



# Isopod mouthpart traits respond to a tropical forest recovery gradient

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## Abstract

Functional trait ecology has the potential to provide generalizable and mechanistic predictions of ecosystem function from data of species distributions and traits. The traits that are selected should both respond to environmental factors and influence ecosystem functioning. Invertebrate mouthpart traits fulfill these criteria, but are seldom collected, lack standardized measurement protocols, and have infrequently been investigated in response to environmental factors. We surveyed isopod species that consume plant detritus, and tree communities in 58 plots across primary and secondary forests in Singapore. We measured body dimensions (body size traits), pereopod and antennae lengths (locomotory traits), dimensions of mandible structures (morphological mouthpart traits), and mechanical advantages generated by mandible shape (mechanical mouthpart traits) for six isopod species found in these plots and investigated if these traits respond to changes in tree community composition, tree diversity, and forest structure. Morphological mouthpart traits responded to a tree compositional gradient reflecting forest recovery degree. Mouthpart features associated with greater consumption of litter (broader but less serrated/rugose lacinia mobilis [an important cutting and chewing structure on the mandible]) were most prevalent in abandoned plantation and young secondary forests containing disturbance-associated tree species. Feeding strategies associated with fungi grazing (narrower and more serrated/rugose lacinia mobilis) were most prevalent in late secondary forests containing later successional tree species. Since morphological mouthpart traits likely also predict consumption and excretion rates of isopods, these traits advance our understanding of environment–trait–ecosystem functioning relationships across contrasting tropical forest plots that vary in composition, disturbance history, and post-disturbance recovery.

**Keywords** Soil invertebrate · Functional traits · Plantation · Mandible · Succession

## Introduction

Functional traits are morphological or physiological traits that moderate the responses of organisms to environmental factors and other organisms, and their impacts on community and ecosystem processes (Violle et al. 2007; Wong et al. 2019). As such, functional trait ecology has the potential to provide insights into ecological phenomena such as ecosystem functioning that are more generalizable and mechanistic than species-based approaches (McGill et al. 2006; Moretti et al. 2017). However, the trait ecology of small, detritivorous soil- and litter-inhabiting invertebrate taxa remains poorly studied (Pey et al. 2014) in comparison to other invertebrate taxa, such as spiders (Pekár et al. 2021), dung beetles (Williamson et al. 2022; deCastro-Arrazola et al. 2023), and ants (Parr et al. 2017) despite their key role in regulating ecosystem functions, such as plant litter decomposition and nutrient cycling (Potapov 2022). As such, establishing

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generalizable trait–environment responses for detritivorous soil or litter invertebrates not only enables reliable predictions of community composition, but potentially also offers insights into the functioning of the ecosystem (Auclerc et al. 2022).

A trait-based bottom–up prediction of ecosystem function is possible only if the trait in focus both responds to environmental factors in question and has an effect on ecosystem functioning—that is, the trait of focus should be both a response and effect trait (Lavorel and Garnier 2002; Suding et al. 2008). Traits relating to resource acquisition and processing such as mouthpart traits are likely to meet this criterion since such traits allow species to exploit different resources which are present at different densities across environments (Brousseau et al. 2019) and are also likely to control species' rates of resource consumption and nutrient excretion (Moretti et al. 2017; McCary and Schmitz 2021). However, few studies to date have examined the responses of mouthpart traits to environmental gradients or developed standardized methods for measuring such traits in detritivorous litter invertebrates.

Many studies have characterized feeding habits among detritivorous species using categorical groups, such as feeding mode (McCary and Schmitz 2021) and mandible type (Malcicka et al. 2017), or ordinal measures, such as mandible strength and cheliceral elongation (Rousseau et al. 2019). However, categorical or ordinal groups mask within-group variability and do not lend themselves well to prediction (McGill et al. 2006; Funk et al. 2017). Measurements of mouthpart morphology that are continuous variables have the potential to act as better standardized mouthpart traits of detritivorous litter invertebrates. Two groups of mouthpart traits that can be measured as continuous variables in a standardized manner are mechanical mouthpart traits and morphological mouthpart traits.

