RESEARCH ARTICLE

Living on the edge: Predicting invertebrate richness and rarity in disturbance-prone aquatic–terrestrial ecosystems

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Abstract

1. Temporal fluctuations in cause the spatial extent of wet and dry habitats to vary in aquatic–terrestrial riverine ecosystems, complicating their biomonitoring. As such, biomonitoring efforts may fail to characterize the species that inhabit such habitats, hampering assessments of their biodiversity and implementation of evidence-informed management strategies.

2. Relationships between the dynamic characteristics of aquatic–terrestrial habitats and their communities are well known. Thus, habitat characteristics may enable estimation of faunal assemblage characteristics such as taxonomic richness, regardless of in-channel water levels.

3. We investigated whether indicators summarizing habitat survey data can predict two metrics representing terrestrial invertebrate assemblages (e.g. taxa richness) in two aquatic–terrestrial habitats: exposed riverine sediments and dry temporary streams. We also compared the performance of unimetric and multimetric habitat indicators in making predictions.

4. In exposed riverine sediments, >88% of predictions were correlated with observed taxa richness and an index of conservation status. Values predicted by exposed riverine sediment samples were correlated with those observed in temporary stream channels with comparable riparian (i.e. largely agricultural) land use, but not those observed in channels with contrasting (i.e. more urban) land use.

5. Unimetric habitat indicators performed similarly to more complex multimetric indicators, with each explaining ≤6% of the variability in taxa richness and the index of conservation status. The different spatial scales at which invertebrates respond to habitat conditions and at which indicators record habitat conditions, and a more comprehensive training dataset that incorporates a full range of habitat conditions (i.e. land use), may improve future predictions.

6. We demonstrate that invertebrate assemblage characteristics can be predicted regardless of in-channel water levels. Agreement between exposed riverine

sediment predictions and temporary stream observations suggests that these predictions are transferable among a range of aquatic–terrestrial habitat types, and could thus be widely applied to aid conservation of riverine biodiversity in dynamic aquatic–terrestrial ecosystems.

1 | INTRODUCTION

Inundation by water—from gradual rewetting to major flood events—characterizes disturbance in aquatic–terrestrial habitats. Inundation promotes high rates of trophic exchange and high habitat heterogeneity at small spatial scales, fostering unique invertebrate communities (Sabo et al., 2005; Schindler & Smits, 2017; Soininen et al., 2015), which include rare and specialist species (Ramey & Richardson, 2017). However, anthropogenic activities are altering the hydrological and morphological characteristics of aquatic–terrestrial habitats, reducing or eliminating inundation-prone areas and their associated communities (Kennedy & Turner, 2011; Paetzold et al., 2008). Effective monitoring strategies are thus needed to characterize and protect biodiversity within aquatic–terrestrial habitats.

Aquatic–terrestrial riverine habitats are inherently difficult to biomonitor due to temporal variability in events such as inundation (Bates et al., 2006; O'Callaghan, Hannah, Boomer, et al., 2013; Sarneel et al., 2019). For example, mobile, inundation-tolerant ground beetles (Coleoptera: Carabidae) colonize newly dry habitats within days (Bates et al., 2007; O'Callaghan, Hannah, Boomer, et al., 2013). However, less-mobile species avoid recently inundated habitats (O'Callaghan, Hannah, Boomer, et al., 2013). Thus, the outcome of terrestrial biomonitoring in disturbance-prone habitats depends on species-specific responses to events like inundation. Additionally, unpredictable inundation can render standard terrestrial sampling techniques ineffective. For example, passive sampling devices (e.g. pitfall traps) left in aquatic–terrestrial habitats for days-to-weeks may be lost if water levels rise. Equally, rapid bioassessment methods (e.g. ground searching: Webb et al., 2022) can only be used when in-channel habitats are not inundated. Thus, the relative timing of inundation and sampling events influence both sampling success and the species captured, hindering estimation of biodiversity.

Difficulties in characterizing communities within aquatic–terrestrial riverine habitats leave them largely excluded from biomonitoring programmes (Skoulikidis et al., 2017; Stubbington et al., 2018). However, terrestrial invertebrates respond predictably to long-term average habitat conditions (Koivula, 2011; Rainio & Niemelä, 2003), and habitat survey data may thus enable estimation of assemblage characteristics such as taxonomic richness, rarity and composition. Professional habitat survey protocols (e.g. United States Environmental Protection Agency, 2017) are typically complex, requiring equipment and

extensive training to complete, which makes them unsuited to the widespread and frequent assessments needed to characterize aquatic–terrestrial riverine habitats. However, simpler standardized habitat surveys that can be conducted with limited training and equipment have been developed for community (i.e. citizen) scientists (e.g. Shuker et al., 2017). Such habitat survey data can be used to calculate simple, unimetric indicators that characterize key habitat features such as water availability, or be combined into multimetric indicators that summarize overall conditions (Gurnell et al., 2020a). Many such habitat indicators represent features that influence terrestrial fauna, such as habitat complexity, which increases both alpha and beta diversity (Lassau et al., 2005; Lengyel et al., 2016), and could thus enable prediction of invertebrate assemblage characteristics in aquatic–terrestrial riverine habitats.

