

Invertebrate functional traits and terrestrial nutrient cycling: Insights from a global meta-analysis

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Abstract

1. Functional traits are useful for characterizing variation in community and ecosystem dynamics. Most advances in trait-based ecology to date centre on plant functional traits, although there is an increasing recognition that animal traits are also key contributors to processes operating at the community or ecosystem scale.
2. Terrestrial invertebrates are incredibly diverse and ubiquitous animals with important roles in nutrient cycling. Despite their widespread influence on ecosystem processes, we currently lack a synthetic understanding of how invertebrate functional traits affect terrestrial nutrient cycling.
3. We present a meta-analysis of 511 paired observations from 122 papers that examined how invertebrate functional traits affected litter decomposition rates, nitrogen pools and litter C:N ratios. Based on the available data, we specifically assessed the effects of feeding mode (bioturbation, detritus shredding, detritus grazing, leaf chewing, leaf piercing, ambush predators, active hunting predators) and body size (macro- and micro-invertebrates) on nutrient cycling.
4. The effects of invertebrates on terrestrial nutrient cycling varied according to functional trait. The inclusion of both macro- (≥ 2 mm) and micro-invertebrates (< 2 mm) increased litter decomposition by 20% and 19%, respectively. All detritivorous feeding modes enhanced litter decomposition rates, with bioturbators, detritus shredders and detritus grazers increasing decomposition by 28%, 22% and 15%, respectively. Neither herbivore feeding mode (e.g. leaf chewers and leaf piercers) nor predator hunting mode (ambush and active hunting) affected decomposition. We also revealed that bioturbators and detritus grazers increased soil nitrogen availability by 99% and 70%, respectively, and that leaf-chewing herbivores had a weak effect on litterfall stoichiometry via reducing C:N ratios by 11%.
5. Although functional traits might be useful predictors of ecosystem processes, our findings suggest context-dependent effects of invertebrate traits on terrestrial nutrient cycling. Detritivore functional traits (i.e. bioturbators, detritus shredders and detritus grazers) are more consistent with increased rates of nutrient cycling, whereas our currently characterized predator and herbivore traits are less predictive. Future research is needed to identify, standardize and deliberately study the impacts of invertebrate functional traits on nutrient cycling in hopes of revealing the key functional traits governing ecosystem functioning worldwide.

KEYWORDS

detritivores, ecosystem processes, functional traits, herbivores, invertebrates, meta-analysis, predators, trophic level

1 | INTRODUCTION

Functional traits are measurable characteristics at the individual level (e.g. phenological, morphological, behavioural or physiological traits) that can be linked to an organism's fitness or effect on the ecosystem (Blaum et al., 2011; Brousseau et al., 2018; Pey et al., 2014). In contrast to a taxonomic framework, a functional trait approach has the potential to better explain variation in community assembly and interspecific effects on ecosystem processes (De Deyn et al., 2008; Funk et al., 2017; Mokany et al., 2008). For instance, functional traits can predict the abundance and distribution of species across environmental gradients (Bernhardt-Römermann et al., 2011; Violle et al., 2011), explain effects of climate change on species range shifts (Lopez-Iglesias et al., 2014; Moor et al., 2015) and clarify patterns between community structure and ecosystem processes (Laigle et al., 2018; Lavorel & Garnier, 2002; Zirbel et al., 2017). Hence, a functional trait framework is now regarded as a promising way of revealing generalities in species distributions, community assemblages and ecosystem processes (McGill et al., 2006; Violle et al., 2007).

Consideration of functional trait-based approaches to explain ecosystem processes began largely in plant ecology (Diaz et al., 2004; Hooper & Vitousek, 1997; Lavorel & Garnier, 2002). Early conceptions of functional traits were based on easily measurable morphological (e.g. stem height, rooting depth), phenological (e.g. early vs. late season, annual vs. perennial life form) and physiological (e.g. nitrogen fixation) traits. This approach was based on the premise that these traits can be surrogates for more difficult-to-measure attributes relating to plant carbon and nutrient economy (uptake, storage and release) that could infer processes like nutrient cycling. These surrogates, however, proved to be less predictive than more refined conceptions such as the leaf economic spectrum (LES; Wright et al., 2004). Although the plant traits (e.g. surface leaf area, nitrogen content, leaf mass per area, etc.) underlying the LES can be more challenging to study than earlier surrogates, these traits are often better at predicting the impacts of plants on ecosystems because they more directly account for interspecific variation in plant leaf acquisition and expenditure of nutrients, life span and foliar nutrient concentrations (Anderegg et al., 2018; Onoda et al., 2017).

By contrast to plant ecology, consideration of the link between animal functional traits and ecosystem function is a more recent endeavour (Blaum et al., 2011; Laigle et al., 2018; Luck et al., 2012) and has largely focused on invertebrates (Brousseau et al., 2018; Moretti et al., 2017; Pey et al., 2014; Schmitz et al., 2015). It is fitting to consider the efficacy of functional traits using terrestrial invertebrates because they are the most abundant and diverse animals on earth (Lunney & Ponder, 1999; Stork, 2018). They are also perceived

as essential players in ecosystems by being critical components of food webs and modulators of nutrient cycling (Coleman et al., 1999; Wardle et al., 2004). In this context, one particular easily measurable functional trait—feeding mode (Schmitz et al., 2017), also referred to as feeding guild (Moretti et al., 2017)—may mediate how invertebrates affect living plant tissue (e.g. leaf chewers, sap-suckers), detritus (litter shredders, grazers) and soil properties (bioturbation), all of which may influence nutrient cycling and soil nutrient retention (Hawlena et al., 2012; Schmitz et al., 2010; Seastedt, 1984). Moreover, another easily measurable functional trait—body size—may determine the magnitude of invertebrate effects on nutrient cycling (Schmitz, 2008b). However, as with the early stages of plant functional trait research, it remains uncertain whether these easily measurable invertebrate functional traits can fulfil the promise of predicting general patterns in ecosystem processes.