Mechanical mouthpart traits refer to the mechanics of movable mouthparts and the amount of force or mechanical advantage provided by muscle–joint–appendage mechanisms. (Perdomo et al. 2012). Measures of oribatid mite cheliceral morphology are associated with their stable  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic signatures, indicating that the feeding niches of oribatid mite species can be predicted using these mouthpart traits (Perdomo et al. 2012). Similarly, morphological mouthpart traits, which refer to the dimensions of biting surfaces and sensory organs on invertebrate mouthparts have been shown to match the traits of resources being consumed by a variety of detritivorous invertebrates (Brousseau et al. 2019; Raymond-Léonard et al. 2019). For example, the size of the molar plate on the mandibles of collembolans is well recognized as an indicator of a plant or fungal diet (Malcicka et al. 2017), and the size and the dentition of oribatid mite chelicerae and rutellae reflect the

degree to which species consume fungal or plant material (Xavier and Haq 2007).

Morphological and mechanical mouthpart traits may be coupled since feeding strategy variations within a given guild may select for particular combinations of mechanical and morphological mouthpart traits. For example, species specializing on more recalcitrant substrates may possess mandibles capable of generating higher force (this force being a mechanical mouthpart trait) and a broader, blade-like incisor surface as opposed to a narrower, piercing one (this incisor surface being a morphological mouthpart trait) (Perdomo et al. 2012). Morphological mouthpart traits may also be easier than mechanical mouthpart traits to measure because the former often feature in the taxonomic descriptions of species, and because the latter often require the observation of soft tissue (muscle attachment points) that are more easily degraded and less easily observed under the microscope.

Traits associated with body size (e.g., total length) and locomotion (e.g., relative leg length) are often measured in invertebrate trait studies (Moretti et al. 2017). Body size is known to affect environmental stress tolerance (Buckingham et al. 2019; Williamson et al. 2022), while locomotory traits are known to relate to vertical stratification in the habitat (Ellers et al. 2018; Hishi et al. 2022), ability to colonize new areas (Buckingham et al. 2019), and predator avoidance (Tuf and Ďurajková 2022). Trade-offs between locomotory and phloem-ingestion abilities have also been demonstrated in sap sucking insects (Huberty and Denno 2006), and it is therefore also possible that body size and locomotory traits interact with mouthpart traits to moderate the responses of invertebrates to environmental factors (e.g., bacterivorous feeding strategies may only be metabolically efficient in small-bodied species), but such interactions have not been explored for detritivorous invertebrates.

Terrestrial isopods (Isopoda: Oniscidea; hereafter 'isopods') are detritivores which collectively feed on a wide range of plant detritus including leaf litter, rotting wood, and saprotrophic fungi, thus playing important roles in decomposition as both primary and secondary decomposers (Zimmer 2002; Potapov 2022). Food preference differences between isopod species are well documented (Dudgeon et al. 1990), but reasons for these preferences are poorly understood. Almost 4000 isopod species are known from all terrestrial biomes except for cold environments such as the poles (Sfendourakis and Taiti 2015). Importantly, the feeding biology of isopods is relatively well known, the body plan and anatomical adaptations are relatively conserved across the suborder, and all known terrestrial species are detritivores that perform comparable functions across ecosystems (Zimmer 2002), thus making morphological trait-based studies on isopods highly generalizable. While moisture and relative humidity are known to exert a strong control on isopod species

distributions and traits in temperate regions (Csonka et al. 2018; De Smedt et al. 2018; Dias et al. 2013), these factors are unlikely to affect litter isopod species distributions as strongly in moist tropical rainforests, where relative humidity in litter layers is almost always high.

In this study, we examined body size, locomotory, mechanical mouthpart, and morphological mouthpart traits of isopods sampled from aseasonal, equatorial forest plots in Singapore that vary in their past anthropogenic disturbances, such as selective logging, intensive agriculture, and agroforestry, as well their recovery from those disturbances (Yee et al. 2019). We focused on traits collected from the mandibles since the highly sclerotized structures on mandibles are the primary food processing surfaces in isopods (Hassall 1977). We hypothesized that differences in the vegetation composition and therefore the availabilities of different types of leaf litter resources along the forest recovery gradient would favor different isopod feeding strategies, and thus lead to a detectable trait–environment interaction between isopod morphological and mechanical mouthpart traits, and the forest gradient. If found to be true, these traits may potentially be used to provide insights about environment–trait–ecosystem functioning associations, and provide insights about how invertebrates affect decomposition and nutrient cycling across tropical forest plots varying in their composition, disturbance history, and post-disturbance recovery.

