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Research

Populations of high-value predators reflect the traits of their prey

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The extent to which prey traits combine to influence the abundance of predators is still poorly understood, particularly for mixed predators in sympatry and in aquatic ecosystems. In this study, we characterise prey use and distribution in iconic bird (grey wagtails and Eurasian dippers) and fish species (brown trout and Atlantic salmon) to assess whether prey traits could predict populations of these four riverine predators. Specifically, we hypothesised that: 1) prey key traits would predict predator populations more effectively than 2) diversity of prey traits, 3) the taxonomic abundance or richness of prey (known as traditional or mass-effect types of biodiversity) or 4) the prevailing environmental conditions. Combined predator population sizes were predicted better by a few key traits – specifically those revealing prey habitat use, size and drifting behaviour – than by prey diversity or prey trait diversity or environmental conditions. Our findings demonstrate that the complex relationships between prey assemblages and multiple predator species can be represented mechanistically when the key prey traits that govern encounter and consumption rates are identified. Given their apparent potential to reveal trophic relationships, and to complement more traditional measures of prey abundance, we advocate further development of trait-based approaches in predator–prey research.

Keywords: aquatic ecosystems, Atlantic salmon, biodiversity, brown trout, ecosystem services, Eurasian dipper, grey wagtails, predator–prey interactions

Introduction

Research into factors affecting the distribution and abundance of predators has been a perennial theme in ecology, focussing often on prey availability and, at least in single species systems, on the dynamics of predator–prey interactions (Volterra 1928, Lotka 1932, Lima 2002, Pintar and Resetarits 2017). In reality, however, predators and their prey seldom occur in isolation, instead forming multispecies communities in complex environments (Blumstein 2006, Rooney et al. 2006). While artificially simplified

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communities provide some insight into mechanisms by which prey numbers can affect predator populations (Petchey 2000, Narwani and Mazumder 2012), extrapolation to more complex communities is difficult in the absence of more extensive field evaluations (Sinclair et al. 2003, Yang et al. 2018). The dearth of synecological studies in real communities also limits the scope to develop or test prey-based models from which to predict predator population sizes (Eisenhauer et al. 2019, van der Plas 2019).

Assessing mechanistic interactions between multiple predators and their prey over large spatial extents is particularly challenging. One option is the use of functional traits – assumed to represent features of organisms that affect ecosystem processes including those related to predator–prey interaction (Kane et al. 2017, Schmitz 2017, Brose et al. 2019). Understanding the influence of prey traits on predator populations requires knowledge of 1) the ability of a prey species to persist in a given environment, and 2) their influence over predator populations while they are present in that environment. These traits can be grouped as 'response traits' and 'effect traits', respectively (Suding et al. 2008). Combined with an ecosystem-level view and data on predator–prey abundances, trait-based approaches could yield insights into multispecies trophic relationships that are both realistic and potentially mechanistic (McGill et al. 2006, Schmitz 2017). So far, however, few studies have used this approach at sufficient scale or with sufficient replication across sites to yield meaningful outcomes.

Together with traditional measures, prey trait-based measures might be used to parameterise bottom–up effects on predators in four hypothetical ways: through key traits, trait diversity, traditional taxonomic diversity and abundance measures alone or alongside measurements of environmental conditions. Key traits include those that determine prey vulnerability and prey nutrient content, which might affect predator populations by mediating predation rates (Blumstein 2006, Kane et al. 2017, Gutiérrez-Cánovas et al. 2020). Other key prey traits might confer resistance and resilience to environmental change in ways that influence prey availability (Suding et al. 2008, McLean et al. 2019). Trait diversity could support predator populations by increasing the opportunity for predators to capture prey more efficiently across a greater array of habitat, morphological and behavioural strategies (Tilman et al. 1997, Petchey 2000, De Crespin De Billy et al. 2002). Large trait diversity might also insure against stressful conditions (McLean et al. 2019). More simply, basic taxonomic diversity and abundance could affect prey availability, irrespective of trait representation, according to the mass-effect hypothesis (Hubbell 2005). Finally, a wide range of environmental conditions are likely to affect predator populations through abiotic filtering (Kraft et al. 2015). To our knowledge, however, there have been few studies to examine the relative utility trait-based bases through these four types of metrics to understand or predict mixed predator distributions.

In addition to the fundamental scientific interest in predator–prey interactions, there is considerable interest in the conservation profile and societal value of predators (Snyder et al. 2006, Ripple and Beschta 2012, Schneider et al. 2012, Hammerschlag et al. 2019). In the case of rivers, many ecosystem services are delivered by biota (Woodward et al. 2012, Perkins et al. 2015, Durance et al. 2016, Hammerschlag et al. 2019) among which apex predators such as birds and salmonid fishes underpin economic and social values ranging from recreational fishing and ecotourism to direct cultural significance or role as indicators of environmental quality (Butler et al. 2009, Green and Elmberg 2014, Harrison et al. 2014, Steven et al. 2015, Gaston et al. 2018, D'Souza et al. 2020, Worthington et al. 2020). In western Europe, river birds such as grey wagtails *Motacilla cinerea* and Eurasian dippers *Cinclus cinclus* exemplify the conservation and cultural significance of river bird species (Green and Elmberg 2014). Among riverine fishes, Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* not only have iconic conservation status, but rank among some of the world's most economically valuable freshwater organisms (Butler et al. 2009). Recreational fishing is a global industry (Cowx 2008), and in rural areas boosts the influx of visitors, employment and local economies (Peirson et al. 2001, Aprahamian et al. 2008).

Despite their ecological, scientific and cultural importance, predators are amongst the most threatened organisms on Earth (Ripple et al. 2014). Because of their apex position in food webs, predator populations are at risk from a range of global changes that arise through bottom–up influences on flows of energy and matter from lower trophic levels (Estes et al. 2011, Perkins et al. 2018, Brose et al. 2019). Particularly in the wake of concerns about changing macroinvertebrate communities (Durance and Ormerod 2007, Sánchez-Bayo and Wyckhuys 2019, Baranov et al. 2020), there is some urgency to understand which features of prey biodiversity are most important both in sustaining predator populations and in appraising risk.

Here, our goal was to identify the prey biodiversity metrics that best predict single and multi-predator population sizes. First, we characterised the diets of four riverine predators (grey wagtails, Atlantic salmon, brown trout and dippers) across continental Europe and the British Isles to compile a comprehensive trait database to reflect their prey spectrum. Next, we used these databases, alongside intensive sampling of 84 Welsh (UK) rivers (Durance et al. 2016), to compare the ability of different prey biodiversity metrics to predict the size of the four predator populations, and to determine to what extent these four predator species could be sustained simultaneously under current environmental conditions. Given that all prey traits may be not equally effective in driving prey–predator encounter and capture rates (Gagic et al. 2015, Kane et al. 2017, Schmitz 2017), we hypothesised that: 1) prey key traits would predict predator populations more effectively than 2) diversity of prey traits, 3) the taxonomic abundance or richness of prey (known as traditional or mass-effect types of biodiversity) or 4) the prevailing environmental conditions.

Material and methods

Predator diets

Data collection
We reviewed 36 publications reporting on over 70 rivers across Europe and the British Isles to assess prey composition in the four selected predators based invariably on large samples (e.g. n = 2156–4850 prey, Ormerod and Tyler 1986, 1991a, b). We recorded sampling locations as well as the mean abundance of macroinvertebrate prey (generally genus or family) found during surveys using methods that included the analysis of guts, faeces or regurgitates. Studies typically provided monthly or seasonal values for all the individual prey collected at each sampling point.