We evaluated whether habitat indicators can predict metrics characterizing terrestrial invertebrate assemblages, and could thus be used to increase their representation in biomonitoring programmes. Specifically, we selected terrestrial beetles (Table S1) to represent invertebrate assemblages, as a ubiquitous, abundant and diverse group within aquatic–terrestrial riverine habitats (Sadler et al., 2004) which have a wide range of well-known habitat preferences (Rainio & Niemelä, 2003; Webb et al., 2018) and which respond to multiple environmental drivers (e.g. moisture, shade, temperature: Koivula, 2011). In addition, some terrestrial beetles are specialists that rely on aquatic–terrestrial riverine habitats for survival (Bates, 2005), many of which are rare (Webb et al., 2018) and thus require effective monitoring and protection.

Beetle community composition differs both spatially between and temporally within aquatic–terrestrial habitats. We therefore selected biotic metrics that characterize communities regardless of compositional differences (e.g. taxonomic richness), to allow application of our predictive method beyond the habitats tested herein. We hypothesized that habitat indicators can be used to predict beetle assemblage taxonomic richness and conservation status (i.e. rarity) in aquatic–terrestrial riverine habitats (H1). We tested this hypothesis in two habitat types: exposed riverine sediments (ERS) and temporary streams. ERS are fluvially deposited sediments within river channels with perennial flow (Bates et al., 2005; Sadler et al., 2004), whereas temporary streams are those in which surface sediments periodically dry. Both are widespread (Datry et al., 2014; O'Callaghan, Hannah, Williams, et al., 2013), biodiverse (Corti & Datry, 2016;

Sadler et al., 2004) and increasingly threatened by anthropogenic activities (Acuña et al., 2014; Paetzold et al., 2008). We also compared the performance of different habitat indicators, and hypothesized that more complex multimetric indicators can characterize variability in faunal ERS metrics more effectively than unimetric indicators (H2).

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | ERS dataset

We used data collated by Buglife (an invertebrate conservation charity) and Natural England (an advisory body to the U.K. government) from baseline surveys that aimed to characterize the beetle fauna of ERS. The dataset comprises 91 terrestrial beetle assemblage samples collected between May and July in 2003–2019 at 39 ERS sites on nine rivers in England and Wales. All sites were rural, being surrounded by arable land, pasture and/or semi-natural scrubland (Figure S1), with >80% of samples collected from sites which are nationally protected for their wildlife, geomorphology or geology (Natural England, 2021).

Samples were collected by pitfall trapping (n = 34) or ground searching (n = 57: Webb et al., 2022). Pitfall traps comprised buried plastic cups (8 cm diameter, 10 cm height), with the cup lip level with the sediment surface. To preserve beetles, each trap contained 100 ml ethylene glycol and 5 ml detergent. At each site, seven to 10 traps set 2 m apart were left in place for 14 days. On retrieval, all traps from a site were pooled into one sample. Ground searches lasted 1 h, during which time all habitats between the base of the bank and the water's edge along approximately 10 m of the channel were manually disturbed and all organisms were collected using an aspirator. Terrestrial beetles were identified to species level and recorded as present.

The Modular River Survey (MoRPh: Shuker et al., 2017) was used to characterize the physical habitat at each site from five to 10 photographs taken by field surveyors at the time of beetle sampling to depict bank-top land use, bank features and the beetle sampling area. MoRPh surveys are usually conducted in the field, but the type and extent of habitat features can be quantitatively estimated using photographs (Hill et al., 2005) and photographs are used to remotely verify MoRPh data (Gurnell et al., 2020a). Thus, given the large number of photographs from each site, which were taken by trained ecologists seeking to record habitat conditions, the photographs provide an adequate record of habitat conditions from which to complete a MoRPh survey. Minor site-specific features may have been absent or unidentifiable from the photographs, aligning with MoRPh's exclusion of features covering <5% of the survey reach in the calculation of indicators.

Three standardized indicators that represent habitats from the water's edge to 10 m lateral to the bank top were calculated from the MoRPh data (see MoRPh Supporting Information for calculations). Each indicator was selected based on evidence that the habitat conditions it characterizes can influence beetle community responses (Table S2). Habitat complexity (hereafter, HabComplex) is a multimetric indicator calculated from four unimetric components: (1) the type and extent of wood habitat (Wood, e.g. fallen trees, exposed roots); (2) the type and extent of bank-top water features (WatFeat, e.g. ponds, side channels); (3) the type and extent of natural bank-face features (Bank face, e.g. vegetated bars, riverine cliffs) and (4) the type and extent of natural bank profiles (Profiles, e.g. overhanging, gentle). The other two indicators are unimetric, characterizing the number of riparian and bank-face vegetation morphotypes (VegMorph, i.e. short grass/herbs, tall grass/herbs, scrub/shrubs, trees/saplings) and the type and extent of anthropogenic land cover (AnthroCover, e.g. industrial buildings, residential buildings, grazed land, plantation woodland). During calculation, the MoRPh method scales indicators so the probable range of values is 0 (extremely low) to 10 (extremely high: Gurnell et al., 2020b).

