestedness (0.30). The diversity of shredder taxa decreased significantly along the urbanisation gradient (impermeable surface coverage within 100 m, 500 m or 1000 m). The strongest correlation was found between total shredder taxa and urbanisation within 500 m (Pearson's -0.70 , $P < 0.001$, Fig. S2).

Most frequently observed taxa with a high affinity for shredding

were *Asellus aquaticus* (Isopoda) and the non-native shrimp *C. pseudogracilis* (Amphipoda), which occurred at 24 (92.3%) and 16 (61.5%) sites respectively with densities of up to 96.7 (mean 19.3) and 36.6 (mean 4.0) individuals g AFDM^{-1} and thus, represented the majority of the shredder community. The native amphipod *Gammarus pulex* was only identified at two sites (17, 23). At these typically peri-urban sites *G. pulex* occurred at low densities (max. 1.5 individuals g AFDM^{-1}), lower than densities of *C. pseudogracilis* (max. 5.6) with which it cohabited.

In a redundancy analysis of the shredder community data and environmental parameters the majority of the explained variance (49.7%) was accounted for on RDA axis 1 (Fig. 2), which was highly significant ($F = 21.8$, $P = 0.001$) (Table 2). Stepwise selection of environmental parameters identified two significant physical and land-use variables correlated with the first two RDA axes respectively: pond surface area and the coverage of impermeable surface within 500 m (each $P < 0.05$) (Table 3). RDA indicated that the majority of variation in the shredder community was due to the dominance of *A. aquaticus* and *C. pseudogracilis*. A number of environmental variables were correlates of pond surface area: pH ($\rho 0.68$, $P < 0.05$), dissolved oxygen ($\rho 0.62$, $P < 0.05$), shading ($\rho -0.58$, $P < 0.05$), temperature ($\rho 0.52$, $P < 0.05$), and with impermeable surface cover within 500 m: hard engineered perimeter ($\rho 0.62$, $P < 0.05$) and macrophyte richness ($\rho -0.41$, $P < 0.05$) (Table S3).

3.3. Macroinvertebrate associations with breakdown rate

Following a model-averaging procedure three shredder species were included in a multiple linear regression (Table S4). The final regression model ($k_{\text{total}} \sim A. aquaticus$ ($\beta 0.40$, $P < 0.05$) + *C. pseudogracilis* ($\beta 0.39$, $P < 0.05$) + *P. corneus* ($\beta 0.25$, $P > 0.05$)) explained 65% of the variance ($R^2 = 0.65$, $F = 13.7$, $P < 0.001$) and it was found that both *A. aquaticus* and *C. pseudogracilis*, significantly and similarly predicted k_{total} .

A strong association was identified between shredder diversity and leaf breakdown rates (k_{total} ; Fig. 3a). Similarly, a strong association was observed between shredder density (all 14 shredder taxa) and k_{total} (Fig. 3b). However, k_{total} was most strongly correlated with the densities (g AFDM^{-1}) of *C. pseudogracilis* (Pearson adj. $R^2 0.63$, $P < 0.001$; Fig. 3d) and *A. aquaticus* (Pearson adj. $R^2 0.43$, $P < 0.001$; Fig. 3c) whose populations covaried significantly (Pearson adj. $R^2 0.59$, $P < 0.05$). Thus, partial correlations were carried out to identify the strength of the correlation between k_{total} and *C. pseudogracilis* whilst controlling for the effect of *A. aquaticus* (Pearson $r 0.58$ $P < 0.001$) and vice versa (Pearson $r 0.45$ $P < 0.05$), thus indicating a closer association of leaf decomposition rates to *C. pseudogracilis* densities.

4. Discussion

Our study suggests that increasing urbanisation had a negative impact on ponds, including a loss in the diversity of shredders and giving a competitive advantage to a non-native species in the most deteriorated water bodies (accept hypothesis 1). The replacement of native shredders with the non-native *C. pseudogracilis* partly decouples the biodiversity-ecosystem functioning link, thereby reducing effects of urban impact on the functional indicator used (leaf-litter decomposition rates). As a consequence, ecosystem functioning was at least partly sustained along the degradation gradient because of the presence of an invasive species, maybe limiting impacts of urbanisation on transformation of organic matter and hence energy transfer through the pond food web (reject hypothesis 2). In the context of biomonitoring and our ability to detect multiple stressors, this study strongly suggests that a combination of structural and functional indicators are needed to detect ecosystem impacts.