Here we undertake a global meta-analysis to evaluate the extent to which current, widely measured functional traits of terrestrial invertebrates can predict their effects on nutrient cycling, including litter decomposition, soil nutrient pools and litter stoichiometry. While the body of literature that we synthesize has mainly examined ecosystem processes at the species level, and thus often does not explicitly link functional traits to functioning, the studies do report enough taxonomic information to characterize them by their easily measurable traits. Accordingly, such reporting allowed us to synthetically evaluate predictions about how functional traits might affect nutrient cycling (Figure 1).

At a broad level, we expect that invertebrate impacts on nutrient cycling are likely a function of body size. We postulate that populations of larger-bodied (≥ 2 mm) macro-invertebrates have a more pronounced effect on terrestrial nutrient cycling compared to populations of smaller micro-invertebrates (< 2 mm; A'Bear et al., 2014). At the population level, we expect that larger invertebrates (Figure 1a) would have an enhanced ability to breakdown and consume larger, complex organic substrates over smaller invertebrates (A'Bear et al., 2014; Figure 1b), thus facilitating the release and recycling of nutrients. However, invertebrate feeding mode will likely mediate the effects of invertebrates on terrestrial nutrient cycling. The feeding mode of invertebrate detritivores should generally increase rates of decomposition and the release of nutrients (e.g. nitrogen availability) irrespective of body size (Suzuki et al., 2013; Tonin et al., 2018; Figure 1c–e), whereas impacts of herbivore feeding mode and predator hunting mode should be more context-dependent (Figure 1f–i). For example, we expect that ambush predators will decrease decomposition and nutrient release compared to active hunting predators (Figure 1h,i), due to their ability to reduce herbivore foraging behaviours and alter prey chemical stoichiometry (Hawlena et al., 2012).

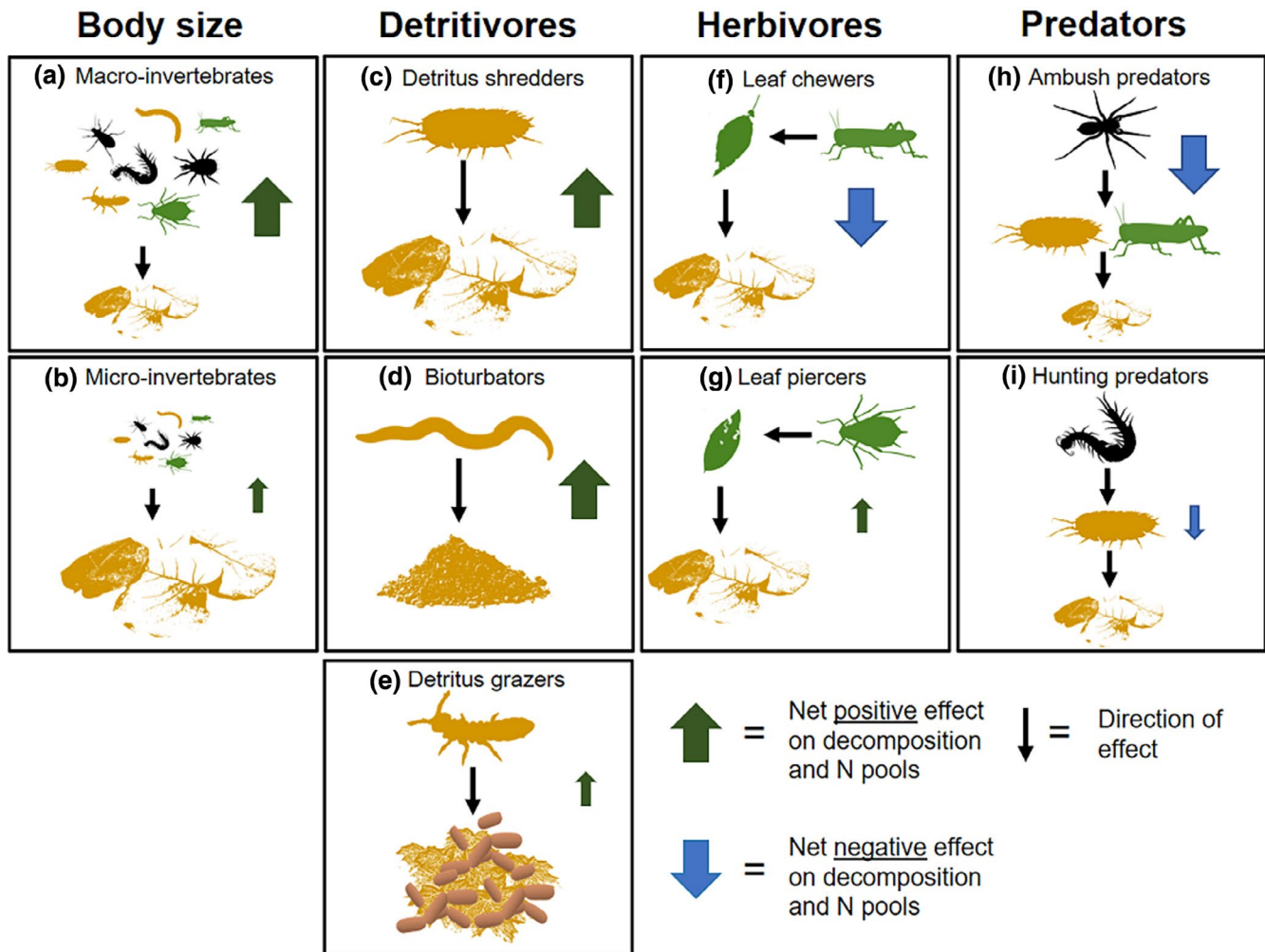


FIGURE 1 Conceptual framework showing our hypothesized effects of invertebrate traits (a) macro-invertebrates, (b) micro-invertebrates, (c) detritus shredders, (d) bioturbators, (e) detritus grazers, (f) leaf choppers, (g) leaf piercers, (h) ambush predators and (i) active hunting predators on terrestrial nutrient cycling. The arrows' directionality indicates the hypothesized net effect on nutrient cycling, with green and blue arrows representing faster and slower nutrient cycling, respectively. The size of these arrows denotes the estimated magnitude of invertebrate effects. The small black arrows show the direction of invertebrate traits' impacts