2.1.2 | Temporary stream dataset

Two temporary stream datasets were combined. The first dataset, published in Bunting et al. (2021), was collected from five sites in one dry stream (Candover Brook) in south central England between June and September 2019 (Figure S2). The catchment is dominated by arable and pastoral agriculture (51% of total catchment land use), with minimal urban areas (4%). Based on observations from site visits by the Environment Agency (a regulatory body in England), sites had dried 2–181 weeks (±1 week) prior to sampling. Beetles were collected by ground searching (n = 5) and pitfall trapping (n = 10) as described for the ERS dataset, except pitfall traps were left in place for 7 days, not 14 days. The second dataset was collected from one site in each of two dry streams (the Rivers Misbourne and Ver) north of London, England between May and September 2019 (Figure S3). These sites were within or in direct proximity to urban areas which comprise 16%–19% of land use, with wider catchment land uses being primarily arable and pastoral agriculture (34%–51%). Sites had dried 1–220 weeks before sample collection. Beetles were sampled by pitfall trapping (n = 8) as described for the ERS dataset; no ground searching was undertaken. For all temporary stream sites, MoRPh surveys were conducted in the field at the same time as beetle sampling. Terrestrial beetles were identified predominantly to species level (61% of individuals), except some small and ambiguous specimens which were resolved to genus (11%) or family (28%).

2.2 | Data analysis

2.2.1 | Data preparation

In calculating metrics to test H1–2, pooled pitfall trap samples were considered comparable regardless of the number of individual pitfall traps they contained because increased sampling effort (i.e. deploying more traps) has a limited impact on capture rates (Brose, 2002; Webb et. al., 2022). Pooled pitfall traps and ground searches can

capture a similar number of taxa (e.g. Melbourne, 1999; Phillips & Cobb, 2005; Privet et al., 2020; Zanetti et al., 2016), so were also considered comparable (also see Webb et. al., 2022).

To test H1–2, two biological metrics were calculated: taxonomic richness (i.e. the number of taxa per sample, using the vegan package: Oksanen et al., 2019) and the sum of species quality scores (sSQS), an index of conservation status (Webb et al., 2018). To avoid inflation of these biotic metrics, beetles in the temporary stream dataset identified to multiple taxonomic levels were assigned to a most likely taxon (Cuffney et al., 2007). To calculate sSQS, a score for each species based on their threat and rarity status was obtained from a national invertebrate conservation database (*Pantheon*: Webb et al., 2018). Scores range between 1 and 32, with higher values indicating rarer, more threatened species (Table S3). A value of 1 (common native species) was assigned to unscored native species and specimens identified to genus or family. Scores for all taxa in a sample were summed as sSQS. Specialist species (e.g. wood specialists) were also identified using Pantheon, and their method of capture was noted.

Stepwise variance inflation factor analysis (threshold = 3, using the usdm package: Naimi et al., 2014; Zuur et al., 2010) was used to identify collinear fixed effect variables. HabComplex was collinear with its four components, which were therefore not included in the same models.

2.2.2 | Predicting terrestrial invertebrate richness and conservation status

To explore the ability of habitat indicators to predict taxonomic richness and conservation status in ERS, a cross-validation modelling process was used, whereby different randomly selected parts of the dataset were used to train and test model outcomes over 500 iterations (Refaeilzadeh et al., 2009). To train the initial model, a subset of 70 samples was randomly selected, and the remaining 21 samples were used to verify the results. This random selection was repeated for each iteration (i.e. 500 times) to quantify the effect of variability within and between the training and verification subsets. Differences (mean ± standard error) in richness and sSQS between training and verification subsets were calculated for each iteration.

Each subset was used to train negative binomial generalized linear mixed-effect models (NB-GLMMs, using the lme4 package: Bates et al., 2015). NB-GLMMs were used because exploratory analyses highlighted the response variables (i.e. richness and sSQS) were non-normally distributed and overdispersed. HabComplex, VegMorph and AnthroCover were used as fixed effects to predict richness and sSQS. The optimal random effect structure was determined by modelling richness and sSQS with combinations of two potential random factors (sampling site and method: see Burnham & Anderson, 2002) and selecting the most parsimonious structure using Akaike's information criterion (AIC). The final structure for both richness and sSQS training models included only method as a random intercept.

Models derived from each of the 500 training subsets were used to predict richness and sSQS for their respective verification subset.

To test whether habitat indicators can predict assemblage characteristics (H1), the number of subsets with predicted richness and sSQS values that were significantly correlated with observed values was determined using Pearson product-moment correlations. The strength of correlations between observed and predicted values was then summarized for each subset using Pearson's r and reduced major axis regression (RMA, using the lmodel2 package: Legendre, 2018). RMA was selected because observed richness and sSQS values were not truly independent (i.e. uninfluenced by external factors, such as temperature during sampling). Thus, RMA, which allows for variability in both the observed and predicted values, was more appropriate to summarize agreement between the two values than more widely used regression methods (Harper, 2016).

Tables 1 and S4 present the minimum, maximum, mean, standard error (*SE*) and standard deviation (*SD*) (i.e. 'summaries') of the strength (RMA slope, where 1 indicates perfectly correlated variables, and Pearson's r) and significance (Pearson's p) of correlations over the 500 subsets. Table 1 presents summaries of RMA slope for subsets with significant Pearson correlations, because RMA cannot robustly summarize non-significant relationships (as tested using a Pearson correlation: Legendre & Legendre, 2012). These summaries encompass >88% of predictions, offer more robust estimates of the strength of the relationship between observed and predicted values than Pearson correlations and are independent of the testing of H1 (i.e. H1 was tested using the number of subsets with a significant Pearson correlation, not the strength of RMA slopes from only subsets with a significant Pearson correlation). Table S4 presents summaries of RMA slope for subsets with non-significant Pearson correlations for comparison with significantly correlated subsets (Table 1), but should not be considered as evidence for assessing correlation strength. To allow comparisons across all subsets regardless of significance, Table S4 also includes summaries of Pearson's r for all subsets.