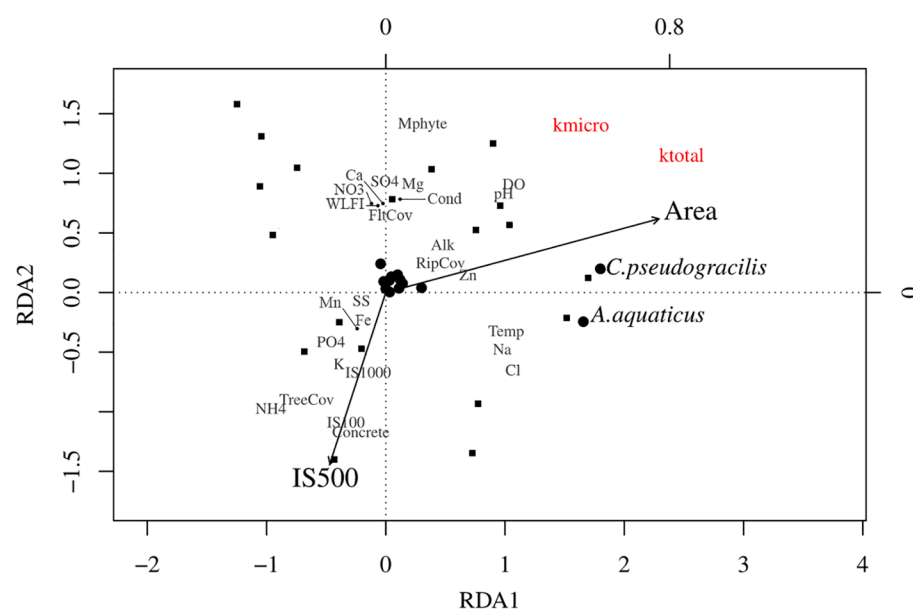


Fig. 2. Redundancy analysis plot for shredder community constrained by environmental variables (variance explained = 49.7%, ANOVA $P = 0.001$, 999 permutations). Significant ($P < 0.05$) environmental variables (with eigenvectors) were selected through forward and backward stepwise selection procedure: Pond surface area (Area, $P = 0.005$) and impermeable surface coverage within 500 m (IS500, $P = 0.03$). Filled squares and dots represents sites and species respectively. All other non-significant variables are displayed in grey, and k rates superficially fitted (i.e. not as part of the RDA).

Table 2

Summary statistics for RDA of shredder community constrained by environmental variables (variance explained = 49.7%).

	RDA 1	RDA 2
Eigenvalues	3.15	0.13
Proportion explained	0.96	0.04
Cumulative proportion explained	0.96	1.00
F	21.8	0.87
P	0.001	0.423

Table 3

Variables significantly correlated to RDA axes 1 and 2 of shredder community constrained by environmental variables (variance explained = 49.7%) following stepwise selection (999 permutations).

	Df	AIC	F	P	RDA1	RDA2
Pond area	1	37.8	17.4	0.005	0.94	-0.35
Impermeable surface (500 m)	1	36.2	3.4	0.030	-0.26	-0.97