Trait database
We built on previous work (Rader 1997, De Crespin De Billy and Usseglio-Polatera 2002, Tachet et al. 2002) to compile an extensive database that characterises instream macroinvertebrates according to their traits, as opposed to traditional taxonomy (Supporting information). We then used this database to assess the prey of wagtails, trout, salmon and dippers according to features that influence their availability to the predators, including behaviours and morphology (referred to as effect traits); and features of life-history that determine the persistence of prey under various environmental conditions (referred to as response traits). For all the macroinvertebrate prey, we recorded ten effect traits and seven response traits.

Effect traits such as body size, drift tendency, mobility and habitat preferences were compiled from all known available databases (Rader 1997, De Crespin De Billy and Usseglio-Polatera 2002, Tachet et al. 2002). The seven response traits were compiled from a single database (Tachet et al. 2002), and describe a taxon's capacity to cope with environmental change: generations per year, lifespan, aquatic stage, reproduction type, respiration, dispersion and resistance forms. Except for drift tendency (Rader 1997) (continuous trait ranging 0–100) and calcium content (single-column, categorical, 'low' or 'high' calcium content), traits were split into various columns representing different affinity categories (e.g. lifespan was divided into '≤ 1 year' and '> 1 year' categories). For each macroinvertebrate genus, total affinity points (i.e. 3, 5, 7) were distributed across the categories of each trait, according to the frequency of occurrence within the genus. This approach is called fuzzy coding (Chevenet et al. 1994), and entails compiling the intraspecific biological information available for the species belonging to each genus (e.g. juvenile and adults, male and female, different species). To standardize the potential differences in the codification scores, fuzzy coded data were converted to percentages of affinity for each trait before analysing data.

All four of the predators studied are visual hunters (Elliott 1973, Bannon and Ringler 1986, Ormerod and Tyler 1986). The rate at which these predators encounter prey items is an important variable for predicting the amount of prey items that can be consumed. This is especially pertinent in unproductive and nutrient-poor upland systems, where prey availability is low (Arscott et al. 2005). Key determinants of encounter rates include: the way prey use habitats, the way they roam and disperse in river currents, and the size of their bodies (Elliott 1973, Rader 1997, Usseglio-Polatera et al. 2000, Woodward and Hildrew 2002, Schneider et al. 2012). Macroinvertebrates drifting in the water column, for example, are more exposed to salmonid predators, while prey that are epibenthic are more susceptible to dippers and wagtails. We used prey effect traits (including body size or the potential to hide or evade predators) as proxies of predator–prey encounter rates (Supporting information). We also explored the putative influence of environmental change on predator–prey interactions through traits that included the duration of prey life cycles, method of respiring and reproductive strategies (Supporting information; Díaz et al. 2008, Verberk et al. 2008, Kearney and Porter 2009).

Prey and predator surveys

Study area
We sampled 84 independent headwater rivers across upland Wales (UK). The study area (11 000 km²) is representative of Piedmont maritime western Europe (mean annual air temperature: 7.2–9.5°C, mean annual precipitation: 1000–1600 mm). Sampling sites were 44–438 m a. s.l. on rivers draining all the main upland land-use types: moorland, pasture, conifer plantation and broadleaf woodland (Durance et al. 2016). All rivers were characterised by riffles or cascades with steep slopes (> 5–200 m km⁻¹), current velocities typically 30–70 cm s⁻¹ and monthly stream temperatures in the range 1–7°C (winter) to 7–20°C (summer) ensuring that oxygen concentrations were always high and fully saturated (Ormerod and Edwards 1987, Rutt et al. 1989, Weatherley and Ormerod 1990, Brewin et al. 1998). At each site, we surveyed the macroinvertebrate community, the abundance of wagtails and dippers, and the biomass of trout and salmon.

Bird surveys
At each site during the breeding season of April to early July 2013, on three mornings separated by at least three weeks, 1 km each way up- and down-stream of sampling sites were surveyed by professional field ornithologists for the abundance of territory-holding pairs of wagtails and dippers. All detections of wagtail and dipper (by sight or sound) were collated; and the counts, activity and exact locations (e.g. pair seen together, two males interacting, family parties) were recorded on fine-scale maps using standard territory mapping protocols (Bibby et al. 2000). At the end of the breeding season, all registrations were assessed by a British Trust for Ornithology ornithologist trained in territory mapping to calculate the total number of occupied territories per site, over the 2 km stretch.

Fish surveys
Up to four electrofishing surveys estimated trout and salmon biomass at 39 (146 surveys) and 32 (121 surveys) of the

84 sites, respectively. Between June and September 2012, and July and September 2013, fish were surveyed under stable base-flow conditions via quantitative electrofishing of representative 30–50 m reaches enclosed with stop nets (mesh size: 10 mm²). Each survey consisted of a standard three-pass depletion procedure, which generally captures a large percentage of individuals present and represents total abundances in upland streams (Kruse et al. 1998).

We used a battery-powered Pulsed DC Electracatch bankside set-up (Smith-Root Europe Ltd. Killney, Ireland) set at 50 Hz (optimal for salmonids; Beaumont 2011), and voltage set according to site conductivity. Fish were identified to species (Maitland 1972), weighed to the nearest gram and measured (fork length) to the nearest millimetre. Length–mass relationships for the data collected in 2012 were used to estimate masses of fish which couldn't be determined accurately. Wet weight was transformed to dry mass using a conversion factor of 0.234 and 0.218 for trout and salmon, respectively (Froese and Pauly 2016). At the 32 coincident sites where wagtails, trout, salmon and dippers were surveyed, the sum of the standardised mean values of their population sizes provided a multi-predator index.

Macroinvertebrate surveys

Macroinvertebrates were gathered via two-minute, semi-quantitative kick sampling of riffles during the springs of 2013 and 2014, preserved in 70% industrialised methylated spirit, and most were identified to genus. This strategy is well-calibrated for detecting biological differences between sites (Bradley and Ormerod 2002). Genus-level information is sufficient to study the major functional patterns of lotic macroinvertebrates (Gayraud et al. 2003).

Testing the four types of prey metrics

We calculated nine metrics to represent the four hypothesised mechanisms that could explain bottom–up influences on predators: key traits, trait diversity, traditional measures and environmental conditions.

Key trait metrics

To estimate the abundance of prey groups with effect trait combinations likely to influence predator populations, we first classified macroinvertebrates (Ward's clustering method) based on their effect traits, via Gower dissimilarity (Pavoine et al. 2009). Effect trait combinations were identified (Supporting information) and, along the first axis, separated organisms from slow flowing water (FG1, FG4) from those in fast flowing water with some tendency to drift (FG2, FG3). Along axis 2, prey with larger bodies (FG2, e.g. Heptageniidae, Perlidae, Rhyacophilidae) were separated from those with smaller bodies of which some drifted between patches (FG3, e.g. Baetidae, Chironomidae or Simuliidae). We then estimated the abundance of taxa belonging to FG2 and FG3 to represent 'key trait' metrics.

Trait diversity metrics

We represented possible trait diversity mechanisms by two metrics, respectively the richness of effect and response traits (TD-e and TD-r, respectively). Effect and response traits were analysed separately using principal coordinate analysis (PCoA, based on 7-dimensional effect and 8-dimensional response trait spaces) based on Gower dissimilarity matrices (Pavoine et al. 2009, Maire et al. 2015). Effect space represented ~68% of the original effect trait variance (mean squared deviation = 0.009), while response trait space accounted for ~75% of the response trait variability (mean squared deviation = 0.007). These metrics were estimated as the portion of effect or response space filled by each community, and ranged between 0 and 1 i.e. functional richness (Villéger et al. 2008).

