



Organic-matter decomposition in urban stream and pond habitats

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ABSTRACT

Organic-matter decomposition is a key ecosystem process in freshwater ecosystems as it influences food web dynamics, represents a considerable flux in the global carbon cycle and can provide a useful measure of the 'health' of freshwater habitats. While organic-matter decomposition has been well studied among lotic ecosystems, research from small standing waterbodies such as ponds is largely missing, and decomposition studies are usually conducted on a single freshwater habitat type. However, there is a need to consider ecosystem processes across multiple freshwater habitats and connected ecosystems to better characterise ecosystem functioning at the landscape-scale, given the interdependence of landscape elements. This study provides a comparative analysis of organic-matter decomposition using a standardised field assay (cotton-strip assay) in the water column, riparian zone and land zone of urban pond and stream habitats. The average daily tensile-strength loss of the cotton strips (a process that corresponds to the catabolism of cellulose by microbes) was significantly higher in the aquatic habitats than riparian and land zones when all sites were considered, and when stream and pond sites were considered separately. Furthermore, the average decomposition rate was significantly higher within the water column in river habitats compared to pond habitats, although no difference was observed among riparian and land zones. Woody debris had a negative unimodal association with average per day tensile strength loss within streams, and a positive unimodal association within pond sites. Both nitrate and shading had positive unimodal associations with average per day tensile strength loss within stream sites. Among pond habitat, urban land coverage within 250m of each site was identified to have a negative association with average per day tensile strength loss. Here we demonstrated that urban freshwater habitats have heterogeneous organic matter decomposition rates, and that the responses can be complex. Understanding key ecosystem processes at a multihabitat scale will ensure the effective inclusion of ecosystem process in freshwater assessment and conservation protocols and improve the health and resilience of urban freshwater ecosystems.

1. Introduction

In freshwater ecosystems organic-matter decomposition is a critical ecosystem process as it influences food-web dynamics through the mineralisation of carbon (Gessner et al., 2010) and represents a considerable flux in the global carbon cycle (Hotchkiss et al., 2015). Despite the significant role that organic-matter decomposition plays in the functioning of freshwater habitats in general (Colas et al., 2019;

Marks, 2019), previous studies examining this process in freshwater have largely focussed on riverine habitats (Zhang et al., 2019), with lentic habitats less studied than lotic systems (Brumley and Nairn, 2018). Furthermore, given that lotic and lentic systems do not exist in landscapes in isolation but as interconnected freshwaters wherein the ecosystem processes in one habitat have implications in others, there is a need to consider ecosystem processes across multiple freshwater habitats, to better characterise ecosystem functioning at larger scales (Sayer

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et al., 2014).

Historically, the quality or 'health' of freshwater systems has been determined through structural measures such as water quality (Wei et al., 2009), taxonomic richness (Hill et al., 2016), indicator species, community composition and specific metrics that assess the biological quality of freshwaters, such as the Predictive SYstem for Multimetrics (PSYM; Biggs et al., 2000) for pond habitats and Walley, Hawkes, Paisley and Trigg metric (WHPT; Paisley et al., 2014) for river systems. For example, the Water Framework Directive in Europe and the United States Clean Water Act use structural metrics (e.g., richness) based on taxonomic composition and ecosystem structure to determine ecological status and ecosystem integrity (USEPA, 2002; Carballo et al., 2009). However, focussing solely on the structure of freshwater habitats, particularly in urban areas, only partially quantifies aquatic health and the human impacts on freshwater habitats, as ecosystem process (e.g., primary production, respiration, decomposition, nutrient and flows) are ignored (Gessner and Chauvet, 2002; Chauvet et al., 2016; Tiegs et al., 2013a). In many cases, structural measures are unreliable proxies for freshwater ecosystem processes such as decomposition, and previous research has shown that human pressures on freshwater may affect the structure and function of aquatic ecosystems differently (Tiegs et al., 2013a). In light of this, assessments of ecosystem health and integrity should be based on both the organisms that are present and ecosystem process to make assessments completer and more reliable (Verdonschot and van der Lee, 2020). In recent years, the importance of structural and functional measures for ecosystem assessment has been recognised and measures of ecosystem processes are now being included in freshwater assessment protocols, complimenting existing structural metrics (Ferreira and Guerold, 2017).

Urbanisation is one of the greatest threats to ecosystem health (Miller and Boulton, 2005) as natural habitat is converted to a more artificial, uniform landscape. As a result of urbanisation, freshwater ecosystems are exposed to a range of stressors including pollution (Hobbie et al., 2017), reduced habitat area and quality (Loke et al., 2014), fragmentation (Gibb et al., 2002), increased disturbance (McKinney, 2008) and colonisation by invasive species (Oertli et al., 2018), all of which can result in a decline in ecological integrity of urban freshwaters. While the response of freshwater diversity to these stressors is well documented in flowing systems (Walsh et al., 2005; Booth et al., 2016), and increasingly understood in lentic habitats (e.g., ponds: Hill et al., 2018; Hyseni et al., 2021; Oertli and Parris, 2019), understanding of the impact of urbanisation on ecosystem process in lentic and lotic habitats is limited (Walsh et al., 2005; Booth et al., 2016). Furthermore, quantifying the differences in decomposition between the water column and the riparian and corresponding land zones of freshwaters has received limited research attention (Tiegs et al., 2019), and is missing from urban landscapes. Given that global urban land coverage is predicted to increase by 1.2 million km² by 2030 (Seto et al., 2012), there is a pressing need to understand how ecosystem processes in diverse freshwater ecosystems and their surrounding terrestrial matrix respond to urbanisation so that their overall health can be accurately assessed, and urban freshwaters are more effectively managed.