At a more refined level, we expect that invertebrate populations capable of shredding dead-leaf tissue (i.e. 'detritus shredders', Figure 1c) into smaller particles (De Oliveira et al., 2010; Hassall et al., 1987) should consistently increase rates of nutrient cycling regardless of the environmental context. We predict similar but weaker effects for invertebrates that can consume and/or graze detritus bacteria or fungal communities (i.e. 'detritus grazers', Figure 1e; Hanlon & Anderson, 1979; Parkinson et al., 1979), thereby stimulating microbial activity via compensatory growth from feeding and causing faster decomposition and nutrient release under most scenarios. On the other hand, we expect invertebrates that can chew living plant tissue (i.e. 'leaf choppers', Figure 1f) to decrease nutrient cycling by selectively consuming higher tissue quality or causing the induction of secondary metabolites (e.g. phenolics) to deter herbivory (Grime et al., 1996; Hättenschwiler & Vitousek, 2000; Wardle & Barker, 2002), thereby changing litterfall stoichiometry and inhibiting the activities of soil fauna and microbes. While there is varying

support for the hypotheses mentioned above, no quantitative synthesis has tested whether these invertebrate functional traits can predict patterns of terrestrial nutrient cycling.

2 | MATERIALS AND METHODS

2.1 | Literature survey and data extraction

We performed a literature search for primary articles in ISI Web of Science that investigated the effects of invertebrate functional traits (feeding mode and body size) on nutrient cycling. Without any restriction on the year of publication (last accessed on 15 November 2020), we used the following string of search terms: (decomp* OR process* OR breakdown OR decay* OR mineral* OR C cycle* OR N cycle* OR nutrient* OR pool* OR stoichiometr*) AND (litter OR leaf OR leaves OR bark OR wood) AND (inverte* OR arthropod*

OR insect*) AND (soil communit* OR soil trophic* OR soil fauna*) AND (trait* OR functional guild* OR trophic* OR food chain* OR food web* OR herbivore* OR detritivore* OR predator* OR omnivore* OR bacterivore* OR fungivore* OR microbivore*). Our initial search yielded 561 published articles. We then assessed each article using title names and abstracts of relevant titles to discern its potential for meeting our selection criteria (detailed below) for inclusion in the meta-analysis. Following our literature search, we then filtered each eligible article's reference lists to uncover other pertinent articles; we used no unpublished datasets in this study. Although it is possible that we did not identify every relevant research article, our survey methods provided thorough coverage of the primary literature testing the impacts of invertebrate traits on nutrient cycling. During our survey, we recorded the number of articles identified and the number of studies included/excluded based on our inclusion criteria (Appendix S1: Tables S1–S4), which followed the Preferred Reporting Items for Systematic Reviews and Meta-analysis (PRISMA; Moher et al., 2009; Appendix S2: Figure S1).

Our meta-analysis focused on surveying peer-reviewed studies that experimentally manipulated the presence/absence of invertebrates to test their effects on ecosystem processes. We focused our study on invertebrates because (a) their functional traits are more diverse than other animal groups, (b) there is more information on their impacts and (c) they are the most abundant terrestrial animals on earth (Berenbaum, 2017; Coleman & Hendrix, 2000; Stork, 2018). Here, each study had to compare treatments with and without invertebrates present. The studies also had to report the method of invertebrate manipulation, which could include the use of different mesh sizes of litter bags, insecticides, physical barriers, hand addition/removal techniques or litter sifting. Because most studies did not

include abundance data for the invertebrates, we could not measure the per capita effects of invertebrate traits; instead, we could only test their effects at the population level. We included all terrestrial invertebrates, which ranged from large decapods such as the wharf crab (*Armases cinereum*; Ewers et al., 2012) to microscopic bacterivores like the *Caenorhabditis elegans* nematode (Mikola & Setälä, 1998; Table 1). We categorized invertebrate functional traits' effects on terrestrial nutrient cycling according to our initial hypotheses (Figure 1).

The ecosystem-process variables we selected were related to changes in nutrient cycling, that is, changes in nutrient fluxes, pools and stoichiometry. Specifically, we considered three variables: nutrient release via litter decomposition (i.e. fluxes), soil and litter nitrogen (i.e. pools) and soil and litter C:N ratios (i.e. stoichiometry). We used carbon and nitrogen as nutrients because they are essential elements in terrestrial ecosystems (Attiwill & Adams, 1993), biotic processes are intimately involved in their cycling through ecosystems (Coleman et al., 1983) and they are commonly studied in nutrient cycling studies (Koltz et al., 2018; Shi et al., 2016). Most studies we screened reported decomposition dynamics of plant litter as mass loss or remaining; thus, we only used studies where proportion mass loss of initial litter weight could be calculated. Few studies reported metrics of respiration, mineralization or nitrification; hence we did not include data from those articles in our final meta-analysis because the sample sizes were too small to provide robust insights. Refer to Appendix S3: Tables S1–S3 for the complete database we used in the meta-analysis.

Articles were included in the meta-analysis if they met the following criteria: (a) The study investigated the effect of invertebrates on nutrient cycling using a comparison between treatments with

TABLE 1 The definition of the invertebrate functional traits used in the meta-analysis. The 'No. observations' column represents the total number of paired observations (including outliers). Refer to Appendix S3: Tables S1–S3 for the taxonomic designations of the representative invertebrates

Functional trait	Definition	Representative invertebrates	No. observations
Ambush predators	Sit-and-wait predators; ambushing characteristics	Funnel-web spiders, sheet-web spiders, nursery-web spiders	6
Bioturbators	Invertebrate detritivores that ingest, move, and defecate soil	Earthworms, mound-building ants, pot worms, termites	53
Detritus grazers	Invertebrates that preferentially consume/ graze microbes on detritus	Bacterivorous nematodes, fungivorous nematodes, oribatid mites, springtails	16
Detritus shredders	Invertebrate detritivores with chewing/ shredding mouthparts	Millipedes, slugs, woodlice	38
Hunting predators	Active hunting invertebrate predators; chase down their prey	Hunting nematodes, predatory crabs, wolf spiders	12
Leaf chewers	Herbivorous invertebrates with leaf/plant chewing mouthparts	Caterpillars, grasshoppers, goldenrod leaf beetles, walking sticks	22
Leaf piercers	Invertebrate herbivores that have piercing/ sucking mouthparts	Aphids, planthoppers, scales	9
Macro-invertebrates	Invertebrates ≥ 2 mm in size	All invertebrates ≥ 2 mm	234
Micro-invertebrates	Invertebrates < 2 mm in size	All invertebrates < 2 mm	121
Total			511