## Materials and methods

### Sample collection

Data were obtained from 58 forest plots each measuring 9 × 12 m in tropical, aseasonal forests in the Republic of Singapore (Fig. S1). Plots were distributed across five forest patches (Fig. S1), and collectively represented a gradient of forest types ranging from forests which were heavily disturbed and cultivated in the past for exotic cash crops such as *para* rubber (*Hevea brasiliensis* Müll.Arg. [Euphorbiaceae]), to forests which show little or no sign of past anthropogenic disturbance. Plot locations were made haphazardly within legally permitted sampling zones spread across the Bukit Timah Nature Reserve, Central Catchment Nature Reserve, and Pulau Ubin Island. Plots were established using a paired design (i.e., 29 pairs of plots, with each pair being located within 10 m of each other). All trees ≥ 1 cm diameter at breast height (DBH, cm) were measured in each plot and identified to species. Sampling was conducted between July 2021 and November 2021. The average monthly total rainfall and the monthly mean temperature in the region were 237 mm and 28.1 °C, respectively (data.gov.sg).

For each plot, leaf litter was collected from six 50 × 50 cm quadrats, which were located equidistant around the perimeter of an interior 5 × 5 m zone of the plots and combined as a single sample. All leaf litter found within each quadrat was collected and sifted through a sieve with a 1-cm screen mesh. Invertebrates were then extracted from the sieved litter through a Winkler extractor over a seven-day period. Collected invertebrates were stored in 70% ethanol. The sifted litters were then dried in a 60 °C oven for another seven days and weighed. Isopods in the samples were counted under a stereomicroscope and identified to genus and species, or where this was not possible morphospecies level, using published guides (Taiti and Ferrara 1986; Ferrara et al. 1995; Taiti et al. 1998) and with the help of experts (see Acknowledgements).

### Functional trait measurement

For each species, trait measurements were made from five well-preserved adult isopod specimens which all originated from different plots. Individuals were considered adults only if they exceeded the 80th percentile total length of all specimens collected of that species. Traits were thus measured from a total of 30 individuals from six isopod species. Four classes of functional traits corresponding to four ecological hypotheses (Table 1), namely body size traits (Fig. S2), locomotory traits (Fig. S3), mechanical mouthpart traits (Fig. S4), and morphological mouthpart traits (Fig. 1), were measured for each specimen. All mouthpart traits were derived from mandible measurements, which were all made on the left mandible to account for asymmetry (Vandel 1960; Hassall 1977; Richter et al. 2002). Specimens were dissected under a stereomicroscope, and anatomical features were imaged using a DVM6 digital microscope (Leica Microsystems, Wetzlar, Germany) with focus stacking completed using default settings in the Leica Application Suite X software. Measurements were made from the resultant images using Fiji ImageJ (Schindelin et al. 2012).

### Statistical analysis—data preparation and dimension reduction

Ordination of the tree communities in each plot was used to numerically characterize the tree species composition across the 58 plots and to identify key axes of tree community composition variation across them. Plot-summed basal areas of all tree species that occurred in at least three of the 58 plots were square root-transformed and double standardized. Pairwise Bray–Curtis distances were calculated from this, and a principal coordinates analysis (PCoA) with Lingoes' correction for negative eigenvalues was performed on the resultant distance matrix. The loadings of each plot on the first (hereafter “PCoA1”) and second (hereafter “PCoA2”) axes

**Table 1** Classification and a priori hypotheses, including the justification for inclusion, trait names, and measurement or derivation of the 14 isopod traits used in this study