Organic-matter decomposition within freshwaters has historically been examined using leaf-litter bag assays (Poi de Neiff et al., 2006). Locally sourced leaves are placed in mesh bags, submerged in the freshwater habitat and then retrieved to quantify organic matter loss over time (Thornhill et al., 2021). However, shortcomings of leaf litter bag assays have been noted, including the differing quality of leaf litter as nutrient and lignin content can be highly variable across tree species, which can cause a lack of standardisation and impede reliable comparisons between leaf litter assays in the same study, and between studies (Colas et al., 2019). Cotton assay strips can address these shortcomings as they are easy to use, can provide a comparable measure of decomposition to leaf litter (Tiegs et al., 2007) and a standardised measure of organic matter decomposition, that facilitates reliable comparison at different spatial and temporal scales and are low cost (Colas

et al., 2019; Tiegs et al., 2019).

Given the paucity of information relating to decomposition (carbon processing) in urban freshwaters and their riparian zones, this study aims to examine the decomposition of a standardised cotton assay strip among pond and stream habitats from the water column, the riparian zone and the land zone in urban landscapes. We further explored how cotton strip decomposition within the water column of urban ponds and streams responded to variation in environmental conditions. We hypothesize that organic matter decomposition in urban freshwaters (i) will be significantly greater in the water column than the riparian zone or the land zone, (ii) will be significantly greater in river habitats than pond habitats and (iii) in the water column will be driven by higher flow velocity, dissolved oxygen, urban land coverage, and nitrate and phosphate concentrations. This information is needed to further fundamental understanding of nutrient cycling, ecosystem functioning and ecosystem health (Tiegs et al., 2013a) within urban freshwaters and their surrounding terrestrial matrix, and for the development of more effective urban freshwater conservation strategies.

2. Materials and methods

2.1. Study sites and study design

This study was undertaken on streams, rivers, and pond habitats within the city of Bristol in the UK. Bristol covers an area of approximately 110 km² and had population of approximately 466,000 in 2020 (bristol.gov.uk, 2021). Bristol has an average annual precipitation of 819 mm, and an average annual minimum and maximum temperature of 7.3 °C and 14.5 °C, respectively (1991–2020, UK Meteorological Office, 2022). The urban pond sites studied were located in urban parks, surrounded by semi-improved grassland, and in high density compact developments, such as roadsides and industrial complexes (Fig. 1). The urban ponds (mean area: 2999.9 m²) mean depth: 0.35 m) studied were perennial and typically had synthetic bases and steep bank sides. The flowing sites (mean wetted width: 3.87 m, mean depth: 0.256 m) were located along several different rivers or streams: River Frome, River Trym, Hazel Brook, Pigeonhouse Stream, Brislington Brook and Malago Stream (Fig. 1). These streams/rivers have been highly modified, with weirs present along their course and parts of their reach being channelised (artificial banks and substrate, straightened, increased bed gradient) and culverted, and are disconnected from the floodplain along most of their reach. Sample sites were not randomly selected but were chosen based on their accessibility, location within an urban matrix, and that they had a riparian zone and corresponding land zone.

Cotton strips were initially placed in the water column and corresponding riparian (transitional vegetation zone between freshwater habitat and land) and land zone (area of land directly adjacent to the riparian zone) of 35 sites (18 stream/river, 17 pond). To secure the three cottons strips in the water column of each freshwater site, we gently eased a cable tie through the end of the fabric and attached it to approximately 30 cm length of paracord at one end, and we attached the other end of the paracord to stainless-steel peg secured in the pond bank or in the stream substrate close to the water's edge. Cotton strips were submerged approximately 30 cm into the water column. We placed a second set of triplicate cotton strips on the soil of the adjacent riparian zone (typically within 1–2 m of the water's edge) and secured it using a stainless-steel peg. Finally, we placed a third set of triplicate cotton strips on the soil of the adjacent land zone. However, in two sites cotton strips were completely lost from at least two of the three zones (water, riparian and land) and were subsequently removed from the study. Therefore, in total, cotton strips from 33 urban sites (17 stream/river, 16 pond) sites (Fig. 1) and considered for analyses.

We placed cotton strips in the water column, riparian and land zones of the sample sites for an average of 25 days (minimum: 22 days, maximum: 35 days – only two sites were exposed for 35 days) between 20th December 2019 and 3rd January 2020. The duration of study