invertebrates absent (i.e. 'control' treatment) and invertebrates present (i.e. 'experimental' treatment). If a study presented multiple abundances of invertebrates for the experimental treatment, we calculated a composite average based on the provided data. Moreover, except for agroecosystem studies, we only included data from ambient conditions (e.g. ambient precipitation vs. experimentally induced drought) identified by the original authors; we did not extract data on environmental disturbances. (b) Details on invertebrate taxonomy, functional guild, feeding mode or body size had to be provided in the study. If a study provided multiple taxonomic units for a given trait, we treated each unit as an individual paired observation. (c) Studies had to incorporate at least one of the three ecosystem processes (i.e. decomposition, nitrogen pools or C:N ratios) related to invertebrate impacts on nutrient cycling. We only extracted data on monocultures and full mixes of plant litter; we did not include data for every litter mix combination. For nitrogen pools, studies had to provide absolute pool sizes; percent changes in nutrient pools were not extracted. If a study reported multiple dates for a given ecosystem process, we used the final time point. Because the studies were inconsistent in how they collected the spatial and temporal scales of their samples, we could not include those factors in our meta-analysis. (d) Studies had to provide complete data, including estimates of mean, variance and sample size for both the control and experimental treatments. Studies without statistical variation were not included in our meta-analysis. Furthermore, sample sizes had to be greater than two. (5) The study had to be an original research article; modelling papers, reviews or other meta-analyses were excluded. See Table S1 in Appendix S4 for full details on our inclusion/exclusion criteria.

We extracted data directly from the text, tables, supplemental materials and figures; data from graphs were obtained using the image processing software ImageJ (Abramoff et al., 2004). We also recorded information on each study's location, climate, ecosystem type and duration.

2.2 | Meta-analysis

We estimated the magnitude of invertebrate functional traits' effects on nutrient cycling by calculating the log response ratio (LRR; Hedges et al., 1999) effect size measure:

$$\text{LRR} = \ln\left(\frac{X_e}{X_c}\right),$$

where X_e and X_c are the sample means of the experimental (invertebrates present) and control (invertebrates absent) treatments, respectively. Here, a positive effect size indicates invertebrate traits increased nutrient fluxes, pools or C:N stoichiometry when present, whereas a negative effect size means that invertebrate traits decreased these measures of nutrient cycling. We also calculated the percent change in nutrient cycling caused by an invertebrate functional trait using the following equation:

$$\text{Percent change} = [e^{\text{LRR}} - 1] \times 100.$$

The variance (V) of LRR was calculated as follows:

$$V = \left(\frac{S_e^2}{n_e X_e^2}\right) + \left(\frac{S_c^2}{n_c X_c^2}\right),$$

where S and n denote the standard deviation and sample size of replicates, respectively. The subscripts 'e' and 'c' refer to the experimental and control group, respectively. We used the LRR as an effect size because it is a measure of the actual difference in responses scaled to the control mean. Furthermore, LRR is commonly used in meta-analyses and allows for symmetrical distributions of effects, equal influence of the experimental and control values on the total effect size, and comparisons of studies with different techniques for measuring nutrient cycling (Hedges et al., 1999; Hedges & Olkin, 1985; Lajeunesse, 2015).

To determine the overall effect of invertebrates on nutrient cycling, we first performed random-effects models (REM) of meta-analysis (Borenstein et al., 2009). We then employed mixed-effects models (MEM) with restricted maximum likelihood (REML) to analyse differences in effects of invertebrate traits on nutrient cycling using weighted mean effect sizes for each trait (Borenstein et al., 2009); invertebrate functional traits were used as moderators to assess their differences in LRR. We included a publication-level random effect as a nested factor to account for multiple effect sizes obtained from a given study. Moderators with fewer than three effect sizes were omitted because small sample sizes can produce erroneous analyses when using mixed models (Borenstein et al., 2009). For better model fits, we removed extreme values (≥ 3 SD of the mean) prior to analysis, although the results were generally similar if they were included (except for nitrogen pools; see Table S1 in Appendix S5 for details). The heterogeneity of effect sizes was evaluated through Q statistics, which are weighted sums of squares tested against a χ^2 distribution and can assess how much the heterogeneity of effects is attributed to unexplained factors (Hedges & Olkin, 1985). The effects of invertebrate trait moderators were examined through p values of Q between statistics that describe the variation in effect size attributed to differences among categorical moderators. Mean effect sizes were considered statistically different from zero if their 95% confidence intervals (CI) did not include zero (Borenstein et al., 2009). All analyses were performed using the METAFOR package in R version 4.0.3 (R Development Core Team, 2020).

2.3 | Publication bias

We tested for publication bias using two methods: (a) Trim-and-Fill funnel plots (Duval & Tweedie, 2000) and (b) Rosenthal's fail-safe number (Orwin, 1983). The Trim-and-Fill method, which plots effect sizes against sample sizes from individual studies (Duval & Tweedie, 2000), showed symmetrical scatter plots for all ecosystem-process variables (see Appendix S5: Figures S1–S3), indicating the

absence of publication bias. Rosenthal's fail-safe number gives the number of missing case studies with non-significant results that would be necessary to nullify the combined effect size (Orwin, 1983). We found no evidence of publication bias using Rosenthal's fail-safe number (Appendix S5: Table S2), as the number of studies needed to offset the results would be 655,133 for litter decomposition, 1,860 for nitrogen pools and 886 for C:N ratios, respectively.

3 | RESULTS

3.1 | Overview of database

The 122 primary articles that met all our inclusion criteria yielded 511 paired observations that could test the effects of invertebrate functional traits on nutrient cycling. The geographical distribution of the observations covered all major biomes, with most research occurring in China (17%), USA (16%) and England (12%). Two-thirds of all observations studied invertebrate effects in woodland ecosystems, which were primarily performed using field experiments (81%) rather than in the laboratory (19%). The most common method of faunal manipulation was the use of litter bags with different mesh sizes (59%), followed by manual addition/removal techniques (25%) and insecticide application (14%), respectively. See Appendix S3: Tables S1–S3 for the complete list and detailed information of studies used in our meta-analysis.