Traditional measures of mass-effect

We calculated macroinvertebrate prey richness (taxon richness = ric) and abundance (number of individuals = abun) as traditional measures commonly used as mass-effect descriptors that could influence predators.

Environmental condition metrics

Our study concentrated on lotic reaches of upland rivers characterised by oxygenated, cool and fast-flowing waters. They are most unpolluted other than through the historical effects of acid rain. We thus focused on abiotic factors that varied strongly across the study sites, specifically acid–base status (pH) and altitude. These factors capture major influences on community composition in our study sites, affecting both fish and river birds through synoptic representation of broader aspects of ionic composition and physiography (Wade et al. 1989, Ormerod and Tyler 1991a, Bussi et al. 2018).

Data analysis

Based on dietary data collected from the literature and using linear mixed-effect models (LMM), we examined how each of the four key trait prey groups (FG1, FG2, FG3, FG4) contributed to the diet of each of the four predators. To account for the lack of independence of diets extracted from the same regions, the 'source study' of each data was considered as random factor. The p-values were estimated using conditional F-tests based on Kenward–Roger approximation for degrees of freedom (Kenward and Roger 1997), using the R package *pbkrtest* (Halekoh and Højsgaard 2014). We used Tukey post hoc tests to assess pairwise comparisons between FG contributions to each predator diet.

To test the four hypothesised mechanisms of prey effects on predators, we assessed whether prey key traits, prey trait diversity, traditional measures of prey richness and abundance or environmental conditions best predicted wagtail, trout, salmon or dipper population sizes using a multi-model inference approach (Burnham et al. 2011). Tests were made for single predator populations (e.g. wagtail only) as well as for all four predators taken together (hereafter the

multi-predator index). We built seven models including one or two predictors according to our hypothesised mechanisms: two models each to represent the concepts of key traits (FG2, FG3) and trait diversity (TD-e, TD-r), two models to represent mass-effect traditional measures (ric, abun) and a single model to represent environmental conditions (both pH and altitude) (Table 2). We also tested models including predictors representing two or more hypothesis simultaneously. We avoided predictor combinations with substantial collinearity (variance inflation factor > 2 (Zuur et al. 2009)). Supporting information shows pairwise collinearity among predictors of each dataset.

For each predator, and also for the multi-predator index, we ranked the models according to their explanatory power and complexity, using the Akaike information criterion corrected for small sample size (AICc) and evidence weights ('MuMIn' package, Bartoń 2016). A generalised linear model (GLM) with a Poisson error distribution was used to model wagtail and dipper abundances, while a LMM with a Gaussian error distribution was used to model trout and salmon biomasses. Prey and environmental metrics were fixed terms and site was a random intercept, to account for repeated measures. For GLM, pseudo-R^2 was calculated based on relative explained deviance out of total deviance. For the LMM, we estimated the variances explained by fixed terms ($r^2_{marginal}$) and by the combination of fixed plus random terms ($r^2_{conditional}$) (Nakagawa and Schielzeth 2013). Residuals were observed for adherence to model assumptions of normality and homoscedasticity. To reduce distribution skewness, we applied a square-root transformation to trout and salmon biomasses and to effect trait diversity (TD-e), and a log-transformation to key trait metrics, response trait diversity (TD-r) and macroinvertebrate abundance. All predictive metrics were standardised (mean = 0, SD = 1) to facilitate model coefficient comparison (standardized effect sizes).

To understand further how macroinvertebrate prey biodiversity might simultaneously affect the four predator populations, we also adopted the multi-threshold approach developed by Byrnes et al. (2014) (*multifunc* package) to investigate the relationships between biodiversity and predator population sizes. Applied to our study, this procedure involves conducting separate linear regressions (Gaussian error term) that relate the number of predator populations simultaneously exceeding a defined threshold relative to population maximum sizes in the study (from 1 to 99%), with one of our prey metrics (Table 1). We selected FG3 abundance and effect trait richness (TD-e) as they were the best prey predictors of the multi-predator index for the key traits and trait diversity hypotheses, respectively, and both traditional measures of mass-effects (macroinvertebrate prey richness and abundance), as they were widely used in literature.

All data analyses were performed using R statistical software (<www.r-project.org>). We provide the code and functions to reproduce the approach presented here in the Supporting information.

Results

Diet analysis

Across continental Europe and the British Isles, macroinvertebrate prey with a preference for fast flows and coarse substrata such as gravel, pebbles and cobbles, were significantly the dominant aquatic items in the diets of grey wagtails, trout, salmon and dippers (FG2 and FG3 in our trait-effect classification; Fig. 1, Supporting information). Brown trout (mean: 54.3 ± 3.3%), Atlantic salmon (74.9 ± 2.4%) and dippers (64.3 ± 4.8%) fed mostly on taxa from FG3, characterised particularly by preference for fast flows, propensity to drift and small-to-moderate body size (Fig. 1). Fast-flow macroinvertebrate prey featuring larger body sizes (FG2) had also a substantial contribution to trout (8.2 ± 1.9%), grey wagtail (7.2 ± 1.1%) and dipper diets (mean: 16.9 ± 1.1%). Modelling revealed a strong consistency between the availability of such favoured prey and the size of the predators' populations.

Comparing the influence of key traits, trait diversity, traditional measures and environment on predator population sizes

Data from intensive sampling in 84 Welsh rivers supported our central hypothesis: predator populations closely tracked the key traits of prey. Key traits outperformed trait diversity and mass-effect traditional measures as predictors of grey wagtail, trout and salmon populations (Fig. 2, 3) and when combined into the multi-predator

Table 1. Proposed mechanisms and associated metrics to explain the population sizes of four riverine predators.