Trait class	Hypotheses	Trait name (abbreviation)	Measurement or derivation
(a) Body size traits (body size)	<p>Body size may affect, and is a general predictor of, many different aspects of isopod biology and physiological processes (Moretti et al. 2017), such as access to microhabitats (Eilers et al. 2018), and susceptibility to desiccation (Dias et al. 2013; Csonka et al. 2018) or predation (Gravel et al. 2013)</p> <p>Cephalon width is a proxy for muscle size and volume (Brousseau et al. 2019) and used to estimate incisor process and molar plate biting forces and mechanical advantages. This trait was not included in the analysis due to its high correlation with other body size traits (Fig. S5)</p>	<p>Length (length)</p> <p>Aspect ratio (aspect)</p> <p>Cephalon width (Cephalon)</p>	<p>Length from the anterior margin of the cephalon or clypeus (where visible) to the posterior margin of the pleotelson, excluding appendages and setae (Fig. S2)</p> <p>Length divided by width of the widest pereon (Fig. S2)</p> <p>Width of the cephalon behind the eyes from a dorsal view, measured while attached to body for runners, and when detached from body for rollers since it is obscured when attached to the strongly convex body (Fig. S2)</p>
(b) Locomotory traits (relative appendage lengths)	<p>Species with relatively longer legs are better adapted to running from predators as a defensive mechanism (Schmalfuss 1998; Tuf and Durajková 2022)</p> <p>Fast-running species may require relatively longer antennae to better and more quickly sense their environment (Schmalfuss 1998). This trait was not included in the analysis due to its high correlation with pereopod length (Fig. S5)</p>	<p>Average total length of pereopods 6 and 7 (Pereopod)</p> <p>Total length of antennae (antenna)</p>	<p>Summed lengths of basis, ischium, merus, and carpus (Fig. S3). Averaged between left and right appendages and pereopods 6 and 7. Divided by body length. Pereopods 6 and 7 are often the longest pereopods (isopod pereopods all have similar locomotory functions (Hessler 1982))</p> <p>Summed lengths of antenna peduncle segments 2, 3, 4, and 5 (Fig. S3). Averaged between left and right appendages and divided by body length</p>
(c) Morphological mouthpart traits (relative sizes of mandible processes)	<p>Morphology of incisor process (IP) may determine how food particles are processed—the extent to which they are scraped, pierced, or cut</p> <p>Morphology of lacinia mobilis (LM) may determine how food particles are processed how effectively they are cut by a pointed and narrow surface or crushed by a blunt and broad surface</p> <p>Size of ciliated lobe and molar penicil may determine sensitivity and thus selectivity of a species toward food sources</p>	<p>Incisor process edge length (IP_e)</p> <p>Incisor process rugosity (IP_r)</p> <p>Contact area of lacinia mobilis (LM_a)</p> <p>Lacinia mobilis rugosity (LM_r)</p> <p>Side profile area of ciliated lobe (CL_area)</p>	<p>Cross sectional length of IP edge (IP_e; Fig. 1b). Divided by cephalon width</p> <p>Side profile length of IP surface (IP_s) divided by side profile maximum width of IP (IP_w; Fig. 1a)</p> <p>Cross sectional area of LM (Fig. 1b). Square-root transformed for normality and divided by cephalon width</p> <p>Side profile length of LM surface (LM_s) minus LM height (LM_h) divided by maximum width of LM (LM_w; Fig. 1a)</p> <p>Side profile area of ciliated lobe. Square root-transformed for normality and divided by cephalon width</p>

**Table 1** (continued)

Trait class	Hypotheses	Trait name (abbreviation)	Measurement or derivation
(d) Mechanical mouthpart traits (proxies of actual force generated by mandible movements)	Species with greater biting force and mechanical advantage may be able to directly consume tougher litter and more recalcitrant substrates (Perdomo et al. 2012; Brousseau et al. 2018, 2019; Raymond-Léonard et al. 2019)	Incisor process biting force (IP_f)	Calculated using formula from Brousseau et al. (2019): $Cephalon \times \frac{W_{ad}}{L_{ip}}$
		Incisor process mechanical advantage (IP_ma)	Calculated using formula from Brousseau et al. (2019): $\frac{W_{ad}}{L_{ip}}$
	Molar process (Mpro) strength affects efficiency of water extraction from leaves with high dry matter content (Koiuhler and Alberti 1990; Perdomo et al. 2012; Brousseau et al. 2019; Raymond-Léonard et al. 2019). Mpro_ma was not included in the analysis due to its high correlation with Mpro_f (Fig. S5)	Molar process biting force (Mpro_f)	Calculated using formula from Brousseau et al. (2019): $Cephalon \times \frac{W_{ab}}{L_{Mpro}}$
		Molar process mechanical advantage (Mpro_ma)	Calculated using formula from Brousseau et al. (2019): $\frac{W_{ab}}{L_{Mpro}}$