3.2 | Litter decomposition

Overall, litter decomposition increased in the presence of invertebrates (REM, log response ratio = 0.17, CI = [0.14, 0.19], $p < 0.001$). However, the magnitude and variation of the impacts differed according to functional trait. Both small (<2 mm) and large invertebrates (≥ 2 mm) increased litter decomposition when present (MEM, log response ratio_{Micro-invertebrates} = 0.18, CI = [0.13, 0.22]; log response ratio_{Macro-invertebrates} = 0.18, CI = [0.14, 0.21], Figure 2), indicating that the inclusion of small or large invertebrates should predictably increase decomposition. Populations of micro- and macro-invertebrates increased decomposition by 19% and 20%, respectively.

Detritivore feeding modes also increased litter decomposition, but the magnitude varied according to the nature of detritus feeding (Figure 2). Highly increased decomposition rates arose when bioturbators and detritus shredders were present (log response ratio_{Bioturbators} = 0.25, CI = [0.16, 0.34]; log response ratio_{Shredders} = 0.20, CI = [0.10, 0.30], Figure 2), with bioturbators and detritus shredders increasing decomposition by 28% and 22%, respectively. The mean effect size of detritus grazers was similar to detritus shredders and bioturbators (log response ratio = 0.14, CI = [-0.02, 0.29]), but grazer effects were weaker and more variable, increasing decomposition by 15% on average.

There was no consistent positive or negative effect of predator hunting mode or herbivore feeding mode on litter decomposition

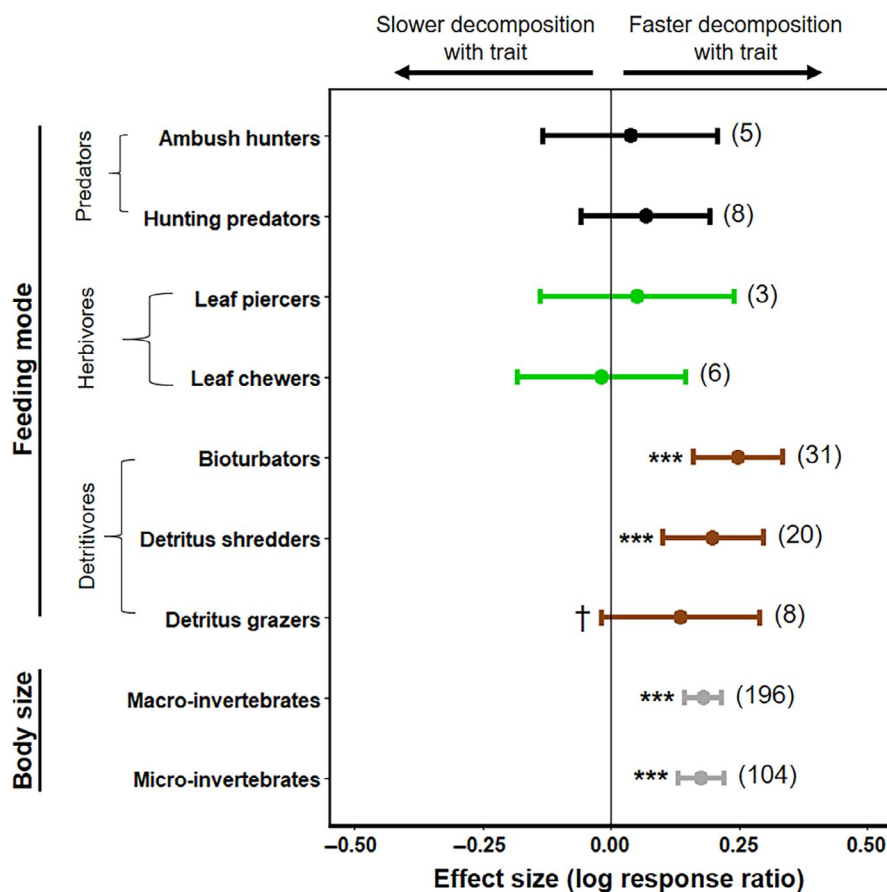


FIGURE 2 The mean effect sizes (log response ratio [LRR]) of invertebrate traits on litter decomposition. Positive effect sizes indicate that the invertebrate functional trait increased litter decomposition rates compared to treatments without the invertebrate trait; negative effect sizes denote the trait decreased decomposition. Means of LRR are shown with 95% CI; the number of paired observations analysed for each functional trait appears in parentheses. (***) indicates $p \leq 0.001$ for the null hypothesis that effect size = 0; (†) denotes $p \leq 0.1$

FIGURE 3 Mean effect sizes (log response ratio [LRR]) of invertebrate traits on nitrogen pools. Here positive values denote the invertebrate functional trait increased soil nitrogen pools when present, whereas negative effect sizes indicate the trait decreased soil nitrogen pools. LRR means are 95% CI, with the number of paired observations for each functional trait appearing in parentheses. (***) indicates $p \leq 0.001$; (*) denotes $p \leq 0.05$. 'NA' indicates not enough paired observations to include in the meta-analysis