| Hypothesis	Description	Mechanism	Metrics
Key traits (Key)	Abundance of prey showing higher encounter rates (fast-flow, drifting prey)	Prey with certain trait combinations are key to sustain predator populations	FG2, FG3
Trait diversity (TD)	Variety of prey morphological and behavioural features affecting encounter rates and/or traits conferring resistance and resilience to environmental change	When predators are complementary, prey trait diversity enhance foraging efficiency and predator populations	TD-e, TD-r
Mass-effect (Mass)	Availability of individuals or taxa (prey abundance or richness)	Prey features are unimportant – prey abundance or richness increases predator populations	ric, abun
Environment (Env)	Local environmental conditions	Prey features are unimportant – environment drives changes in predator populations	pH, altitude
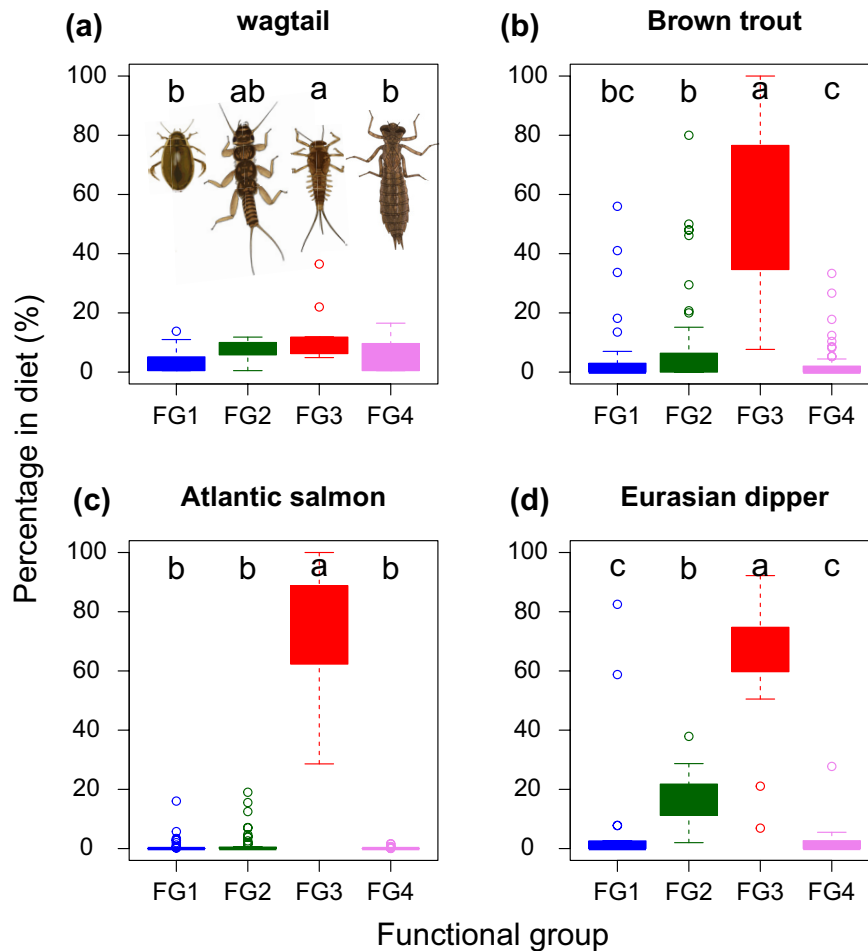
Figure 1. Diet characterisation for four riverine predators. Variation in the relative contribution (percentage) of the four functional groups of aquatic invertebrates to the diet of predator species, based on data extracted from the literature and our databases. Letters above each bar represent post -hoc results. Macroinvertebrate illustrations show representative taxa for each prey group (FG1: Dytiscidae, FG2: Perlidae; FG3: Baetidae; FG4: Aeshnidae).

index (Fig. 4a, Table 2). Both key traits and mass-effect traditional measures were effective predictors of dipper populations (Fig. 2b, 3b). Environmental conditions were of lesser importance ($r^2 = 0.02$–0.26), although explained some variation in grey wagtail ($r^2 = 0.06$) and salmon ($r^2 = 0.20$) populations, as well as the multiple predator index ($r^2 = 0.25$) (Fig. 2 , Supporting information). Models including predictors that represented multiple hypotheses were less explanatory than the best models including some of these metrics in isolation.

In all cases, wagtail, trout, salmon and dipper population sizes increased with metrics of key traits and mass-effect traditional measures up to a certain point of saturation (Fig. 3, 4, Table 2). Of the key trait metrics, the abundance of FG3 prey (small organisms of fast flowing waters) was generally the best predictor of all predator population sizes ($r^2 = 0.04$–0.32). Among the traditional measures, macroinvertebrate abundance generally explained more variation among predator populations ($r^2 = 0.03$–0.31), but macroinvertebrate richness was the best predictor of dipper populations ($r^2 = 0.18$). Metrics of trait diversity had low explanatory

power ($r^2 = 0.00$–0.12), sometimes correlating positively and negatively with predator population sizes.

Predator population size co-variation

Measures of the four predator populations varied independently. At the 32 sites where all four predators were recorded, we found a mean pairwise Spearman rank correlation of $r_s = 0.16$ among their numbers (ranging from $r_s = -0.18$ to $r_s = 0.37$). In the full bird dataset (n = 84), dipper and wagtail were weakly correlated ($r_s = 0.27$). Similarly, there was a very weak rank correlation between mean trout and salmon biomasses ($r_s = 0.12$), for the coincident sites (n = 32).

Multi-threshold analysis revealed that the abundance of FG3 prey, the most explanatory key traits metric in our models, could maintain simultaneously up to 23% of the maximum population sizes of the four predators. Metrics representing traditional measures (macroinvertebrate richness and total abundance) and trait diversity (TD-e) could not support all four predator populations simultaneously; nor could they support three predator population sizes
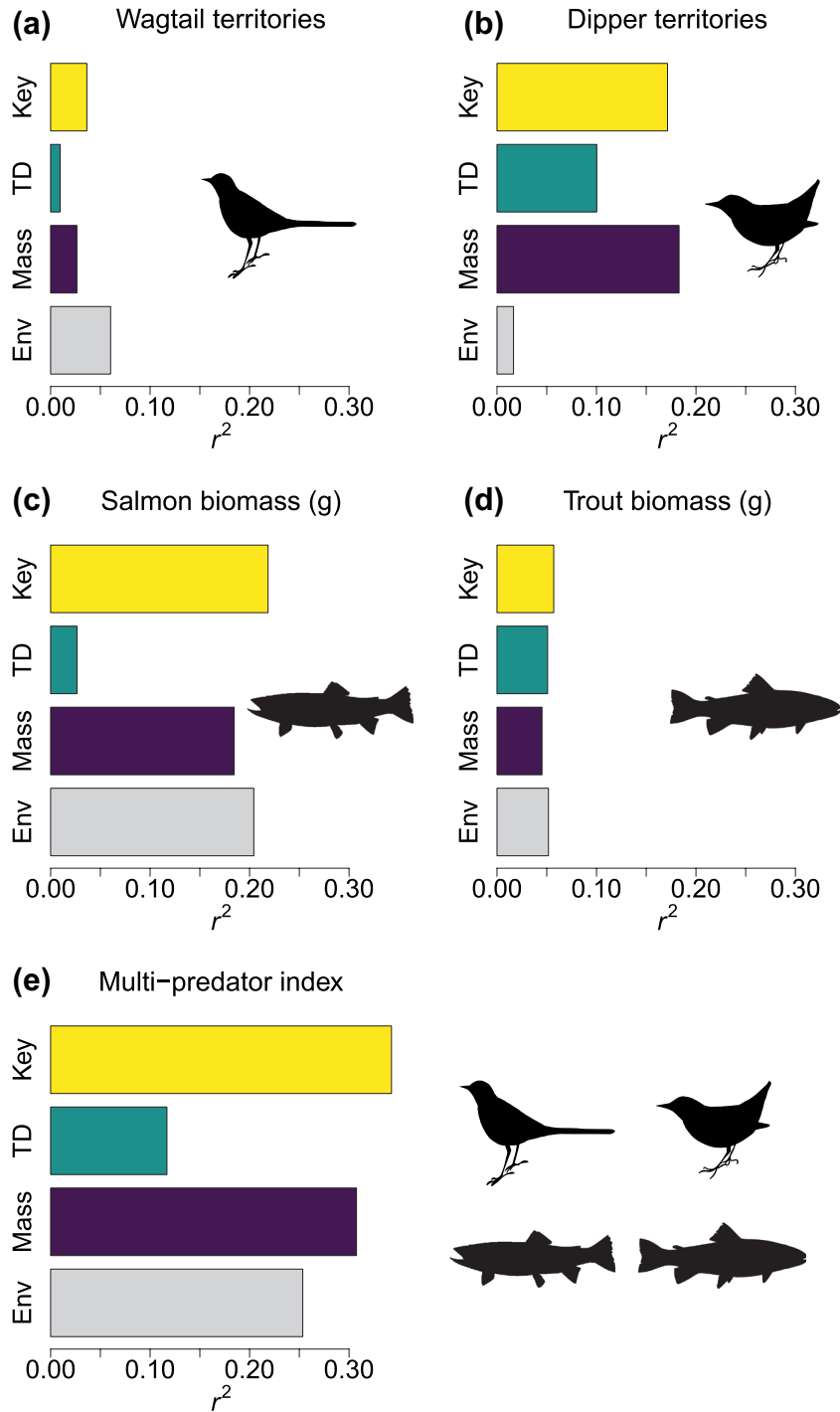
Figure 2. Predictor explanatory capacity (r²) of the best prey and environmental metrics predicting the population sizes of riverine predators alone or in combination (a–e). Yellow: key traits (Key); green: trait diversity (TD); purple: traditional measures of mass-effect (Mass); grey: environmental conditions (Env).

at the same performance level as the abundance of FG3 prey (Fig. 4b).