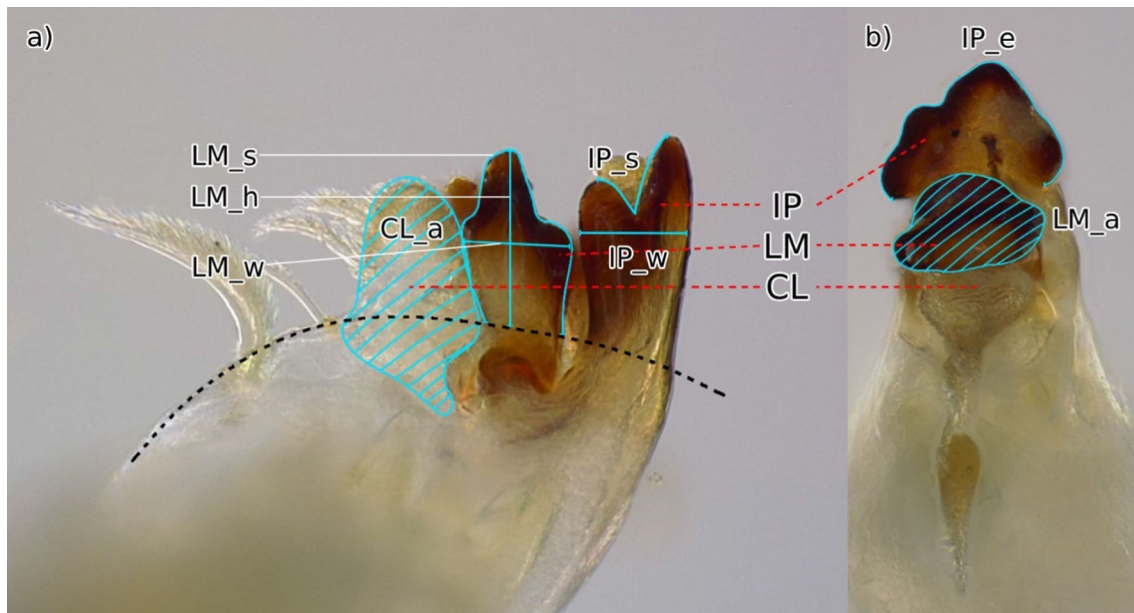
$W_{ad}$  basal width of mandible from insertion point of adductor muscle,  $W_{ab}$  basal width of mandible from insertion point of abductor muscle,  $L_{Mpro}$  length of mandible base to molar process,  $L_{ip}$  length of mandible base to incisor process

PCoA axes were extracted for use in subsequent analyses. Three other environmental variables were also derived for each plot: (1) species richness (SR) of the tree species present; (2) total basal area (BA) or the summed basal area of all trees present; and (3) dry weight of all the leaf litter fragments which had been sifted through the 1-cm litter reducer mesh (determined after invertebrates had been extracted from the litter). This acts as a proxy for the amount of leaf litter present in the plots. These three environmental variables were log-transformed, and all environmental variables including PCoA1 and PCoA2 scores were scaled to standard deviation units and centered on zero for subsequent analyses. PCoA was performed using the *ape* R package (Paradis and Schliep 2019).

Principal components analysis (PCA) was used to reduce the dimensionality of the traits that were measured across the 30 isopod individuals, and to visualize the niches of species in multivariate (“functional”) space. PCA was first performed on isopod traits from all trait classes, and subsequently also on the following subsets of traits: body size and locomotory traits only, morphological mouthpart traits only, and mechanical mouthpart traits only. Pearson correlation coefficients and false discovery rate-adjusted *p*-values (Benjamini and Hochberg 1995) were calculated for all pairwise combinations of traits, and traits which were found to be strongly correlated with other traits within the same trait class (i.e., Cephalon, Antenna, Mpro\_ma; Fig. S5) were removed before the analysis as these explain the same variances within the data. The first and the second principal component score of each isopod individual was extracted for each of the PCAs performed, averaged by species, and used for subsequent analyses. Body size and locomotory traits were grouped together despite being categorically different classes of traits because a relatively strong tradeoff was evident between the two trait classes, so that a single principal component was enough to summarize a high amount of variance present in traits from both trait classes. A redundancy analysis (RDA) on traits from all trait classes and with species identity as the constraining variable was performed to estimate the contribution of species identity to explaining variation in trait values across the isopod individuals. PCAs and the RDA were performed using the *vegan* R packages (Oksanen et al. 2016).