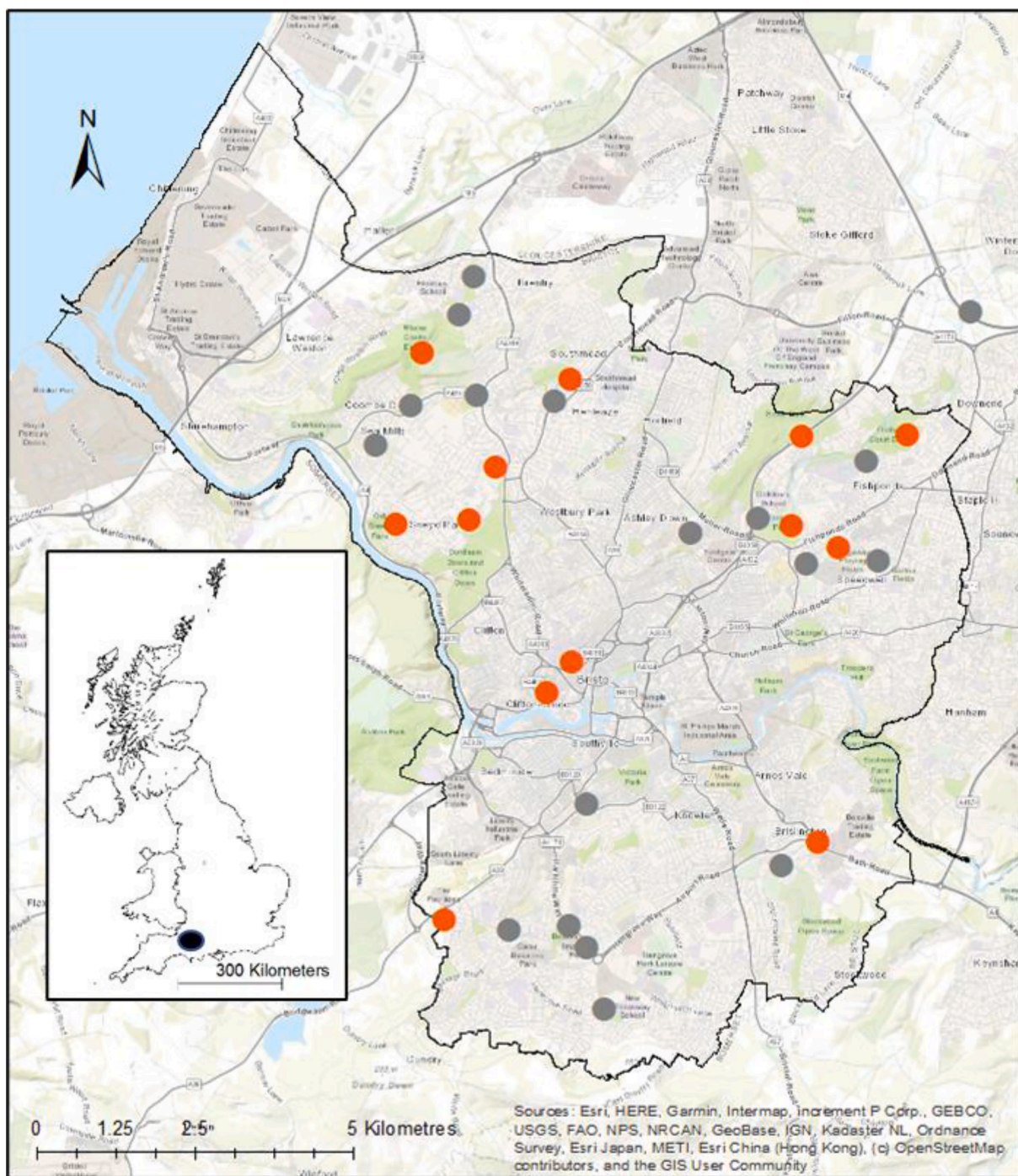


Fig. 1. Location of the 33 surveyed urban ponds (16) and streams (17) across Bristol and its location in relation to the UK (inset). Black circles = pond sites, red circles = stream and river sites. Grey areas represent urban location and green areas represent green spaces (e.g., urban parks). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reflects previous studies that have been conducted over 20–27 days (Colas et al., 2019), and 14 or 27 days (Tiegs et al., 2013a). The study period was immediately after senescence, which is arguably a critical period for ecosystem functioning, when allochthonous input is at its greatest.

Within the final 33 sites, we examined 273 cotton strips across the study area, 95 from the land zone, and 90 from the riparian zone and 88 from within the freshwater habitat. When we considered ponds and streams separately, we analysed a total of 133 cotton strips from pond habitats (45 in the land zone, 40 in the riparian zone and 48 within the pond water) and 140 from stream habitats (50 from the land zone, 50

from the riparian zone and 40 from the stream channel). The differences in total number from each zone were caused by individual cotton strips being lost from sites or were removed from the analysis as they were damaged. Average per day tensile strength loss (TLD: where faster rates of decomposition are indicated by loss in cotton strip tensile strength) was selected as the response variable in this study (see section 2.3).

2.2. Cotton strip assay preparation

We deployed a cotton-strip assay using cotton strips (8 × 2.5 cm) made from a single bolt of 12 oz medium grain artists ‘duck’ canvas

(Pegasus Art Supplies, UK) or ‘Artist’s fabric’. Cotton strips were prepared following Tieggs et al. (2013a). Cotton strips have been shown to provide a standardised and reliable measure of organic matter decomposition (Tieggs et al., 2007). Each cotton strip was fringed by 3 mm of fray along each length of the cotton strip. This was achieved by removing three short threads from the short and long ends of the cotton strip (but ensuring that the cotton strip consisted of 27 long threads); frayed edges ensures that cotton strip does not unravel. The assay quantifies the capacity of ecosystems to process organic matter, i.e., their organic-matter decomposition potential.

2.3. Quantifying average daily tensile strength loss

To determine the tensile strength of each cotton strip, we placed the ends of each strip within the grips of a tensiometer (Checkline brand, Model #G1008, Enschede, The Netherlands) which was mounted on a motorized test stand (Fig. S1). We ensured that the tensiometer grips were tight enough to secure the cotton strip during the pulling process, but not so tight to tear the strips at their point of contact with the grips. Furthermore, we lined the grips with cotton-based tape to prevent slippage. Following Tieggs et al. (2013a), we pulled the cotton strips at a fixed rate of 2 cm min⁻¹ and a maximum tensile strength was recorded. To account for the different length of time the cotton strips were submerged at different sites an *average per day tensile loss* (TLD) was calculated, using the equation presented in Tieggs et al. (2013a).

During transport from the sample site to the laboratory a total of 41 cotton strip assays were partially creased. In addition, 19 cotton stripped slipped during the pulling process. To determine whether slipping in the tensiometer or creasing influenced the results, we compared the average daily tensile strength loss of slipped/creased samples to undamaged samples using a Kruskal-Wallis test, and a Nemenyi post hoc test (based on the Bonferroni correction) using the function *kwAllPairsNemenyiTest* in the PMCMRplus package (Pohlert, 2021). Preliminary analyses indicated that there was no significant difference in average daily tensile strength loss between creased/slipped samples and undamaged samples among each habitat type (within the freshwater habitat, in the riparian zone and in the land zone) when all freshwaters were considered, and when ponds and stream habitats were considered separately ($p > 0.05$, see supplementary Table S1, S2 and S3), although a significant difference was recorded among creased and slipped samples among ponds ($p < 0.05$). As a result, partially creased samples and samples that slipped during the pulling process were retained in the final analyses.