Discussion

Our results support the 'key traits' hypothesis by revealing how the presence of key prey traits related to prey susceptibility or quality predicted predator populations more effectively than the diversity of prey traits, the taxonomic abundance or richness of prey or the prevailing environmental conditions. Despite widespread advocacy for studies of this type (Duncan et al. 2015, Schmitz 2017, Hammerschlag et al. 2019), to the best of our knowledge this is the first large-scale assessment of multiple prey–predator relationships in
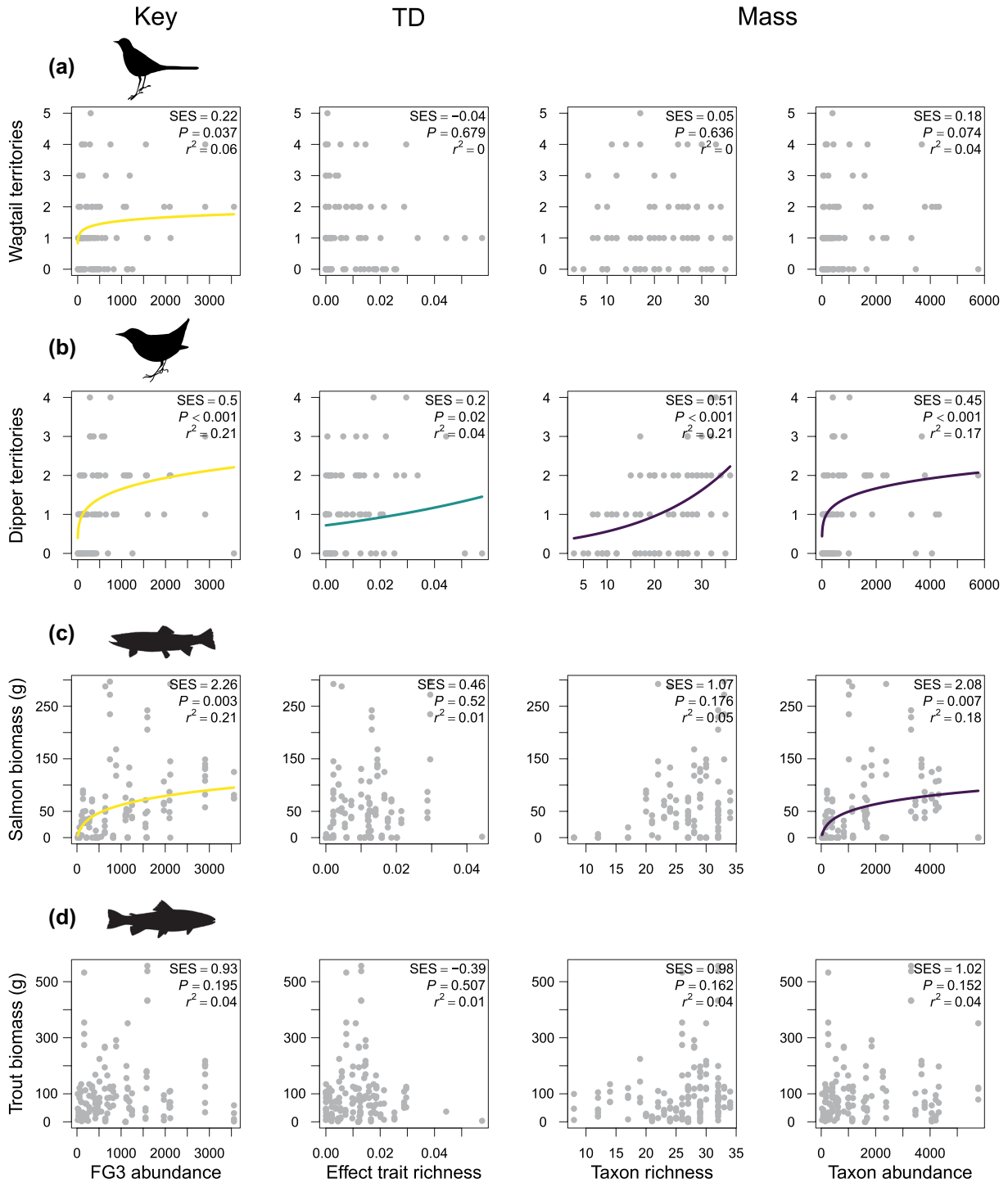
Figure 3. Relationships between the population sizes of riverine predators and selected metrics (a–d). Fitted values for grey wagtail (a, n = 84), Eurasian dipper (b, n = 84), Atlantic salmon (c, n = 121) and brown trout (d, n = 146) are represented only for significant relationships (p ≤ 0.05) as a yellow line for key traits (Key), green line for trait diversity (TD) and purple line for traditional measures of mass-effects (Mass) models. Standardised effect size (SES), p-value (p) and explained variance by fixed factors (R^2) are shown for each predictor.

freshwater ecosystems using a range of ecologically meaningful freshwater metrics.

Our results indicate that out of four potential bottom–up influences on predators, the key trait hypothesis held best.