### Statistical analysis—modeling trait–environment interactions

To test the hypothesis that isopod traits moderate the responses of isopods to measured environmental variables, the abundance of each isopod species in each plot was modeled using generalized linear mixed-effects models (GLMMs) with negative binomial error structures and the log link function against environmental variables, species mean trait values, and the



**Fig. 1** Measurements taken to calculate morphological mouthpart traits from side (a) and cross-sectional (b) profiles of a *Burmoniscus* sp. 1 left mandible. Red dotted lines indicate three key anatomical structures of the mandible: *IP* incisor process, *LM* lacinia mobilis, *CL* ciliated lobe. Lengths (blue curved lines outlining the structures)

and areas (blue shaded areas covering the structures' surfaces) show where the measurements were taken, and the abbreviations are described in Table 1. Black dotted curved line indicates the basal margin of the mandible, beyond which various processes and structures protrude

interactions between these two sets of variables. To account for the non-independence of the plot pairs, random intercepts of plot pair nested within forest patch were fitted. To account for residual variations in species responses not caused by traits, a random slope of species identity against the environmental variable was fitted. The plot-level environmental variables used were: PCoA1 and PCoA2 (representing tree community composition), SR (representing tree diversity), and BA and reduced litter dry weight (representing forest structure). The isopod traits used were: first (allPC1) and second (allPC2) principal components of traits from all trait classes measured; first (morphPC2) and second (morphPC2) principal components of the morphological mouthpart traits; first (mechPC1) and second (mechPC2) principal components of the mechanical mouthpart traits; and first (locPC1) and second (locPC2) principal components of the body size and locomotory traits. For all traits, the species mean value from the five isopod individuals measured was used for the analysis. Thus, for species  $i$  in plot  $p$  in plot pair  $q$  and forest patch  $r$ ,

$$Y_{ipqr} \sim \text{NegBinom}(\mu_{ipqr}, \theta), \quad (1)$$

$$\ln \mu_{ipqr} = \beta_{0,i} + \beta_{0,qr} + \beta_{1,i}X_{pqr} + \beta_{2}Z_iX_{pqr}, \quad (2)$$

where  $Y$  is abundance,  $\mu$  is the linear predictor,  $\theta$  is the dispersion parameter,  $\beta_{0,i}$  is the species-specific random intercept,  $\beta_{0,qr}$  is the plot pair–forest patch nested random intercept,  $X_{pqr}$  is either of the five environmental variables

listed above,  $\beta_{1,i}$  is the species-specific response to the environment (random slope),  $Z_i$  is either of the six traits listed above, and  $\beta_2$  is the trait–environment interaction coefficient. All possible pairwise combinations of each environmental variable and trait were fitted separately, null models containing environmental variables but not traits (i.e.,  $\ln \mu_{ipqr} = \beta_{0,i} + \beta_{0,qr} + \beta_{1,i}X_{pqr}$ ), and a global null model containing neither environmental variables nor traits (i.e.,  $\ln \mu_{ipqr} = \beta_{0,i} + \beta_{0,qr}$ ), were also fitted, resulting in 46 different models of isopod abundances. Models were implemented in R with the package *lme4* (Bates et al. 2015). Models that successfully converged (35 of the 46 fitted models) were ranked using Akaike's information criterion with correction for small sample sizes (AICc), and inferences were made using models with  $\Delta\text{AICc} < 2$ , according to Burnham and Anderson (2002) and using the R package MuMIn (Barton 2022).

To check for the potential effect of interspecific interactions on these results, a Bayesian generalized linear latent variable model was fitted to the data, with almost identical specifications to the best GLMM model, with the only difference being the inclusion of a latent variable model component to account for interspecific interactions and joint responses to unmeasured environmental variables (Hui 2016). This model and its results are described in detail in the Supporting Information (Appendix S1). All analyses were performed in R version 4.0.3 (R Core Team 2020).