Due to the limited number of temporary stream samples ($n = 23$), all ERS samples were used to train a new NB-GLMM following the structure outlined for ERS. This training model was then used to predict richness and sSQS for all temporary stream sites and for rural (i.e. Candover Brook) temporary stream sites only, based on their habitat indicator values. The agreement between observed and predicted values was assessed using ranged major axis regression (RaMA: Legendre, 2018; Legendre & Legendre, 2012), which scales variables prior to regression, thus accounting for differences in taxonomic resolution between ERS and temporary stream datasets.

2.2.3 | Characterization of richness and sSQS by multimetric and unimetric indicators

To test whether the multimetric habitat indicator characterized variability in ERS richness and sSQS more effectively than unimetric indicators (H2), an NB-GLMM was developed for each habitat indicator with richness or sSQS as the response variable and method as a random intercept. The habitat indicator best characterizing variance in richness

TABLE 1 Descriptive statistics summarizing significant reduced major axis (RMA) slopes and associated Pearson product-moment correlation p-values assessing agreement between predicted and observed richness and sum of species quality scores (sSQS) for terrestrial beetle assemblages sampled from exposed riverine sediments

		Minimum	Mean ± SE	Maximum	SD
Richness	RMA slope	0.251	0.638 ± 0.009	1.422	0.200
	Pearson p	0.001	0.009 ± <0.001	0.049	0.011
sSQS	RMA slope	0.258	0.629 ± 0.008	1.405	0.187
	Pearson p	0.001	0.009 ± 0.001	0.049	0.011

and sSQS was identified by AIC, and models with ΔAIC < 2 were considered comparable. Marginal and conditional R^2 (R^2_m and R^2_c) were calculated to quantify the variance explained by each model (using the MuMIn package: Bartoń, 2020).

All analyses were performed in R (R Core Team, 2020), and the DHARMa package (Hartig, 2020) was used to check the assumptions of all NB-GLMMs.

3 | RESULTS

3.1 | Habitat indicators

In ERS, all indicators except Bank face, Profiles and WatFeat occupied the lower range (<5) of values, with Bank face and Profiles being the only indicators exceeding the range of probable MoRPh values (maximum: 12.5). In temporary streams, HabComplex, VegMorph and AnthroCover values were comparable to those in ERS, except one site with a VegMorph value of 4.5 (ERS VegMorph maximum + 0.5) and another site with an AnthroCover value of 6.0 (ERS AnthroCover maximum + 2.0).

3.2 | Assemblage composition

The ERS assemblages comprised 344 species from 22 families. Most species were rove beetles (Staphylinidae: 43.9%) and ground beetles (Carabidae: 28.2%), with the remaining 20 families comprising 27.9%. Richness varied between 2 and 60 (mean ± SE: 22 ± 1.4) species per sample. *Bembidion tetracolum*, *Gastrophysa viridula* and *Paranchus albipes* were the most common species, occurring in 53%–68% of samples. Individual species quality scores ranged from 1 (common) to 16 (Nationally Rare/Scarce and IUCN Endangered; International Union for the Conservation of Nature, 2021; 1.6 ± 0.1), and sSQS from 2 to 66 (28 ± 1.8) per sample. Wood specialists *Barynotus moerens*, *Glischrochilus hortensis* and *Phyllobius glaucus* each occurred in three to five samples, across seven sites at which the Wood indicator ranged from 0 to 1.4, and were only captured by pitfall trapping. These species were not recorded at five sites with comparable or higher Wood indicator values (0–2.9) at which only ground searching was undertaken.

Temporary stream samples contained 114 taxa from 18 families. Most taxa were ground beetles (46.5%) and rove beetles (31.6%), with

the remaining 21.9% including 16 families. Richness varied between 2 and 27 taxa (12 ± 1.9) per sample. Individual species quality scores ranged from 1 to 8 (Nationally Rare/Scarce and IUCN Vulnerable; International Union for the Conservation of Nature, 2021; 1.2 ± 0.1), and sSQS from 2 to 33 (14 ± 2.1) per sample.

3.3 | Predicting taxonomic richness and conservation status in ERS

Five of the 500 ERS iterations were discounted because one of the two sampling methods was represented by insufficient samples to generate accurate estimates. Of the remaining 495 models, 444 (90%) and 438 (88%) predictions of richness and sSQS, respectively, were significantly correlated with observed values from their verification subset, supporting H1. The maximum, mean ± SE and SD of RMA slopes were comparable for richness and sSQS (Table 1, also see Table S4 for corresponding Pearson correlation summaries). Predicted richness and sSQS were on average 0.2 ± 0.1 and 0.3 ± 0.1 lower than observed values, respectively, with predictions of sSQS being more variable than predictions of richness (SD = 14.9 and 11.3, respectively).