4.1. Leaf breakdown rates in urban ponds

Leaves of the family of plants Fagaceae, including oak (*Quercus* spp.) and beech (*Fagus* spp.) are classified as slow degraders ($<0.005 \text{ k d}^{-1}$ Petersen and Cummins 1974) and the rates here ($k_{\text{total}} 0.002 \text{ k d}^{-1}$) accord with a review of Fagaceae breakdown rates across both lentic and lotic systems (0.0025 k d^{-1} ; Webster and Benfield 1986). However, the decomposition rate can vary greatly due to the influence of physical and/or chemical parameters such as nutrient and dissolved oxygen concentrations (Suberkropp and Chauvet, 1995), which likely explains the variability in k rates, with some urban pond sites as low as 0.0003 k d^{-1} (site 29, k_{total}). We did not measure oxygen exactly where leaf bags were placed, and this might have introduced some unexplained variability in breakdown rates among ponds. However, we expect, as the bags were deployed in a similar manner in all ponds, that unmeasured oxygen levels at this local scale will not have any influence on overall patterns. Nevertheless, few studies are available to compare decomposition rates in still water systems that contrast markedly with running water sites within which flow is considered an additional key influence due to physical abrasion and higher oxygen availability (Paul et al., 2006; Webster and Benfield, 1986). Indeed, breakdown rates of Fagaceae leaves in flowing systems are typically faster (e.g. Lecerf et al.,

2007; Schindler and Gessner, 2009) and a likely explanation, among others such as physical lower abrasion, could be lower oxygen levels in and around leaf bags.

4.2. The importance of a non-native invertebrate

Studies indicate that *C. pseudogracilis* may be excluded from areas of good water quality by native Gammaridae, but can proliferate where water quality is poor (Vermonden et al., 2010), particularly where temperatures are high and dissolved oxygen low (Dick et al., 1998; Gledhill et al., 1993; MacNeil et al., 2000). Dissolved oxygen levels were frequently low across the studied sites (mean 47.4%) and phosphate high (mean 0.54 mg/L), indicative of eutrophic conditions. Positive and significant associations between pH and dissolved oxygen respectively with leaf breakdown rates have also been observed in constructed (Mackintosh et al., 2016) and natural wetlands (Harbourd et al., 2015; van der Lee et al., 2017). Overall shredder diversity decreased as sites became more urban, with the loss of active dispersing species (mostly Trichoptera) and pollution sensitive taxa (e.g. *G. pulex*; Maltby 1995). Such loss of specialist shredding taxa has also been observed in urban streams (Cook and Hoellein, 2016). Thus, it would suggest that *C. pseudogracilis* is highly important for the maintenance of leaf litter breakdown, an important aspect of ecosystem functioning, in these stressed environments.

The native isopod *A. aquaticus* has a weaker association with leaf breakdown rates, and has been shown to be an inferior shredder when compared to specialist shredding taxa at the individual level and per g animal biomass (Bjelke and Herrmann, 2004). Here, total leaf breakdown rates were chiefly driven by the abundance of a non-native amphipod *C. pseudogracilis* and in the absence of native Gammaridae in all but two sites, to which *C. pseudogracilis* may become intraguild prey (MacNeil et al., 2000). The feeding habits of *C. pseudogracilis* are well established, whereby it primarily feeds upon plant detritus (Pardo and Armitage, 1997; Tachet et al., 2010), although at a potentially slower rate than native amphipods (Gama et al., 2017).

4.3. The influence of urbanisation

The extent of urbanisation surrounding the pond was a relatively weak influence upon the composition of the shredder assemblage. This might be attributed to not having sampled the entire macroinvertebrate community in each pond but rather collected from our leaf packs where