## Results

A total of 2827 stems from 237 identified tree species were recorded in vegetation surveys of the 58 plots. The first two PCoA axes collectively explained 23.7% of tree community composition variation (Fig. 2). Most notably, in PCoA1, tree species associated with native species-dominated secondary and primary forests loaded negatively on PCoA1 (e.g., *Prunus polystachya* [Rosaceae], *Gironniera nervosa* [Cannabaceae], many uncommon species not displayed in Fig. 2), native tree species associated with slowed or arrested forest recovery (e.g., *Adinandra dumosa* [Pentaphylacaceae], *Rhodamnia cinerea* [Myrtaceae]), and tree species found in recently abandoned rubber plantations (e.g., the pará rubber tree *Hevea brasiliensis* [Euphorbiaceae], a non-native plantation species; Fig. 2), loaded positively on PCoA1. We thus interpreted PCoA1 as a forest recovery gradient. In addition to the observed floristic compositions described above, the selection of plot locations across sites with highly dissimilar land use histories (ranging from historically protected areas to recently abandoned monoculture plantations) necessitates that the forest recovery gradient becomes projected onto PCoA1—the axis which explains the greatest variation in the sample—since no other known environmental gradient can reasonably explain the same amount of tree compositional variation across the geographic extent of our study.

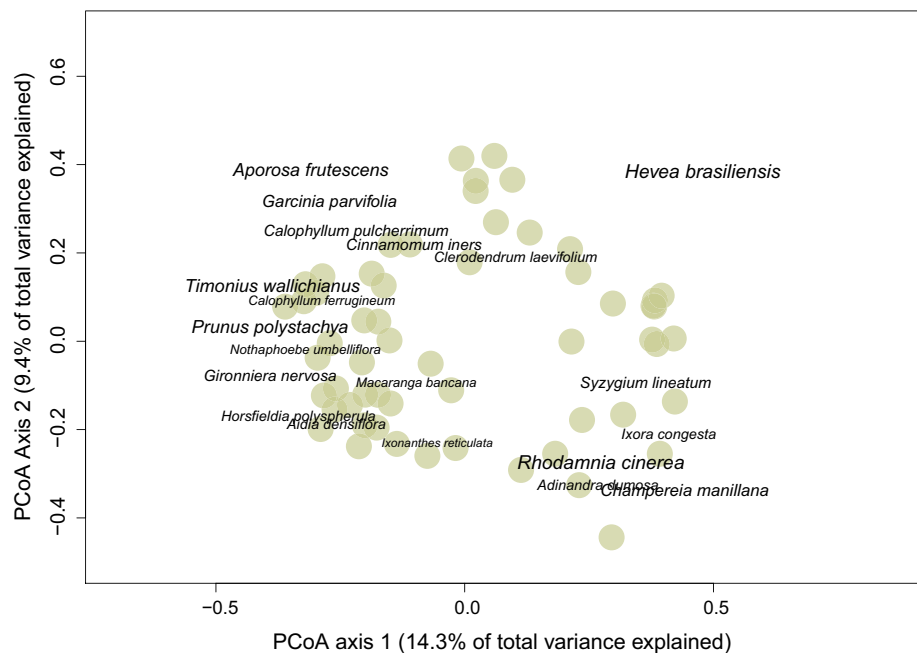
From leaf litter samples, 174 isopod individuals from seven morphospecies and three families, namely Armadillidae, Philosciidae and Scleropactidae were collected, although only six of these species were present in sufficient