2.4. Environmental and Land-use data

We visited all sites during autumn and winter (Oct 2019-Jan 2020) to record physical and chemical parameters. At each stream and pond site we measured water depth (m) and flow (streams only) in triplicate within the water column where we placed the strips. In the same location and in triplicate, we measured water temperature, pH, conductivity (μScm^{-1}) and dissolved oxygen (%) using a Hach HQd multi-parameter probe (Hach, Colorado, USA), calibrated daily before use. Additionally, we collected three 1 litre water samples at each site visit and filtered them with a Whatman No. 2 filter. For these samples we measured nitrogen as $\text{NO}_3\text{-N}$ (mg l^{-1}) using an ion selective probe (after Bartram and Balance, 1996) and total phosphorus (TP: mg l^{-1}), using the molybdenum blue reaction. We acidified filtered samples using 1 % nitric acid in an oven at 100 °C overnight and the addition of ammonium molybdate. We then measured the blue-coloured complex with a spectrophotometer at 880 nm (Jenway, Staffordshire, UK).

We recorded water velocity (m s^{-1}) (Geopacks Advanced Stream Flow Meter, Devon, UK) only from stream sites, and estimated coverage of woody debris (%) and emergent, submerged or floating macrophytes (all in %), and the percentage of open water free from vegetation (see Table S4). We estimated the degree of urbanisation around each sample

site using the urban land coverage (%) within a 250 m buffer of each freshwater site by deriving it from the Centre for Ecology and Hydrology National River Flow Archive (<https://nrfa.ceh.ac.uk/content/land-use>).

In addition to the degree of urbanisation within a 250 m buffer, the micro-scale habitat where the riparian and land zone cotton strips were located was quantified (irrespective of whether the associated water body was a stream or pond). These micro-scale habitats (aligned to habitat classifications from the Phase 1 Habitat Survey- a standardised survey used to record vegetation and other habitats in the UK: Joint Nature Conservation committee, 2010), comprised of amenity grassland (J.1.2, $n = 13$), broadleaved woodland and hedgerows (A.1.1.1 or J.2.1.2, $n = 6$), improved grassland (B.4, $n = 5$), scattered scrub (A.2.2, $n = 4$), car park (J.3.6, $n = 1$) and allotments (J.1.1, $n = 1$).

2.5. Statistical analyses

For each stream and pond site, we averaged the average daily tensile-strength loss (TLD) values of the three cotton strip replicates, resulting in a single average TLD value for the water column, riparian zone and land zone for each site. We examined differences in average TLD among the water zone, riparian zone and land zone for all urban freshwaters together and urban ponds and streams separately using a Kruskal-Wallis test (in the PMCMR package: Pohlert, 2021a). We performed pairwise comparisons using Nemenyi post hoc tests with Bonferroni correction (in the PMCMRplus package in R: Pohlert, 2021) to determine where significant differences among the three habitats: water, riparian zone and land zone occurred. We also employed Kruskal-Wallis tests with Nemenyi post hoc test to test for differences in TLD between the three habitats. Finally, we carried out comparisons of TLD between the riparian zone and specific habitats present within the land zone corresponding to Phase 1 habitat categories (amenity grassland, improved grassland, broadleaved woodland or hedgerows, and scrub; too few data were available to compare car parks and allotments) using a paired samples Wilcoxon Test.

Environmental data was only available from the water column in stream and pond sites; subsequently, environmental-decomposition relationships were only assessed within these two habitats. We undertook preliminary analysis to minimise multicollinearity among environmental variables using Variance Inflation Factor analysis (VIF: using the function *vif* in the car package: Fox et al., 2021). We used a stepwise procedure, where we calculated a VIF value for each environmental variable and removed the variable with the highest value. We repeated this procedure until all VIF values were 7 or lower (Dormann et al., 2012). In addition, we identified outliers among each environmental variable as values that were greater than three times the interquartile range (White et al., 2021), which we subsequently removed from the analysis. This preliminary analysis resulted in: (1) the removal of conductivity, % coverage of floating macrophytes, pH, and NO_3 as it demonstrated significant collinearity (based on VIF analysis) with other environmental variables among pond sites, and the removal of conductivity, percentage coverage of floating macrophytes, dissolved oxygen concentration and temperature as they demonstrated collinearity with other environmental variables among stream sites and (2) the removal of one shading outlier and two submerged macrophyte outliers among stream sites (submerged macrophyte coverage was subsequently removed from the analysis as no values were greater than zero after outliers were removed), and one woody debris outlier and one total phosphorus outlier among pond sites.

We examined the response of the average daily loss of tensile strength (dependent variables) in relation to the individual effect of each environmental variable (*both pond and stream sites*: urban land coverage within 250 m, percentage coverage of emergent macrophytes, total phosphorus, depth, shading, percentage coverage of woody debris; *stream sites only*: flow velocity, pH, NO_3 ; *pond sites only*: dissolved oxygen, temperature, coverage of submerged macrophytes) (independent variables) via separate sets of statistical models each testing a unique

dependent-independent pairwise combination ($n = 18$; flowing: 9 independent \times 1 dependent, pond: 9 independent \times 1 dependent variable) to make sure that models were not overfitted (White et al., 2017). Each of these statistical sets initially comprised four regression models, where the independent variable was modelled via linear, exponential, logarithmic and quadratic statistical functions. We determined the optimal statistical function for each environmental variable in each statistical set from the model exhibiting the lowest AIC (Fornaroli et al., 2019). Once we determined the optimal statistical function for each environmental variable, we used pairwise regression analyses for all explanatory (dependent) and response (independent) variables in their optimal structure (exponential, logarithmic, quadratic and linear). We determined the proportion of statistical variation explained (R^2) and significance of the optimal model within each statistical set. To minimise the likelihood of Type I errors, we adjusted the α significance level by (1) multiplying the degrees of freedom of statistical models by 0.05 and (2) dividing this value by the total number of tests (see Dolédec et al., 2006).