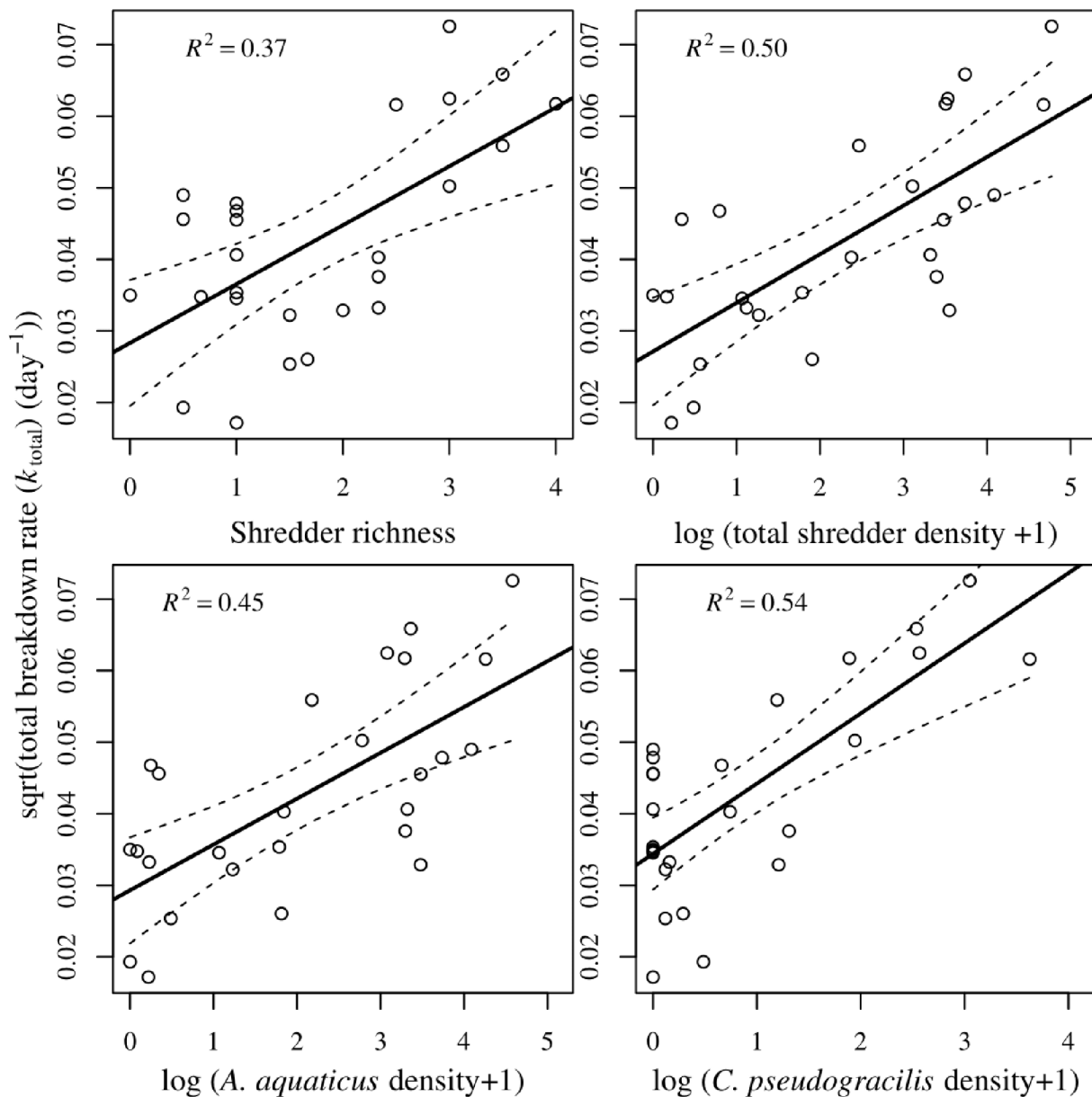


Fig. 3. Relationship between total leaf breakdown rate (k_{total}) and a) the average diversity of shredders per leaf pack, per site, and b) density (individuals g AFDM⁻¹) of all shredders (13 taxa) including two most abundant shredder species c) *A. aquaticus* and d) *C. pseudogracilis*.

both the homogeneity of the substrates and allochthonous food source would filter for a subset of the macroinvertebrate assemblage. However, there was a clear correlation between the extent of impermeable surface and the diversity of shredders, and those species lost were typically less pollution tolerant and active dispersers. This may be symptomatic of the urban stream syndrome (Walsh et al., 2005) where taxa richness is reduced in urban stream catchments due to multiple stressors associated with urban run-off, and has been found in urban environments compared to forested or agricultural areas (Paul et al., 2006).