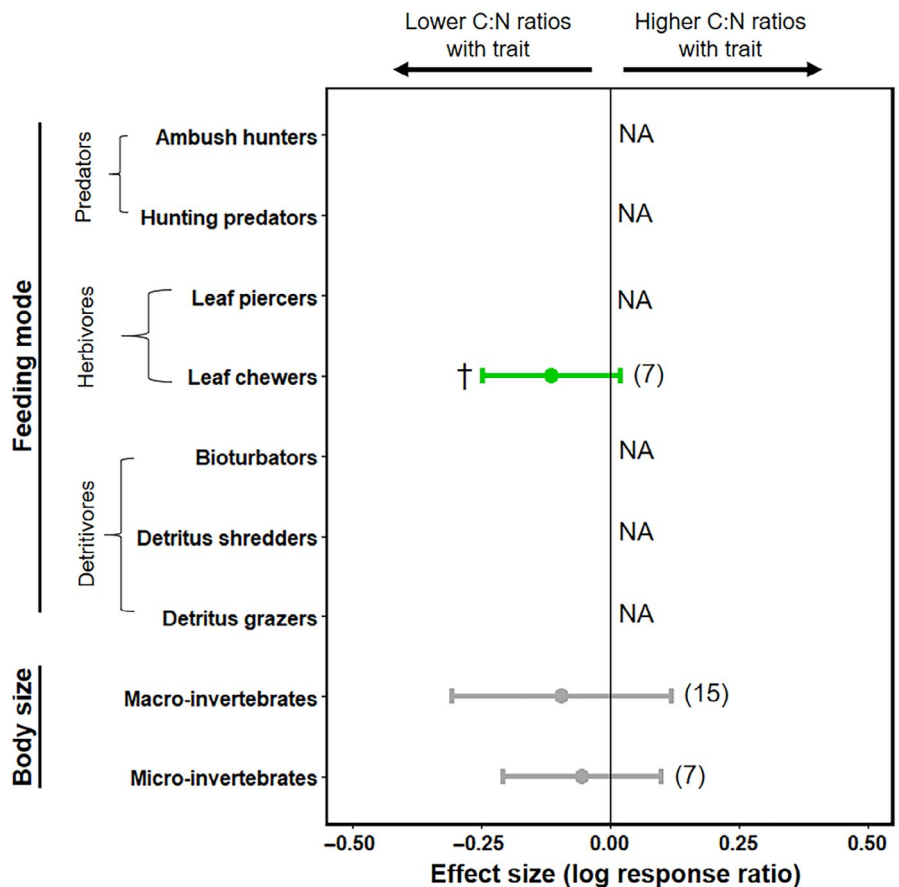
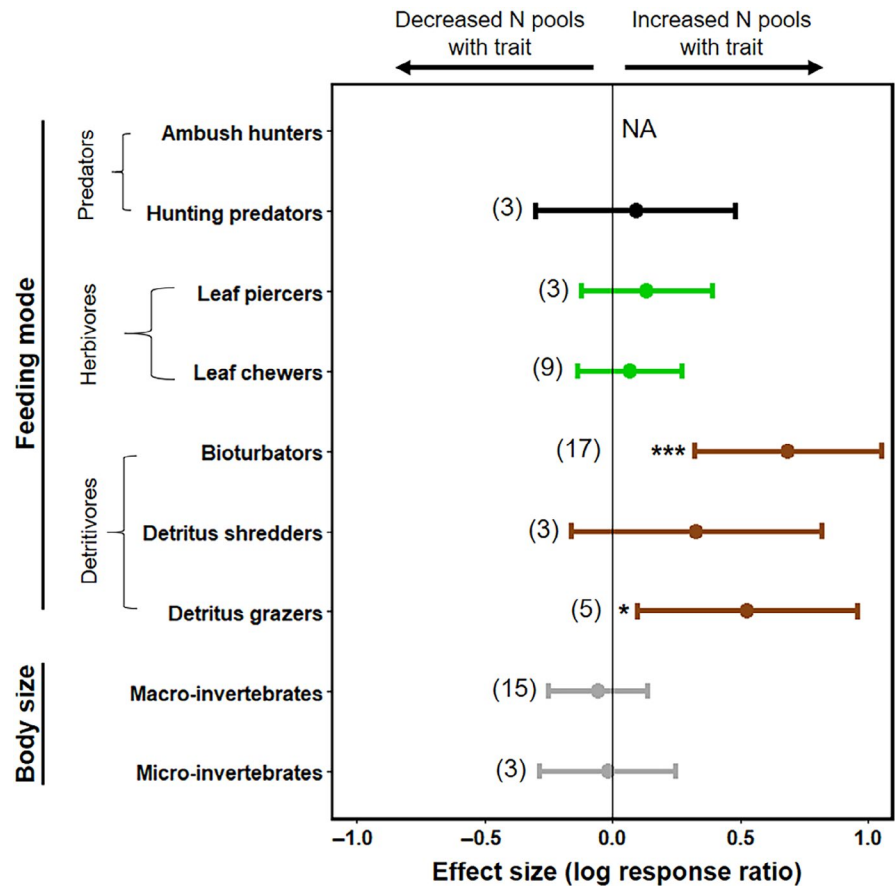


FIGURE 4 Mean effect size (log response ratio [LRR]) of invertebrate traits on C:N ratios. Refer to Figures 2 and 3 for details on symbols and interpretation of this figure. (†) denotes $p \leq 0.1$. 'NA' indicates not enough paired observations to include in the meta-analysis

rates (all CIs overlap zero, p values > 0.25 , Figure 2). The overall residual heterogeneity of effect sizes was large for litter decomposition ($Q_{\text{Total}} = 24,240.32$, $df = 372$, $p < 0.001$), indicating that the traits' effects were not the only factors contributing to decomposition.

3.3 | Soil nitrogen pools

The presence of invertebrates had an overall positive effect on nitrogen pools when not considering moderators of functional traits (REM, log response ratio = 0.19, CI = [0.10, 0.28], $p < 0.001$). Only bioturbators and detritus grazers were found to influence the size of nitrogen pools (MEM, log response ratio_{Bioturbators} = 0.69, CI = [0.32, 1.06]; log response ratio_{Grazers} = 0.53, CI = [0.10, 0.96], Figure 3), with bioturbators and detritus grazers increasing nitrogen availability by 99% and 70%, respectively. None of the other functional traits influenced the size of nitrogen pools (MEM, all CIs overlap zero, p values > 0.15). Overall, the heterogeneity of effects was large for nitrogen pools ($Q_{\text{Total}} = 176.74$, $df = 50$, $p < 0.001$), again suggesting that the functional traits were not the only factors determining nutrient cycling.