3. Results

3.1. Decomposition of organic matter among water, riparian and land zones in urban stream and pond habitats

We found significant differences in average daily tensile-strength loss (TLD) of the cotton strips among the land zone, riparian zone and in water samples when we considered both freshwater habitats together (Kruskal Wallis Test, $df = 2$, $\chi^2 = 34.82$, $p < 0.001$), and when we considered pond (Kruskal Wallis Test, $df = 2$, $\chi^2 = 7.14$, $p < 0.05$) and stream (Kruskal Wallis Test, $df = 2$, $\chi^2 = 31.04$, $p < 0.001$) habitats separately (Fig. 2). Pairwise Nemenyi post hoc tests indicated; (1) TLD of the cotton strips was significantly ($p < 0.001$) higher in the water zone (median TLD: 2.572) than riparian (median:1.423) and land (median: 1.451) zones when all freshwater sites were considered, (2) TLD of cotton assay strips was significantly ($p = 0.027$) higher in the water zone (median: 1.755) than land (median: 1.544) zones among pond habitats, but not compared to the riparian zone (median: 1.431) and (3) TLD of cotton assay strips was significantly ($p < 0.001$) higher in the water zone (median: 3.727) than riparian (median: 1.418) and land (median:1.207) zones among stream habitats (Fig. 2).

3.2. Differences in decomposition in the water, riparian and land zones between urban pond and stream habitats

The TLD of cotton strips was significantly higher (Kruskal-Wallis Test, $df = 1$, $\chi^2 = 52.793$, $p < 0.001$) within the water column in river habitats compared to pond habitats (Fig. 3). No significant difference in TLD was recorded between ponds and rivers habitats from riparian (Kruskal Wallis Test, $df = 1$, $\chi^2 = 0.108$, $p > 0.05$) and land zones (Kruskal Wallis Test, $df = 1$, $\chi^2 = 2.381$, $p > 0.05$; Fig. 3).

When comparing the TLD between the riparian zone and Phase 1 habitat categories, average daily tensile strength loss was significantly greater in the riparian zone than amenity grassland ($p < 0.05$; Wilcoxon paired-sample test), with tensile strength loss being on average 21.6 % faster in the riparian zone than amenity grassland.

3.3. Environmental and spatial drivers of cotton strip decomposition in the water, riparian and land zone among ponds and streams

The percentage coverage of woody debris was significantly negatively associated with the TLD in the stream water column (adj. $R^2 = 0.288$, $F = 3.842$, $p = 0.05$; Table 1). NO_3 (adj. $R^2 = 0.342$, $F = 4.636$, $p < 0.05$; Table 1) and percentage shading (adj. $R^2 = 0.486$, $F = 7.163$, $p < 0.05$; Table 1) demonstrated a unimodal relationship TLD (Fig. 4), with TLD peaking at intermediate values of NO_3 and shading. The percentage coverage of urban land within 250 m of each site, total phosphorus, flow velocity, pH, depth and the percentage coverage of

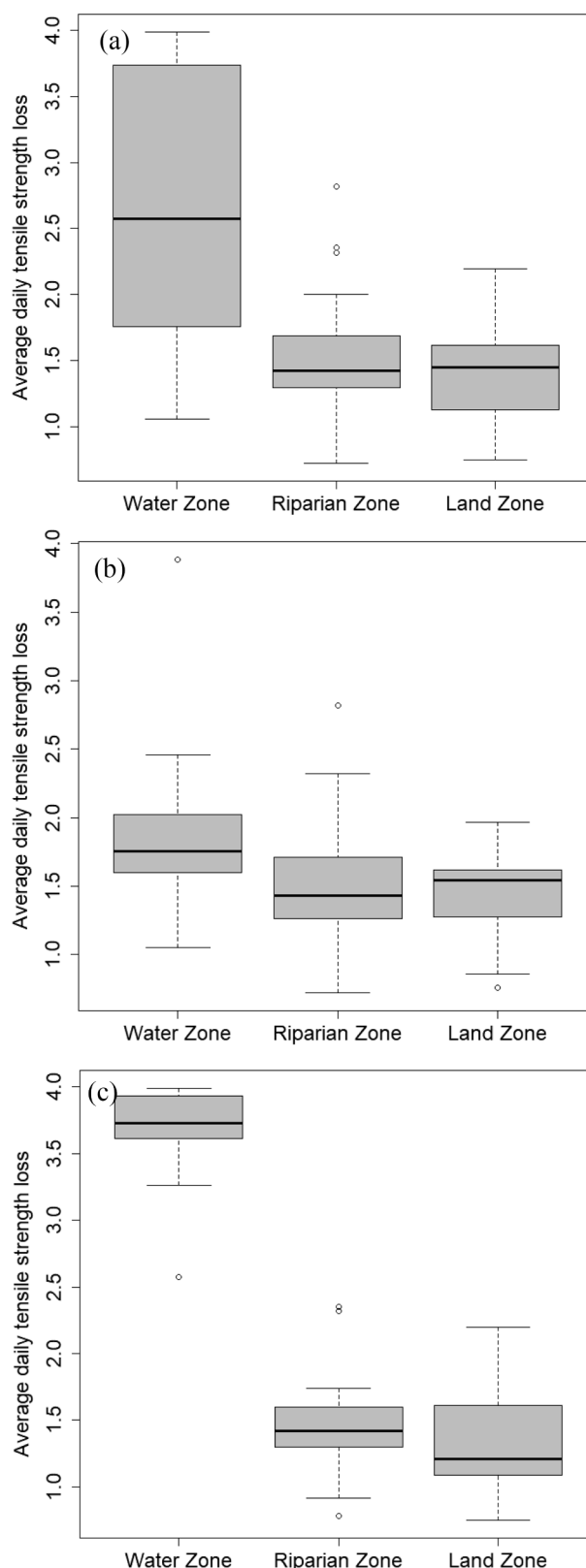


Fig. 2. Median cotton strip per day tensile strength loss recorded from the water zone, riparian zone and land zone when all freshwaters were considered together (a) and when pond (b) and stream habitats (c) were considered separately. Boxes show 25th, 50th, and 75th percentiles and whiskers show 5th and 95th percentiles.