The extent of urbanisation did not however influence breakdown rates. Similarly, Harboud et al. (2015) did not find any differences in breakdown rates between urban and agricultural wetlands in South Australia (Harboud et al., 2015). However, these results contrast to previous stream studies that identified significant changes in breakdown rates in response to catchment urbanisation, with either increases (Chadwick et al., 2006) or decreases (Del Arco et al., 2011; Martins et al., 2015) observed. The use of impermeable surface cover as an indicator of urbanisation is well established (Hahs and McDonnell, 2006;

Oertli and Parris, 2019). Thus, the results indicate that leaf processing rates in these urban ponds are less sensitive to factors stemming from urban land-use than other aspects of the ecosystem (e.g. biodiversity) or that the strong effect of surface area or the persistence of *C. pseudogracilis* may have masked the influence of urbanisation.

4.4. Important physical and chemical factors

Many of the physical and chemical factors studied across the study ponds were highly covariant (Table S3). Thus, whilst surface area was identified as a key driver, it is likely that the effect of area upon leaf breakdown rates was realised through biochemical factors such as dissolved oxygen and pH and their determining of the shredding taxa community via their interaction with local physical parameters (Table 4). For example, shading disproportionately increases with decreasing surface area, and thus does the relative load of organic input whilst inhibiting macrophytic growth (Gee et al., 1997). Fish presence is typically expected to increase with surface area (Søndergaard et al.,

Table 4

General effects of surface area upon key physical and chemical parameters within larger (A) and smaller (B) urban ponds with the same depth of overhanging vegetation (black ring). Cascading effects and their directions are shown by the linkages (with the exception of fish, of which populations and community composition is not known in the present study). See also Supplementary Information Table S3.

A

B

Parameter	Effect	Effect
Sunlight Shade	50% 50%	25% 75%
Plant growth	Moderate	Low
Organic input	Moderate	High
pH	Neutral – alkaline	Neutral – acidic
Nutrients (PO ₄)	Low – moderate	Moderate – high
Microorganisms	Fewer	More
Dissolved oxygen (benthic)	Aerobic	Anaerobic
Fish	Presence	Absence

2005), which was observed here, however little was known about the composition of the fish community which could significantly vary the impact upon invertebrate assemblages (e.g. through predation) and the physical and chemical environment (e.g. bioturbation; Cline, East & Threlkeld 1994). Our results suggest that monitoring of ponds along stress gradients should be stratified by area to avoid that features related to pond size mask anthropogenic impact (Table 4).

In conclusion, our study suggests that an invasive species can sustain ecosystem functioning in heavily impacted freshwater ecosystems when native species are lost and can provide ecosystem resilience in response to urbanisation, thereby masking impacts to the native macro-invertebrate community. This has implications for the transfer of energy to higher trophic levels that are less impacted by degradation such as certain fish, amphipods and birds. However, it is likely that these heavily impacted systems relying on a non-native shredder are temporally unstable due to the increased likelihood of pollution events in urban areas, and are more likely to lose ecosystem function at intervals if environmental conditions are not improved. The decoupling of the biodiversity-ecosystem functioning link by a non-native species furthermore suggests that monitoring of functional attributes in isolation to assess ecosystem health could be dangerous and our study clearly indicates that measures of both community structure and ecosystem functioning are needed. We showed that small ponds in an urban landscape can be severely degraded, and lack functional redundancy, as such they should receive more attention in future despite not being regularly monitored as part of legislation such as the WFD. Urban ponds provide an important range of ecosystem services and support human health and well-being in urban areas, which are rapidly increasing globally with more than 50% of the World’s population already living in cities.

5. Author’s contributions

IT carried out the fieldwork, statistical analyses and led the writing of the manuscript. NF provided critical input to frame and scope the manuscript and analyse the data. VT assisted both fieldwork and laboratory analyses. ME and LB oversaw and advised on the fieldwork and provided valuable edits of several iterations of the manuscript

6. Data Accessibility

The data that support the findings of this study are openly available in Figshare at <http://doi.org/10.17870/bathspa.8203751>

CRedit authorship contribution statement

Ian Thornhill: Conceptualization, Investigation, Methodology. Nikolai Friberg: Conceptualization, Funding acquisition. Lesley Batty: Funding acquisition, Supervision, Writing - review & editing. Victoria Thamia: Investigation, Methodology. Mark E. Ledger: Supervision, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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