3.4 | Stoichiometric ratios

For the subset of functional traits for which studies measured effects on stoichiometry, we found that the inclusion of invertebrates led to decreased mean C:N ratios (REM, log response ratio = -0.06, CI = [-0.11, -0.003], $p = 0.04$). However, of the three traits that had enough observations to test C:N ratios, we found that herbivores with leaf-chewing abilities caused a marginal 11% decrease in C:N ratios when present (MEM, log response ratio = -0.11, CI = [-0.24, 0.02], Figure 4). The lack of general significance was attributable to large heterogeneity in magnitudes of effect sizes for nutrient stoichiometry ($Q_{\text{Total}} = 243.23$, $df = 26$, $p < 0.001$).

4 | DISCUSSION

Understanding the patterns of ecosystem functioning is thought to be limited when using a classic species-centric approach (McGill et al., 2006; Naeem & Wright, 2003). In the last few decades, it has been proposed that investigating the nature of species' roles in ecosystems using morphological, behavioural and/or physiological traits will improve prediction of ecosystem processes (de Bello et al., 2010; Eviner & Chapin III, 2003; Petchey & Gaston, 2006; Wong et al., 2019). This has been mostly upheld in concerted analyses to resolve relationships between functional traits and ecosystem functioning across the diversity of plants (De Deyn et al., 2008; Diaz et al., 2004; Funk et al., 2017; Lavorel & Garnier, 2002; but see van der Plas et al., 2020). Whether or not trait-based approaches apply to animals remains less clear because efforts to deliberately link animal functional traits to ecosystem processes have lagged

(Brousseau et al., 2018; Laigle et al., 2018; Moretti et al., 2017; Pey et al., 2014; Schmitz et al., 2015). Therefore, the intent of this study was to determine whether functional traits of one major group of animals—terrestrial invertebrates—affect aspects of a key ecosystem function: nutrient cycling.

We focused on two easily measurable functional traits—body size and feeding mode—that have been suggested to predict nutrient cycling (Moretti et al., 2017; Schmitz, 2008a; Schmitz et al., 2015) and then assessed their impacts on decomposition, nitrogen pools and C:N ratios. The focus on these particular traits stems from the fact that, even though there are a broader set of traits that ought to be considered (Brousseau et al., 2019; Laigle et al., 2018; Moretti et al., 2017), this subset was evaluated in most studies or were traits that could be easily discerned using the available taxonomic information. We found that whenever these functional traits had non-zero mean net effects, the trait generally increased litter decomposition and the size of nitrogen pools while lowering the stoichiometric balance of soil carbon to nitrogen (i.e. lower C:N ratios) relative to organism-excluded control conditions (Figures 2–4). Thus, in general, the functional traits of the invertebrates reviewed either had no significant link to nutrient cycling or tended to enhance nutrient cycling.

Counter to expectations, there were no differences in the mean and variance of effect magnitudes between small and large invertebrates on the three components of nutrient cycling. It remains uncertain whether this lack of difference is solely attributable to body size. Because the studies systematically manipulated invertebrate size by excluding all animals of a given size range, they did not consider other functional trait dimensions that could be important influencers of nutrient cycling, such as trophic group or feeding mode. These additional trait dimensions are necessary to consider alongside body size, as different feeding modes can have varying magnitudes and directionality of effects (Schmitz, 2008b) after controlling for body size (Schmitz & Price, 2011). This is supported by some of our analyses comparing effect sizes between the feeding modes, where the mean effects of different functional traits varied widely according to trophic group (i.e. detritivores, herbivores and predators).

Among the trophic groups considered, detritivores tended to have the highest magnitudes of effects, likely owing to their direct influence on the breakdown of organic matter and subsequent nutrient release. Of the three functional trait designations within detritivores, bioturbators (e.g. earthworms or enchytraeids) and litter shredders (e.g. millipedes or woodlice) affected decomposition most predictably. Bioturbators acting as 'ecosystem engineers' (Ojha & Devkota, 2014; Ransom, 2011) can ingest a combination of soil, litter and microbes, thereby altering soil structure and leading to the rapid breakdown of organic matter into smaller fragments (Barthod et al., 2020; Cortez, 1998; Haimi & Huhta, 1990), increasing soil nitrogen reserves (Eisenhauer, 2010). Detritus shredders can also significantly increase litter decomposition when present, as they can ingest and breakdown large organic compounds similar to bioturbators (Cárcamo et al., 2000; Zimmer et al., 2002). Detritus grazers, such as springtails and oribatid mites, had the weakest and most

variable effects on decomposition of the three detritivore traits. Detritus grazers can either promote or slow fungal and bacterial growth via foraging, through overgrazing or inducing compensatory microbial growth after feeding. Thus, detritus grazers' net effect on nutrient cycling likely depends on the environmental context (Bakonyi et al., 2002; Hishi & Takeda, 2008). For example, springtails are more likely to overgraze fungal hyphae under drought conditions leading to slower decomposition, whereas fungal grazing by springtails in litter with sufficient moisture can promote hyphal growth and enhance litter decomposition (Lensing & Wise, 2006).

The herbivore trophic group had weak effect sizes overall. Their net effects and direction were largely unpredictable due to large variances around the mean, producing both positive and negative outcomes on the three components of nutrient cycling. Some of this variation may arise because body size effects were not considered in addition to their feeding mode. Indeed, herbivore body mass and foraging mode together can explain uncertainty in the magnitude and direction of their effects on ecological processes (Meyer, 1993; Schmitz, 2008b; Schmitz & Price, 2011), suggesting that several traits of an individual herbivore should be considered concurrently to enhance prediction. For example, larger herbivores probably consume more plant tissue than smaller herbivores, and the degree to which an herbivore will eat a particular plant will likely depend on its dietary preferences (i.e. specialism vs. generalism). Further resolving each herbivore feeding mode within a multi-dimensional trait framework might better forecast their effects on nutrient cycling (Schmitz, 2008b).