3.4 | Predicting taxonomic richness and conservation status in temporary streams

In temporary streams, predicted and observed values were not correlated for richness (RaMA: slope = −0.185, $p = 0.352$) or sSQS (slope = −0.446, $p = 0.267$; Figure 1a,c), contrary to H1. Rural temporary stream assemblages had richness values of 2–25 (mean ± SE: 14 ± 2.0) and sSQS values of 2–31 (16 ± 2.3), whereas in the more urban assemblages, both metrics were lower, ranging from 2 to 7 (4 ± 0.7). As such, only rural temporary stream assemblages were comparable to those in equivalent ERS samples (i.e. pitfall trap samples: richness 13–59 [31 ± 1.8], sSQS 13–66 [39 ± 2.6]). Removing the more urban samples resulted in correlations between values predicted for rural ERS sites and observed in rural temporary stream sites, for both richness and sSQS (richness slope = 0.906, $p = 0.003$, sSQS slope = 1.007, $p = 0.010$; Figure 1b,d), supporting H1. Richness and sSQS in rural temporary streams were over-predicted (richness +5, sSQS +17; Figure 1b,d), likely due to the higher taxonomic resolution of the ERS training samples.
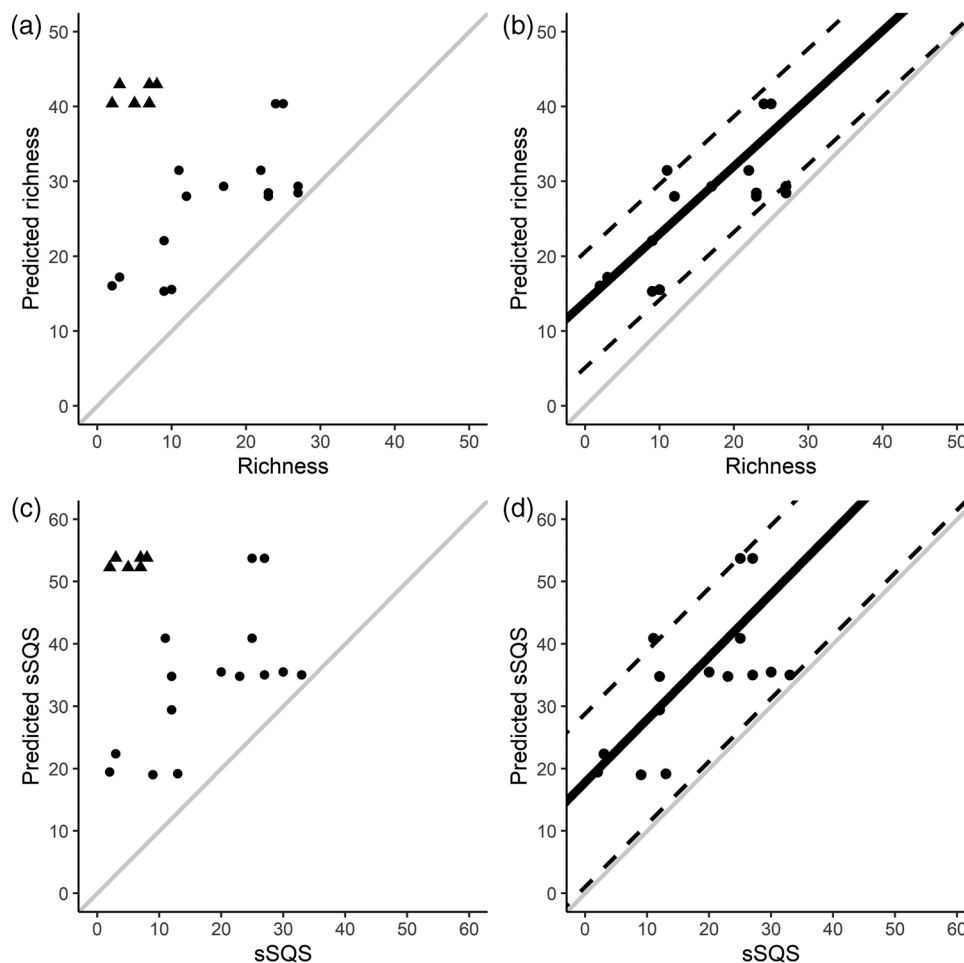
FIGURE 1 The relationship between observed and predicted taxonomic richness (a, b) and sum of species quality scores (sSQS: c, d) for temporary streams including (a, c) and excluding (b, d) assemblages from more urban sites. Triangles and circles represent assemblages from more urban and rural sites, respectively. Grey lines indicate the optimal 1:1 correlation, and solid and dashed black lines indicate the observed correlation and 95% confidence interval

3.5 | Characterization of richness and sSQS by multimetric and unimetric indicators

Richness and sSQS responded to two habitat indicators, increasing with both the multimetric indicator HabComplex and the unimetric indicator WatFeat (Figure 2; Table S5). HabComplex had a 3.7× and 4.4× greater effect than WatFeat on richness and sSQS, respectively. HabComplex and WatFeat each explained 6% of the variance in richness, with other indicators accounting for $\leq 2\%$ (R^2_m) and method for $\geq 20\%$ (R^2_c). HabComplex and WatFeat explained 7% and 5% of the variance in sSQS, respectively, with other indicators accounting for $\leq 2\%$ (R^2_m) and method for $\geq 19\%$ (R^2_c). Contrary to H2, the unimetric WatFeat best characterized differences in taxonomic richness, but characterizations by the multimetric HabComplex were comparable (i.e. <2 ΔAIC from the WatFeat model). HabComplex best characterized differences in sSQS, and was not comparable to the WatFeat model (ΔAIC > 2), supporting H2. To assess the influence of the two samples with HabComplex values <1 (Figure 2a,c), we reran the richness and sSQS models with these values removed.