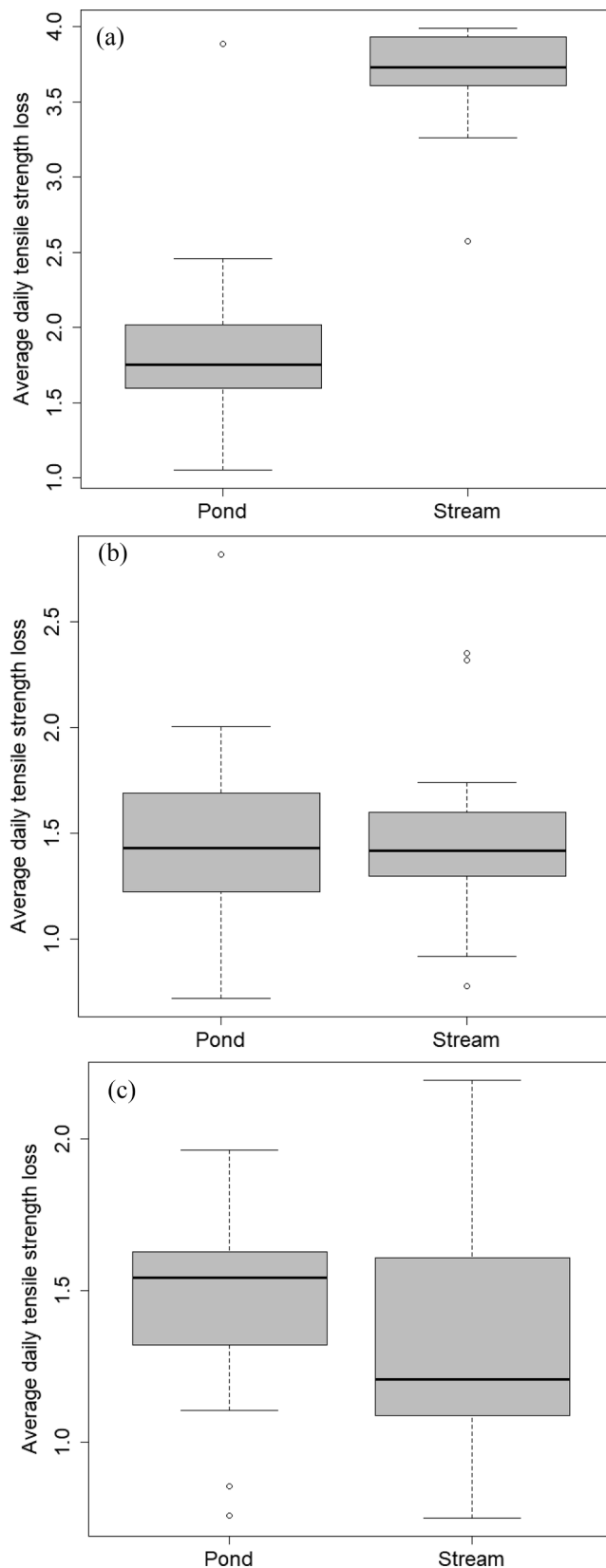


Fig. 3. Median cotton strip per day tensile strength loss recorded from (a) the water zone, (b) the riparian zone and (c) the land zone among stream and pond habitats. Boxes show 25th, 50th, and 75th percentiles and whiskers show 5th and 95th percentiles.

submerged macrophytes were not significantly associated with TLD of cotton strips ($p > 0.05$; See Table S5).

The percentage urban land within 250 m of each site (adj. $R^2 = 0.384$, $F = 7.846$, $p < 0.05$; Table 1, Fig. 4) was identified to be significantly negatively associated with cotton assay strip TLD within the water column of pond sites. The percentage coverage woody debris (adj. $R^2 = 0.7$, $F = 12.7$, $p < 0.01$; Table 1, Fig. 4) demonstrated a significant unimodal association with TLD, with greater TLD at moderate woody debris coverages in ponds, and the opposite pattern recorded in streams. Total phosphorus, shading, water depth, temperature, dissolved oxygen, and percentage of submerged macrophyte coverage and emergent macrophyte coverage were not significantly associated with decomposition rates in the water column of pond sites (Table S5).

4. Discussion

4.1. Differences in decomposition in the water, riparian and land zones among urban pond and stream habitats

Understanding the functioning of freshwater ecosystems, and their proximal terrestrial habitat in urban areas is critically needed given the predicted future increase in urban land coverage (Seto et al., 2012), and the associated urban pressures facing freshwater and riparian habitats (Groffman et al., 2003; Reid et al., 2019). This study demonstrated that organic-matter decomposition (carbon processing) was fastest within the water column and slowest across the terrestrial landscape (riparian and land zone) among urban pond and stream habitats (accept hypothesis 1). This corresponds to findings by Nakajima et al. (2006), and Tiegs et al. (2019) who found carbon processing rates to be approximately twice as fast in river sites compared to adjacent riparian zones. Given that freshwater habitat and their riparian zones are closely connected and readily exchange organic carbon, the large difference in carbon processing between freshwater and riparian zones indicates that streams and ponds are relative hotspots for organic-matter decomposition while riparian zones provide greater organic carbon storage, beyond the periods (autumn in the temperate region of this study) of organic matter input (Tiegs et al., 2019).

Although not tested here, differences in organic-matter decomposition between freshwater and terrestrial zones may be explained by temperature. Carbon processing has been demonstrated to be more sensitive to temperature in rivers (Yvon-Durocher et al., 2012; Tiegs et al., 2019), and warmer temperatures in stream sites during winter (when samples were taken in this study) may promote greater organic matter decomposition in streams and ponds through biological and chemical activity (Martins et al., 2015), while lower temperatures in riparian and land sites may slow decomposition, promoting organic-matter storage. Furthermore, increases in water temperature in urban areas due to urbanisation, thermal pollution and removal of riparian vegetation may further increase litter decomposition in urban landscapes (Ferreira et al., 2020). Water limitation may also explain the similarly slow organic-matter decomposition in riparian and land zones relative to ponds and streams, reflecting findings observed by others (e.g., Tiegs et al., 2019). The sometimes-restricted availability of water in riparian and land zones may limit biological activity and nutrient content of leaf litter, and by extension, organic-matter decomposition (Capps et al., 2014).