This is a development from previous experimental research on single predator populations where prey diversity and abundance were identified as likely influences on predator population size and stability (Petchey 2000, Pintar and
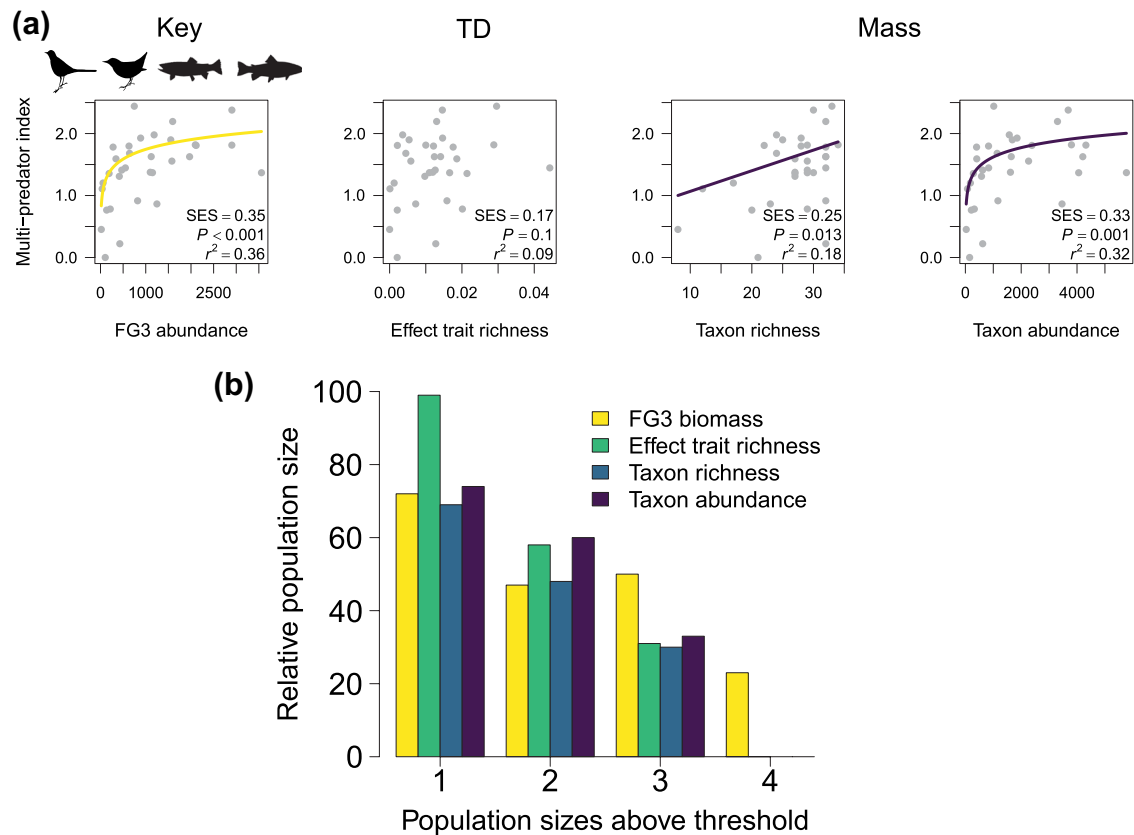
Figure 4. Relationships between the multi-predator index for rivers (a) and various prey metrics using the multi-threshold analysis (b) (n = 32). Fitted values are represented only for significant relationships (p ≤ 0.05) as a yellow line for key traits (Key), green line for trait diversity (TD) and purple line for traditional measures of mass-effects (Mass) models. Standardised effect size (SES), p-value (p) and explained variance by fixed factors (r²) are shown for each predictor. We show the maximum performance level (relative population size) at which predator population sizes can be sustained simultaneously for each prey biodiversity aspect.

Resetarits 2017). That said, we found the best predictions for single predator populations included a key trait (the smaller, abundant macroinvertebrates from fast flowing water, FG3) but also some traditional measures (total invertebrate richness and abundance).

Variation in diets aside (Ormerod and Tyler 1987, Ormerod 1996, Dineen et al. 2007, Eros et al. 2012), prey typical of fast flowing water appeared to be important for all four predator populations. Key prey trait metrics were less effective in tracking the population sizes of the more generalist grey wagtail and brown trout. This may be explained by the their known reliance on combinations of aquatic and terrestrial prey that were not captured completely by our benthic measurements (Tyler and Ormerod 1991, Dineen et al. 2007, Perkins et al. 2018).

The multi-predator index, which represents the combined populations sizes of grey wagtail, trout, salmon and dipper, was also best explained by prey key traits. Other studies exploring prey biodiversity effects on multi-predator systems in natural systems found contrasting results that support either mass-effects of prey diversity (Sinclair et al. 2003, Yang et al. 2018) or key prey groups (Hörnfeldt et al. 2005, Delibes-Mateos et al. 2008). However, because the majority of previous studies did not consider prey traits, we cannot make comprehensive comparisons.

There is evidence that predators in very productive systems might benefit from a diverse prey trait representation to allow predator co-existence (Sinclair et al. 2003, Bluhm and Gradinger 2008). In less productive ecosystems such as the uplands studied here, or even in Artic (Hörnfeldt et al. 2005) or semi-arid systems (Delibes-Mateos et al. 2008), the scarcer top predators might be adapted to certain prey groups which are abundant and vulnerable. Our findings suggest that studies focusing on overall species richness or abundance as sole predictors of predator populations may have misrepresented the capacity of these less productive ecosystems to support multiple predator populations, and the ecosystem services they provide. Here lies a clear priority for manipulative experiments to validate.

Broadly, our data suggest that the loss from the prey assemblage of drifting macroinvertebrates specialised for fast flows could impact riverine ecosystem services, through the reduction of bird and fish predator populations of high cultural and economic importance (Butler et al. 2009, Green and Elmberg 2014, Steven et al. 2015). Our multi-threshold analysis results seem to confirm that bottom–up regulation

Table 2. Results of the models relating prey metrics and environmental conditions with a multi-predator index of four river species. Models are ranked following decreasing statistical support based on AICc values. Standardised regression coefficients (standardized effect sizes), goodness-of-fit (r²), ΔAICc values (difference with the model with the lowest AIC value), and model weight are also showed.

| Intercept | Key traits | | Trait diversity | | Mass effects | | Environment | | r² | ΔAICc | Weight |
	FG2	FG3	TD-e	TD-r	ric	abun	alt	pH			
1.43		0.35							0.34	0.00	0.26
1.43						0.33			0.31	1.67	0.11
1.43		0.31					−0.09		0.34	1.68	0.11
1.43		0.32	0.06						0.33	2.13	0.09
1.43		0.34			0.01				0.32	2.62	0.07
1.43		0.34		0.01					0.32	2.62	0.07
1.43			0.09			0.29			0.30	3.41	0.05
1.43						0.29	−0.08		0.30	3.51	0.04
1.43					0.05	0.30			0.29	4.10	0.03
1.43				0.03		0.31			0.29	4.20	0.03
1.43		0.30	0.04				−0.07		0.32	4.33	0.03
1.43		0.32		−0.02			−0.09		0.32	4.47	0.03
1.43							−0.19	0.23	0.25	5.61	0.02
1.43	0.27								0.19	6.63	0.01
1.43			0.10				−0.14	0.21	0.25	7.46	0.01
1.43	0.22		0.12						0.20	7.69	0.01
1.43					0.25				0.16	7.76	0.01
1.43	0.18				0.13				0.20	8.01	0.00
1.43				0.06			−0.16	0.21	0.23	8.15	0.00
1.43	0.21						−0.11		0.19	8.17	0.00
1.43	0.21			0.10					0.18	8.47	0.00
1.43					0.19		−0.11		0.16	9.28	0.00
1.43				0.22					0.12	9.45	0.00
1.43			0.21						0.11	9.85	0.00
1.43	0.19		0.10				−0.08		0.19	10.02	0.00
1.43	0.16					0.10	−0.08		0.18	10.31	0.00
1.43	0.18			0.08			−0.09		0.18	10.50	0.00

in these unproductive systems seems to be related to the availability of these prey. Together, these results indicate that certain groups of macroinvertebrate prey could offer a useful tool for environmental managers seeking to enhance multiple cultural services, which has proven elusive to date (Duncan et al. 2015). Further work is needed to assess whether the abundance of these key prey groups can predict a wider complement of ecosystem services, especially for traits that map onto multiple ecosystem functions (de Bello et al. 2010).

Although our models reveal the value of a trait based approach to understand and predict prey–predator interactions, they also highlight some limitations, particularly over knowledge of predator diets. Currently available dietary data typically vary over different time periods (annual values, seasonal, bi-monthly, monthly), which is why we could only make comparisons based on annually aggregated data. In reality, however, prey use can vary substantially through the annual cycle of organisms as their specific resource needs change. In dippers, for example, mineral-rich prey are required during egg formation, small accessible prey are important during spates, and energetic efficiency becomes important when provisioning young (Ormerod and Tyler 1991b). Niche segregation through time can also be compounded by usage of allochthonous sources of prey (Perkins et al. 2018), for example grey wagtail and salmonids can source a significant dietary contribution through terrestrial prey subsidies (Tyler and Ormerod 1991, Ormerod et al. 2004). Further knowledge of specific prey use throughout the lifecycle of a predator is thus likely to yield more accurate prey–predator models.