Models with and without these values had comparable relationship strength (change: ≤ 0.06), significance (≤ 0.003), goodness of fit (≤ 0.01) and relative ranking in terms of AIC. Although non-significant, Wood and Bank face had marginally stronger relationships with sSQS (estimate $\pm$ SE: 0.07 ± 0.06 and 0.06 ± 0.04) than richness (0.04 ± 0.06 and 0.05 ± 0.04).

4 | DISCUSSION

Aquatic–terrestrial riverine habitats support unique terrestrial biodiversity (Sabo et al., 2005; Schindler & Smits, 2017; Soininen et al., 2015), but can be difficult to biomonitor due to temporally variable faunal responses to environmental conditions (Bates et al., 2006; O'Callaghan, Hannah, Boomer, et al., 2013). To address this challenge, we explored two frequently inundated riverine habitats, ERS and temporary streams, to evaluate whether indicators based on habitat survey data could predict metrics characterizing terrestrial invertebrate assemblages. In ERS, significant correlations between observed
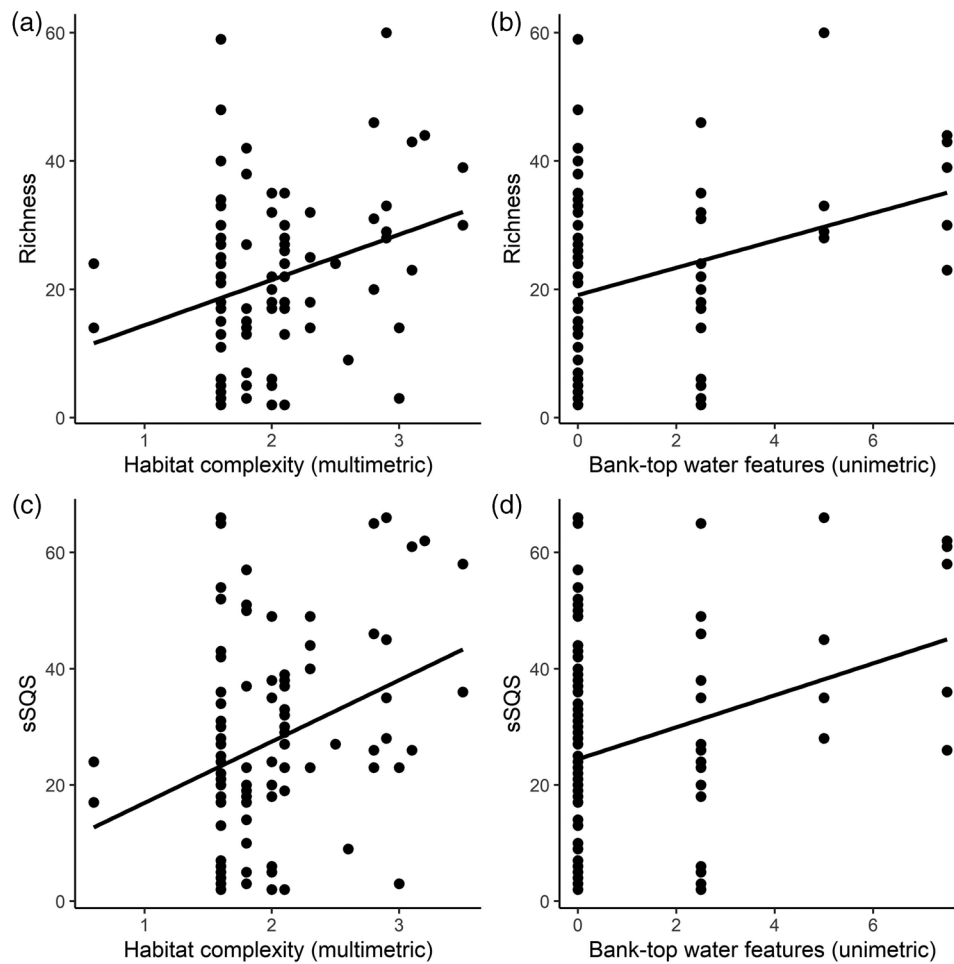
FIGURE 2 The relationship between richness (a, b) and the sum of species quality scores (sSQS: c, d) and the multimetric indicator habitat complexity (a, c) and the unimetric indicator representing the type and extent of bank-top water features (b, d) for terrestrial beetle assemblages sampled from exposed riverine sediments

and predicted taxonomic richness and sSQS, an index of conservation status, suggest that habitat indicators can predict these assemblage characteristics, supporting H1. Correlations between observed and predicted richness and sSQS in rural temporary streams also supported H1 and suggested that predicted assemblage characteristics may enable assessment of biodiversity in a range of aquatic–terrestrial riverine habitats, not just ERS. However, predictions including more urban temporary streams were uncorrelated with observed richness and sSQS, suggesting that better representing human pressures such as land use in habitat indicators could improve future predictions. The effectiveness of unimetric and multimetric habitat indicators (H2) differed for richness and sSQS, suggesting that both may enable monitoring of communities in aquatic–terrestrial riverine habitats.