Three separate classes of organic matter decomposition emerged from this study, reflecting rapid decomposition in the stream water column, intermediate decomposition in pond habitats and slow decomposition in terrestrial sites. While no previous studies have been undertaken in an urban context that used a directly comparable assay in these diverse habitats, similar differences in decomposition among pond and river habitats have also been recorded across floodplain habitats (McArthur et al., 1994; Baldy et al., 2002; Langhans et al., 2008) and decomposition rates in pond habitats on the Copper River Delta, Alaska, have been recorded to be slow relative to published values for different

Table 1

Significant predictors of cotton-strip tensile-strength loss (average per day), within the water column for pond and stream sites. The statistical function employed for each significant environmental variable is presented in parenthesis.

	Variable	F value (df)	p value	Adjusted R ²	Directional response
Stream – Water zone					
Decomposition (Average per day cotton strip tensile strength loss)	Woody debris (Quadratic)	3.842 _(2,12)	=0.051	0.288	Unimodal
	NO ₃ (Quadratic)	7.563 _(2,12)	=0.007	0.483	Unimodal
	Shading (%) (Quadratic)	7.163 _(2,11)	=0.010	0.486	Unimodal
Pond – Water zone					
Decomposition (Average per day cotton strip tensile strength loss)	Urban coverage (%) (logarithmic)	7.846 _(1,10)	=0.018	0.384	-
	Woody debris (Quadratic)	12.7 _(2,8)	=0.003	0.705	Unimodal

freshwater habitats (Tiegs et al., 2013b). Although, similar leaf decomposition coefficients among ponds and river were recorded from the Garrone River System in France (Baldy et al., 2002). Decomposition in freshwater systems is the result of the combined effect of the chemical, biological and physical components of aquatic ecosystems (Martins et al., 2015). In this study, the significantly greater organic matter decomposition in urban streams compared to ponds (accept hypothesis 2) may be driven by water flow, providing nutrient and oxygen delivery at rates greater than that of passive diffusion that characterizes other aquatic habitats, increasing abrasion-based organic matter breakdown, and providing a steady delivery of microbial inoculants (Langhans et al., 2008; Martins et al., 2015).

4.2. Environmental drivers of organic matter decomposition among ponds and streams

The third hypothesis of this study could partially be accepted as the presence of woody debris, NO₃ concentration, shading and the percentage urban land coverage were identified to significantly influence organic matter decomposition. The presence of woody debris was a significant driver of TDL in stream and ponds, but in contrasting ways. In the study stream sites woody debris was strongly indicative of slower flow (Fig. S2; Braudrick and Grant, 2001). As a result, in areas where woody debris is present there is likely to be a reduced influence of flow-driven organic-matter breakdown in streams, reducing the overall rate of tensile strength loss. However, among pond habitats, greater TDL was associated with moderate coverages of woody debris (10–15 %). This may be because woody debris provides suitable habitat to support high populations of bacteria, fungi and macroinvertebrates required for organic matter decomposition (Harmon et al., 1986; Czarnecka, 2016). The unimodal relationship between shading and TDL in streams may reflect the thermal buffering capacity of trees, mediating extreme cold water temperatures during winter (this has been recorded across different terrestrial habitats; Hu et al., 2013; De Frenne et al., 2019; Lin et al., 2020). The reduction in thermal fluctuations due to shading in the winter may provide stable and warmer temperatures encouraging organic matter decomposition.

Increases in nutrient concentrations have been associated with increased leaf-litter breakdown in temperate headwater streams (Gulis and Suberkropp, 2003) and Mediterranean streams (Menéndez et al., 2011). Ferreira et al. (2015) identified an average 50 % increase in the rate of leaf litter decomposition in the presence of elevated nutrient conditions across a review of 840 case studies. In this study, NO₃ demonstrated a unimodal association with decomposition in streams, similar to the findings of Woodward et al. (2012). A peak loss in tensile strength was observed at approximately 13 mg l⁻¹. These findings suggest that subsidy-stress relationships have been observed (Woodward et al., 2012) in the studied stream, and such a decline with further enrichment might suggest how increases in concomitant pollution syndromes, such as smothering, or disappearance of pollution sensitive taxa may counteract the stimulating effects of nutrient enrichment (Lecerf et al., 2006). Additionally, high nutrient concentrations are commonly

associated with other environmental stressors, which may have contributed to the hump-shaped response we observed.

The extent of urbanisation within 250 m was a significant predictor of average TLD within ponds. Urbanisation can be an indirect, underlying influence resulting in a cocktail of stressors upon freshwater environments such as nutrients, heavy metals, Polycyclic aromatic hydrocarbons, pH, temperature, and dissolved oxygen concentrations (Martins et al., 2015; Mackintosh et al., 2016), where the direct effect of any single stressor may not be significant, but together with others, can act synergistically to have pronounced effects (Jackson et al., 2016).

4.3. Implications for freshwater conservation in urban areas

The monitoring, assessment and conservation of lake and stream ecosystems are predominantly based on structural measures such as taxonomic richness and composition, and taxonomic-based metrics (Biggs et al., 2000). Given that urban freshwaters are often subjected to multiple anthropogenic stressors, incorporating measures of ecosystem functioning alongside structural measures is critical to accurately determine the effects of different human activities on the health and resilience of freshwater ecosystems (Thornhill et al., 2018) as structural measures are often unreliable proxies for ecosystem functioning. Cotton-strip assays have been widely used in terrestrial and aquatic systems, having been deployed in hundreds of streams across the planet, providing an effective, standardised and accurate way to quantify the capacity of an ecosystem to process organic matter, and assess the effect of anthropogenic stressors on freshwater functioning (Imberger et al., 2010), although additional comparative studies are needed between natural and artificial assays. The cotton strip assay can be applied rapidly to freshwaters and are simple to analyse, creating a significant opportunity for management agencies and policy makers to include a functional indicator in freshwater ecosystem monitoring and conservation assessments. Including a functional indicator alongside taxonomic based monitoring will help ensure that the full impact of different anthropogenic stressors is understood, and that effective management and conservation strategies can be implemented to support freshwater ecosystems in urban landscapes.