Our understanding of population dynamics was formalised during 'The golden age of theoretical ecology' (Scudo 1984). Many developments since then, including trait-based approaches and computers capable of analysing substantial volumes of data have opened the door for further advance. Here, we demonstrate that the complexity that forms the relationship between a multispecies prey assemblage and multispecies predator assemblage can be represented mechanistically, by identifying the key traits that govern their encounter and consumption rates. This result sheds light on the level of bottom–up control exerted within the multispecies predator–prey nexus.

Data availability statement

Author contributions

Cayetano Gutierrez-Canovas: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Thomas A. Worthington**: Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Ifan B. Jams**: Writing – review and editing (supporting). **David G. Noble**: Data curation (equal); Funding acquisition (equal); Investigation (supporting); Writing – review and editing (supporting). **Daniel M. Perkins**: Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – review and editing (equal). **Ian P. Vaughan**: Methodology (equal); Writing – review and editing (equal). **Guy Woodward**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Steve J. Ormerod**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Isabelle Durance**: Conceptualization (lead); Funding acquisition (lead); Investigation (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

References

Aprahamian, M. W. et al. 2008. Life history changes in Atlantic salmon from the River Dee, Wales. – Hydrobiologia 602: 61–78.

Arscott, D. B. et al. 2005. Lateral organization of aquatic invertebrates along the corridor of a braided floodplain river. – J. N. Am. Benthol. Soc. 24: 934–954.

Bannon, E. and Ringler, N. H. 1986. Optimal prey size for stream resident brown trout *Salmo trutta*: tests of predictive models. – Can. J. Zool. 64: 704–713.

Baranov, V. et al. 2020. Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. – Conserv. Biol. 34: 1241–1251.

Bartoń, K. 2016. MuMIn: multi-model inference. – R package ver. 1.15.6, <https://CRAN.R-project.org/package=MuMln>.

Beaumont, W. R. 2011. Electric fishing: a complete fuide to theory and practice. – Game & Wildlife Conservation Trust.

Bibby, C. J. et al. 2000. Bird census techniques, 2nd edn. – Academic Press.

Bluhm, B. A. and Gradinger, R. 2008. Regional variability in food availability for arctic marine mammals. – Ecol. Appl. 18: S77–S96.

Blumstein, D. T. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. – Ethology 112: 209–217.

Bradley, D. C. and Ormerod, S. J. 2002. Evaluating the precision of kick-sampling in upland streams for assessments of long-term change: the effects of sampling effort, habitat and rarity. – Arch. Hydrobiol. 155: 199–221.

Brewin, P. et al. 1998. River habitat surveys and biodiversity in acid-sensitive rivers. – Aquatic Conserv. Mar. Freshwater Ecosyst. 8: 501–514.

Brose, U. et al. 2019. Predator traits determine food-web architecture across ecosystems. – Nat. Ecol. Evol. 3: 919–927.

Burnham, K. P. et al. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. - Behav. Ecol. Sociobiol. 65: 23–35.

Bussi, G. et al. 2018. Modelling the effects of climate and land-use change on the hydrochemistry and ecology of the River Wye (Wales). – Sci. Total Environ. 627: 733–743.

Butler, J. R. A. et al. 2009. Evaluating an ecosystem service provided by Atlantic salmon, sea trout and other fish species in the River Spey, Scotland: the economic impact of recreational rod fisheries. – Fish. Res. 96: 259–266.

Byrnes, J. E. K. et al. 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. – Methods Ecol. Evol. 5: 111–124.

Chevenet, F. et al. 1994. A fuzzy coding approach for the analysis of long-term ecological data. – Freshwater Biol. 31: 295–309.

Cowx, I. 2008. Recreational fishing. – In: Hart, P. and Reynolds, J. (eds), Handbook of fish biology and fisheries, Vol. 2: fisheries. Blackwell Science Ltd, pp. 367–390.

D'Souza, J. M. et al. 2020. Food web transfer of plastics to an apex riverine predator. – Global Change Biol. 26: 3846–3857.

de Bello, F. et al. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. – Biodivers. Conserv. 19: 2873–2893.

De Crespin De Billy, V. and Usseglio-Polatera, P. 2002. Traits of brown trout prey in relation to habitat characteristics and benthic invertebrate communities. – J. Fish Biol. 60: 687–714.

De Crespin De Billy, V. et al. 2002. Invertebrate accessibility and vulnerability in the analysis of brown trout (*Salmo trutta* L.) summer habitat suitability. – River Res. Appl. 18: 533–553.

Delibes-Mateos, M. et al. 2008. Key role of European rabbits in the conservation of the western Mediterranean Basin hotspot. – Conserv. Biol. 22: 1106–1117.

Díaz, A. M. et al. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. – Freshwater Biol. 53: 1–21.

Dineen, G. et al. 2007. Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. – J. Fish Biol. 71: 17–38.

Duncan, C. et al. 2015. The quest for a mechanistic understanding of biodiversity–ecosystem services relationships. – Proc. R. Soc. B 282: 20151348.

Durance, I. and Ormerod, S. J. 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. – Global Change Biol. 13: 942–957.

Durance, I. et al. 2016. The challenges of linking ecosystem services to biodiversity: lessons from a large-scale freshwater study. – Adv. Ecol. Res. 54: 87–134.

Eisenhauer, N. et al. 2019. A multitrophic perspective on biodiversity–ecosystem functioning research. – Adv. Ecol. Res. 61: 1–54.

Elliott, J. M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *Salmo gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. – Oecologia 12: 329–347.

Eros, T. et al. 2012. Forest-stream linkages: effects of terrestrial invertebrate input and light on diet and growth of brown trout *Salmo trutta* in a boreal forest stream. – PLoS One 7: e36462.

Estes, J. A. et al. 2011. Trophic downgrading of planet earth. – Science 333: 301–306.

Froese, R. and Pauly, D. 2016. FishBase ver. (12/2019). – <www.fishbase.org>.

Gagic, V. et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. – Proc. R. Soc. B 282: 20142620.

Gaston, K. J. et al. 2018. Population abundance and ecosystem service provision: the case of birds. – Bioscience 68: 264–272.

Gayraud, S. et al. 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. – Freshwater Biol. 48: 2045.

Green, A. J. and Elmberg, J. 2014. Ecosystem services provided by waterbirds. – Biol. Rev. 89: 105–122.

Gutiérrez-Cánovas, C. et al. 2020. Large home range scavengers support higher rates of carcass removal. – Funct. Ecol. 34: 1921–1932.

Gutiérrez-Cánovas, C. et al. 2021. Data from: Populations of high-value predators reflect the traits of their prey. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.d51c5b02k>.

Halekoh, U. and Højsgaard, S. 2014. A Kenward–Roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package pbkrtest. – J. Stat. Softw. 59: 1–32.

Hammerschlag, N. et al. 2019. Ecosystem function and services of aquatic predators in the Anthropocene. – Trends Ecol. Evol. 34: 369–383.

Harrison, P. A. et al. 2014. Linkages between biodiversity attributes and ecosystem services: a systematic review. – Ecosyst. Serv. 9: 191–203.