4.1 | Predicting characteristics of terrestrial invertebrate assemblages

Correlations between observed and predicted values of taxonomic richness and sSQS in both ERS and rural temporary streams suggest that standardized habitat indicators may predict assemblage characteristics in a range of frequently inundated habitats. Such correlations reflect similar habitats in ERS and rural temporary streams (i.e. relatively undisturbed semi-vegetated gravels: Figures S1 and S2), and thus similar community characteristics. Furthermore, the capacity of our habitat indicators (which include the 10 m lateral to the channel) to characterize ERS and rural temporary stream community characteristics suggests that these in-channel communities assemble from nearby riparian zones (Corti & Datry, 2016; Steward et al., 2011, 2022). These similar community characteristics likely arise because ERS, dry temporary streams and adjacent riparian zones have key habitat features in common, such as exposed damp sediments and riparian vegetation that encroaches into the channel as streams dry (Räpple et al., 2017). Thus, biotic metrics (e.g. richness and rarity) predicted from habitat indicators may enable assessment of terrestrial biodiversity in ERS, temporary streams and their adjacent riparian zones by allowing inference of terrestrial community characteristics when time-restricted sampling campaigns coincide with periods of inundation. However, relationships require characterization in a more comprehensive range of temporary stream habitat types and landscape settings to further enhance predictions.

No relationship was detected between observed and predicted richness or sSQS values in more urban temporary streams, likely because (1) urban land use led to habitat conditions (e.g. compacted sediments: Figure S3) that decreased richness relative to rural sites (Martinson & Raupp, 2013) and (2) small-scale differences in habitat characteristics, such as sediment composition, were not detected by the reach-scale habitat indicators used, reducing the accuracy of predictions made from ERS samples. Additionally, 10% and 12% of ERS richness and sSQS predictions were uncorrelated with observed values because their training subsets were less representative of verification subsets, and thus could not be accurately predicted. These uncorrelated cases highlight that training datasets which incorporate a full range of habitat conditions and species occurrences could improve prediction of biotic metrics such as richness and sSQS.

4.2 | Improving future predictions: Evaluating characterizations of terrestrial invertebrate assemblages

We identified positive relationships between richness and both the multimetric HabComplex and unimetric WatFeat indicators. These relationships align with well-known beetle responses to habitat complexity (Lengyel et al., 2016; Staudacher et al., 2018) and water availability (Lassau et al., 2005), increasing confidence that habitat indicators can be used to represent species–habitat relationships. However, the lack of response to VegMorph, AnthroCover, Wood, Bank face and Profiles contrasts with established relationships between community composition, including its taxonomic richness, and vegetation characteristics (e.g. complexity and composition: Greenwood et al., 1995; Rouabah et al., 2015), agriculture and urbanization (French et al., 2001; Magura & Lövei, 2021; Martinson & Raupp, 2013), the type and distribution of woody habitats (Hering et al., 2004; Seibold et al., 2016) and bank face features (e.g. side bars and bank profile: Ramey & Richardson, 2017; Srößig et al., 2020). Thus, community responses may have been masked by both the methods of beetle sampling and of recording these habitat characteristics.

Contrary to H2, WatFeat characterized variability in richness more effectively than HabComplex, but differences were slight. As the only unimetric indicator eliciting a biotic response, WatFeat likely drove the relationship between richness and HabComplex. The marginally weaker performance of the multimetric indicator may thus reflect its inclusion of three non-significant habitat indicators (Bank face, Profiles, Wood), which obscured responses to WatFeat. In contrast, HabComplex best characterized variability in sSQS, supporting H2, and likely reflecting the marginally better performance of two additional components of the multimetric indicator (Wood and Bank face). A multimetric indicator's values depend upon each unimetric component contributing to effects on the response variable, and identification of unimetric indicators that effectively characterize species–habitat relationships is therefore fundamental to accurate, consistent predictions.

Some unimetric indicators calculated using habitat data may be too simplistic to represent species–habitat relationships. For example,

VegMorph summarizes vegetation complexity as the number of morphotypes (Gurnell et al., 2020b), which does not represent vegetation cover, composition or structural diversity, all of which influence beetle distributions (Brose, 2003; Schaffers et al., 2008). Additionally, some beetles require specific habitat resources (e.g. saproxylic taxa on decaying wood: Alexander, 2004; Fowles et al., 1999), which were excluded from calculation of our indicators if covering <5% of the survey area. This coarse characterization of some habitat features may have prevented identification of relationships with biotic communities.

We calculated indicators based on a reach-scale habitat survey, and their detection of beetle responses may have been limited by the differing spatial scales at which habitats are surveyed and at which beetles respond to environmental conditions. For example, although habitat indicators including AnthroCover suggested that ERS and more urban temporary stream survey areas were comparable, catchment-wide urban land uses may have reduced beetle richness and sSQS in temporary streams, for example by disconnecting sites from potential colonist sources (Niemelä & Kotze, 2009). In contrast, VegMorph represents the structural richness of plant communities within a survey area, and was likely too coarse to detect beetle responses to variability in plant densities and community composition within and between habitat patches, which influence beetle movement and predation risk (Allema et al., 2019; Heydemann, 1957).