This study has demonstrated that local habitat diversity in urban areas is of critical importance to create and maintain spatial variability in ecosystem functioning (organic matter decomposition) at a landscape-scale. Increasing development pressure on semi-natural areas and modification to freshwater habitats (such as alterations to flow regimes and morphological changes) across urban landscapes, will likely result in reduced habitat diversity, and concomitant functional diversity. These impacts will likely reduce the heterogeneity in decomposition rates (Langhans et al., 2008) and may influence ecosystem health at larger scales. Maintaining habitat heterogeneity across urban landscapes is critical to ensure that overall functioning is maintained at a connected multihabitat scale. Furthermore, the addition of a riparian zone to the urban landscape improved ecosystem functioning across the wider landscape, especially when compared to amenity grassland that is frequently encountered in urban parks. Thus, any future conservation

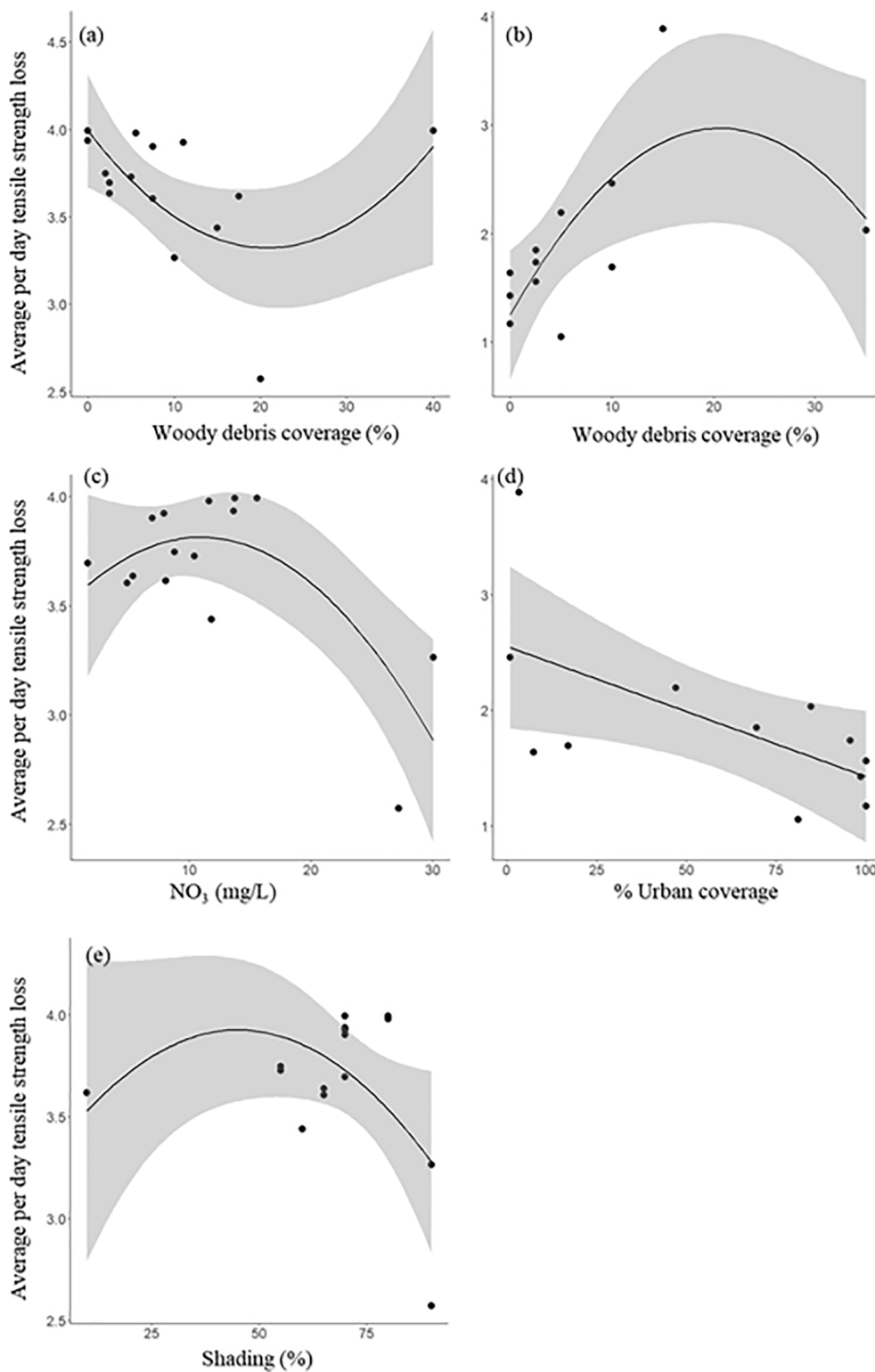


Fig. 4.

strategies that aim to ensure full ecosystem functioning need to consider the wider terrestrial landscape surrounding freshwater habitats.

CRediT authorship contribution statement

Matthew J. Hill: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft. **Ian Thornhill:** Funding acquisition, Project administration, Conceptualization, Methodology,

Data curation, Writing – original draft. **Scott D. Tiegs:** Methodology, Data curation, Formal analysis, Writing – review & editing. **Ana Castro-Castellon:** Writing – review & editing. **J. Salvador Hernández-Avilés:** Writing – review & editing. **Arantza Daw:** Writing – review & editing. **Victor Hugo Salinas-Camarillo:** Writing – review & editing. **Sarah Hobbs:** Data curation, Writing – review & editing.

Declaration of Competing Interest

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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