Hörnfeldt, B. et al. 2005. Fading out of vole and predator cycles? – Proc. R. Soc. B 272: 2045–2049.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. – Funct. Ecol. 19: 166–172.

Kane, A. et al. 2017. A recipe for scavenging in vertebrates – the natural history of a behaviour. – Ecography 40: 324–334.

Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. – Ecol. Lett. 12: 334–350.

Kenward, M. G. and Roger, J. H. 1997. Small sample inference for fixed effects from restricted maximum likelihood. – Biometrics 53: 983.

Kraft, N. J. B. et al. 2015. Community assembly, coexistence and the environmental filtering metaphor. – Funct. Ecol. 29: 592–599.

Kruse, C. G. et al. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. – N. Am. J. Fish. Manage. 18: 940–946.

Lima, S. L. 2002. Putting predators back into behavioral predator–prey interactions. – Trends Ecol. Evol. 17: 70–75.

Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food supply. – J. Wash. Acad. Sci. 22: 461–469.

Maire, E. et al. 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. – Global Ecol. Biogeogr. 24: 728–740.

Maitland, P. S. 1972. A key to the freshwater fishes of the British Isles. – Sci. Publ. Freshwater Biol. Assoc. 27: 1–137.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – Trends Ecol. Evol. 21: 178–185.

McLean, M. et al. 2019. Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. – Global Change Biol. 25: 3424–3437.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.

Narwani, A. and Mazumder, A. 2012. Bottom–up effects of species diversity on the functioning and stability of food webs. – J. Anim. Ecol. 81: 701–713.

Ormerod, S. J. 1996. Dippers *Cincus cinclus* as predators in upland streams. – In: Greenstreet, S. P. R. and Tasker, M. L. (eds), Aquatic predators and their prey. Fishing News Books (Blackwells), pp. 33–43.

Ormerod, S. J. and Edwards, R. W. 1987. The ordination and classification of macroinvertebrate assemblages in the catchment of the River Wye in relation to environmental factors. – Freshwater Biol. 17: 533–546.

Ormerod, S. J. and Tyler, S. J. 1986. The diet of dippers *Cinclus cinclus* wintering in the catchment of the River Wye, Wales. – Bird Study 33: 36–45.

Ormerod, S. J. and Tyler, S. J. 1987. Aspects of the breeding ecology of welsh grey wagtails *Motacilla cinerea*. – Bird Study 34: 43–51.

Ormerod, S. J. and Tyler, S. J. 1991a. The influence of stream acidification and riparian land-use on the feeding ecology of gray wagtails *Motacilla cinerea* in Wales. – Ibis 133: 53–61.

Ormerod, S. J. and Tyler, S. J. S. J. 1991b. Exploitation of prey by a river bird, the dipper *Cinclus cinclus* (L.), along acidic and circumneutral streams in upland Wales. – Freshwater Biol. 25: 105–116.

Ormerod, S. J. et al. 2004. The effects of riparian forestry on invertebrate drift and brown trout in upland streams of contrasting acidity. – Hydrol. Earth Syst. Sci. 3: 578–588.

Pavoine, S. et al. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. – Oikos 118: 391–402.

Peirson, G. et al. 2001. Economic evaluation of inland fisheries in England and Wales. – Fish. Manage. Ecol. 8: 415–424.

Perkins, D. M. et al. 2015. Higher biodiversity is required to sustain multiple ecosystem processes across temperature regimes. – Global Change Biol. 21: 396–406.

Perkins, D. M. et al. 2018. Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs. – Ecol. Lett. 21: 1771–1780.

Petchey, O. L. 2000. Prey diversity, prey composition and predator population dynamics in experimental microcosms. – J. Anim. Ecol. 69: 874–882.

Pintar, M. R. and Resetarits, W. J. 2017. Prey-driven control of predator assemblages: zooplankton abundance drives aquatic beetle colonization. – Ecology 98: 2201–2215.

Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. – Can. J. Fish. Aquat. Sci. 54: 1211–1234.

Ripple, W. J. and Beschta, R. L. 2012. Trophic cascades in Yellowstone: the first 15years after wolf reintroduction. – Biol. Conserv. 145: 205–213.

Ripple, W. J. et al. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484.

Rooney, N. et al. 2006. Structural asymmetry and the stability of diverse food webs. – Nature 442: 265–269.

Rutt, G. P. et al. 1989. Microhabitat availability in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. – Freshwater Biol. 22: 247–261.

Sánchez-Bayo, F. and Wyckhuys, K. A. G. 2019. Worldwide decline of the entomofauna: a review of its drivers. – Biol. Conserv. 232: 8–27.

Schmitz, O. 2017. Predator and prey functional traits: understanding the adaptive machinery driving predator–prey interactions. – F1000Research 6: 1767.

Schneider, F. D. et al. 2012. Body mass constraints on feeding rates determine the consequences of predator loss. – Ecol. Lett. 15: 436–443.

Scudo, F. M. 1984. The 'Golden Age' of theoretical ecology; a conceptual appraisal. – Rev. Eur. Sci. Soc. 22: 11–64.

Sinclair, A. R. E. et al. 2003. Patterns of predation in a diverse predator–prey system. – Nature 428: 288–290.

Snyder, W. E. et al. 2006. Predator biodiversity strengthens herbivore suppression. – Ecol. Lett. 9: 789–796.

Steven, R. et al. 2015. Birdwatching and avitourism: a global review of research into its participant markets, distribution and impacts, highlighting future research priorities to inform sustainable avitourism management. – J. Sustain. Tour. 23: 1257–1276.

Suding, K. N. et al. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. – Global Change Biol. 14: 1125–1140.

Tachet, H. et al. 2002. Invertébrés d'eau douce (2nd corrected impression). – CNRS éditions.

Tilman, D. et al. 1997. The influence of functional diversity and composition on ecosystem processes. – Science 277: 1300–1302.

Tyler, S. J. and Ormerod, S. J. 1991. The influence of stream acidification and riparian land-use on the breeding biology of grey wagtails *Motacilla cinerea* in Wales. – Ibis 133: 286–292.

Usseglio-Polatera, P. et al. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. – Freshwater Biol. 43: 175–205.

van der Plas, F. 2019. Biodiversity and ecosystem functioning in naturally assembled communities. – Biol. Rev. 94: 1220–1245.

Verberk, W. C. E. P. et al. 2008. Life-history strategies in freshwater macroinvertebrates. – Freshwater Biol. 53: 1722–1738.

Villéger, S. et al. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – Ecology 89: 2290–2301.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. – ICES J. Mar. Sci. 3: 3–51.

Wade, K. R. et al. 1989. Classification and ordination of macroinvertebrate assemblages to predict stream acidity in upland Wales. – Hydrobiologia 171: 59–78.

Weatherley, N. S. and Ormerod, S. J. 1990. Forests and the temperature of upland streams in Wales: a modelling exploration of the biological effects. – Freshwater Biol. 24: 109–122.

Woodward, G. and Hildrew, A. G. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. – J. Anim. Ecol. 71: 1063–1074.

Woodward, G. et al. 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. – Science 336: 1438–1440.

Worthington, T. A. et al. 2020. Testing the ecosystem service cascade framework for Atlantic salmon. – Ecosyst. Serv. 46: 101196.

Yang, J. W. et al. 2018. Predator and prey biodiversity relationship and its consequences on marine ecosystem functioning – interplay between nanoflagellates and bacterioplankton. – ISME J. 12: 1532–1542.

Zuur, A. F. et al. 2009. A protocol for data exploration to avoid common statistical problems. – Methods Ecol. Evol. 1: 3–14.