Biotic sampling is essential in mapping assemblage responses to environmental drivers, here represented by habitat indicators. The biotic assemblages analysed herein were sampled using two well-tested, widely used methods: ground searching and pitfall trapping (Ramírez-Hernández et al., 2018; Skvarla & Dowling, 2017). However, these methods preferentially capture different species, and species with different conservation statuses (Bunting et al., 2021; Webb et al., 2022), potentially hindering characterization of species–habitat relationships. For example, the wood specialists *B. moerens*, *G. hortensis* and *P. glaucus* were caught only by pitfall trapping. These species may have been absent from the five sites (where the Wood indicator ranged from 0 to 2.9) at which only ground searching was undertaken, or present but not sampled, reducing responsiveness to the Wood indicator.

Over-estimation of richness and sSQS in rural temporary streams by ERS training samples (identified to mixed and species level, respectively) highlights taxonomic resolution as an additional source of variance that can potentially hinder prediction of assemblage characteristics and characterization of species–habitat relationships. Therefore, new samples collected to improve prediction of assemblage characteristics from habitat indicators should be collected using a standard multi-method protocol (e.g. Webb et al., 2022) and be identified to the taxonomic resolution at which predictions are required, to avoid introducing variability which could obscure biotic responses.

4.3 | Applications and future directions

This study demonstrates that indicators calculated from habitat survey data can predict terrestrial invertebrate assemblage characteristics.

These predictions are currently sufficient to provide managers with coarse assessments of key assemblage metrics such as richness. While we focused on beetles as a model group, invertebrate taxa including true bugs, true flies and ants contribute to the biodiversity of both ERS and temporary streams (Steward et al., 2022) and respond predictably to habitat conditions (e.g. Buczkowski & Richmond, 2012; Mulieri et al., 2011). Thus, future biodiversity assessments that include a range of terrestrial invertebrate taxa may be used alongside those from aquatic monitoring programmes to provide more comprehensive assessments of the biodiversity within aquatic–terrestrial riverine habitats (Bunting et al., 2021).

Further developing our predictive approach could, for example, enable more precise habitat-survey-based predictions of assemblage characteristics for beetles and other invertebrate taxa, allowing preliminary assessment of habitat quality by managers, researchers and community scientists outside of invertebrate survey seasons, or when site access is not safe or practical. Development of sufficiently accurate predictive models could also enable identification sites at which predicted richness and rarity (or other metrics) are higher or lower than expected based on habitat conditions, informing implementation of conservation and management interventions. In practice, a large and representative training dataset will be required to further improve predictions. Community science initiatives have the capacity to collect large, high-quality biological and environmental datasets (e.g. Brooks et al., 2019; Ratnieks et al., 2016; Shuker et al., 2017) and may thus enable both generation of this training dataset and application of predictive techniques to increase our understanding of the biodiversity within aquatic–terrestrial riverine habitats.

AUTHOR CONTRIBUTIONS

Kieran Gething conceptualized the study (lead), curated the data, designed the methodology, performed formal analysis, wrote the original draft, administered the project and reviewed and edited the manuscript (equal). Chloe Hayes and Jonathan Webb performed investigation (equal) and reviewed and edited the manuscript (equal). Tim Sykes and Judy England reviewed and edited the manuscript (equal). Rachel Stubbington conceptualized the study (supporting) and reviewed and edited the manuscript (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xwdbrv1hg (Gething et al., 2022).

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PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Number of species, percent of total species and frequency of occurrence in samples per family.

Table S2. Literature highlighting the role of habitat complexity (HabComplex), no. of vegetation morphotypes (VegMorph) and anthropogenic land cover (AnthroCover: equivalent to indicators 10—12 in Gurnell et al., 2020b) in influencing beetle communities.

Table S3. Quality scores attributed to species of differing conservation status, adapted from Webb et al. 2018.

Table S4. Descriptive statistics of non-significant reduced major axis regressions (RMA) and Pearson product-moment correlations between predicted and observed richness and the sum of species quality scores (sSQS) for terrestrial beetle assemblages sampled from exposed riverine sediments.

Table S5. Negative binomial generalised linear mixed-effect model results for richness and the sum of species quality scores (sSQS) as predicted by habitat complexity (HabComplex), the number of vegetation morphotypes (VegMorph), the type and extent of anthropogenic land cover (AnthroCover), the type and extent of bank-top water features (WatFeat), the type and extent of natural bank-face features (Bank face), the type and extent of wood habitat (Wood) and the type and extent of natural bank profiles (Profiles).

Figure S1. Examples of channel characteristics and surrounding land use at Exposed riverine sediment sampling sites, photographs courtesy of Natural England, Bug life and Staffordshire Wildlife Trust.

Figure S2. Channel characteristics and surrounding land use at rural temporary stream sites.

Figure S3. Examples of channel characteristics and surrounding land use at urban temporary stream sites.

Table M1. Wood habitat features and their contribution to the Wood index when present or extensive within a surveyed reach.

Table M2. Bank-top water features and their contribution to the WatFeat indicator when present or extensive within a surveyed reach.

Table M3. Bank face features and their contribution to the Bank face indicator when present or extensive within a surveyed reach.

Table M4. Anthropogenic land cover types and their contribution to the AnthroCover indicator when present or extensive within a surveyed reach.