Moreover, herbivore effects on soil processes may be less direct than for detritivores. Their effects can be mediated by changes in plant chemistry induced from feeding. Leaf-chewing herbivores can stimulate a change in leaf chemistry via secondary metabolites, which in some cases have inhibitory effects on nutrient cycling due to litter becoming more recalcitrant (Findlay et al., 1996; Hättenschwiler & Vitousek, 2000). Other studies have found that leaf chewers can enhance the production of nitrogen-rich compounds leading to faster decomposition and nitrogen mineralization (Brown, 1994; Chapman et al., 2003). Sap-feeding insects may have similar effects on leaf chemistry (Hall et al., 2017), although our meta-analysis did not have enough case studies to evaluate their impact. Given the high diversity and variation of plant-herbivore relationships worldwide (Barbehenn & Constabel, 2011; Coppock et al., 1983), our findings suggest that the impacts of herbivore feeding mode on nutrient cycling are likely context-dependent. Thus, to resolve these context-dependent effects, we need also to consider herbivory in relation to interspecific variation in plant leaf acquisition and expenditure of nutrients, life span and foliar carbon and nitrogen balance—that is, the leaf economic spectrum (Burghardt et al., 2018). This further implies that enhancing prediction requires taking a food-web approach that jointly considers both animal and plant functional traits (Schmitz et al., 2015), an approach now known as trait-matching (Brousseau et al., 2019; Laigle et al., 2018).

None of the traits associated with predators were important indicators of nutrient cycling, which runs contrary to our initial

hypotheses for ambush or active hunting predators. This may stem from analyses of predator effects failing to take a trait-matching approach. At a fundamental level, the body size of the prey and predator can be a strong predictor of a potential predator effect (Schmitz et al., 2017). But within a body size, the effects of predator functional traits (e.g. hunting mode) will be mediated by additional prey functional traits—for example, mobility and vulnerability to predation—that creates additional context dependency in the magnitude of effects (Gravel et al., 2016; Green & Côté, 2014; Klecka & Boukal, 2013; Melguizo-Ruiz et al., 2020). There are other components of feeding modalities—mandible size, structure, force—that can further influence the nature and strength of predator-prey interactions (Brousseau et al., 2019; Schmitz et al., 2017). Furthermore, predator effects will depend on whether they are mediated by herbivores in the plant-based food chain, by detritivores in the detritus-based food chain, or by a cascading chain of effects among both prey groups. For example, predator-prey interactions can determine herbivore effects on plant biomass and chemistry via changes in litter quality, thereby altering detritivore impacts on soil nutrient availability (Buchkowski et al., 2019). Incorporating such a food-web framework will likely uncover important predator effects on terrestrial nutrient cycling.

4.1 | Future directions for finding more predictive invertebrate functional traits

Our meta-analysis included 122 primary articles with over 511 paired observations. The distribution of the data among animal taxa was skewed. There were noticeably fewer data for herbivore and predator functional traits (Table 1), making it challenging to resolve context-dependent effect sizes, especially given the potential for these species to have indirect, rather than direct, effects on nutrient cycling (Schmitz et al., 2015). More generally, however, the studies included in our meta-analysis did not account for the potential confounding or conflating effect of other functional traits. The challenge in adopting a functional trait approach is to recognize that a given species can be characterized by multiple, interrelated functional traits (Brousseau et al., 2019; Laigle et al., 2018); hence, there is a need for more studies to experimentally account for their independent and combined effects (Moretti et al., 2017; Pey et al., 2014; Schmitz & Price, 2011). This will also require studying less easy-to-measure animal traits, which might more finely resolve the nature of organismal foraging, nutrient demands, movement and abundance.

Although there are too many invertebrate functional traits to list here that could potentially influence processes like nutrient cycling, we would like to highlight two research areas that might offer fruitful insights. One of the primary impediments to identifying key invertebrate functional traits is that studying invertebrates in nature is difficult, due to their cryptic lifestyle (Coleman et al., 1999). Basic life-history traits—such as diet composition, consumption rates, morphological variation, death rates and life span—can be challenging to measure compared to plants or vertebrates. DNA metabarcoding

has become increasingly mainstream to study diet composition and food-web interactions in larger vertebrates (De Barba et al., 2014; de Sousa et al., 2019), but the application of this method to soil invertebrates has lagged (Sow et al., 2020; Toju & Baba, 2018). DNA metabarcoding can help discern the degree of generalism or specialism and detect shifts in diet as a response to the environmental context or spatial/temporal scale (Pringle & Hutchinson, 2020). Second, geometric morphometrics can be used to map intraspecific and interspecific variation in invertebrate morphology (Benítez et al., 2020). This method can be explicitly used for mapping and providing three-dimensional coordinates of invertebrate mouthparts, leg length, exoskeleton density, etc., allowing for quantitative analyses of morphological traits between and within invertebrate species/groups (Tatsuta et al., 2018). Because these two methods allow for a more detailed analysis of intraspecific and interspecific variation across environmental contexts, they are likely to uncover the herbivore and predator traits most associated with terrestrial nutrient cycling.

5 | CONCLUSIONS

The promise of using functional traits to resolve context-dependent effects of animals on ecosystem functioning is an exciting venture in ecology (Moretti et al., 2017; Schmitz et al., 2015; Wong et al., 2019). To this end, several frameworks have been developed to guide a universal, explicit effort to characterize and carefully measure the suite of animal functional traits that could impact ecological processes (Gravel et al., 2016; Pey et al., 2014). Our meta-analysis, however, reveals that this promise of a functional trait approach is not yet realized across trophic groups of invertebrates. This is because the resolution of traits in the studies is relegated to the easily measurable subset of the broader suite of traits that could affect nutrient cycling. As in the early plant functional trait research, the easily measurable traits currently being considered are too crude to resolve context-dependent animal effects on nutrient cycling. We have pinpointed ways to enhance the evaluation of functional trait effects. This includes identifying matches of plant and animal traits in a food-web context to better characterize the dynamic interplay between consumers and their resources, as well as conducting experiments that systematically control for the potential confounding or conflating effects of multiple interrelated functional traits. Given that community-level interactions can cascade to affect ecosystem functioning (Schmitz, 2008b), we hope that new experimental research will consider a broader suite of functional traits to help realize the promise of animal functional traits to predict ecosystem functioning.

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AUTHORS' CONTRIBUTIONS

M.A.M. and O.J.S. conceived and designed the study; M.A.M. conducted the literature search and performed the meta-analysis; O.J.S. provided intellectual guidance and assisted with the meta-analysis; M.A.M. wrote the first manuscript draft; both authors contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Access to all analyses and accompanying scripts are available on Zenodo <https://doi.org/10.5281/zenodo.4620062>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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