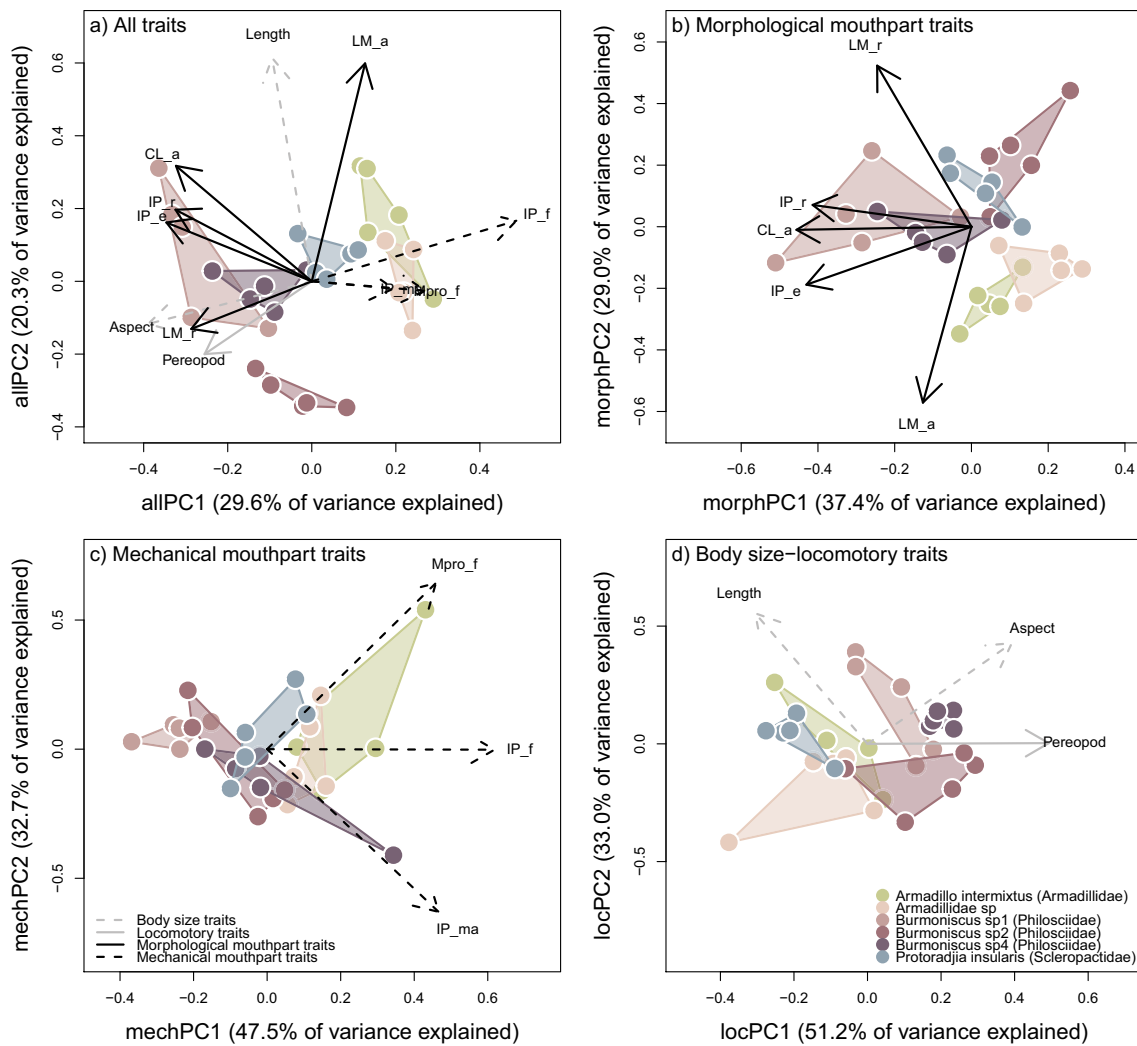
quantities for use in the subsequent analysis (Table S1). Interspecific variation accounted for most of the between-individual trait variations (Fig. 3), with species identity explaining 56.2% of variance in the RDA of traits from all trait classes. Species were generally well-resolved when PCAs were run with only traits from each of the three trait classes i.e., morphological mouthpart, mechanical mouthpart and body size–locomotory trait classes (Fig. 3b–d).

The model with the lowest AICc value was the model containing PCoA1, morphPC2, and the interaction between these two variables (Table 2). All other models had AICc values that were more than 1.5 units larger than this model's AICc, and this model consequently accounted for 64% of the total Akaike weights, thus the data overwhelmingly supported this single model over all other competing models.

We focus on the inferences that could be made from only the top model since it received overwhelming support from the data (Burnham and Anderson 2002). The trait–environment interaction coefficient ( $\beta_2$  in Eq. 2) in this model was  $-4.04$  (95% confidence interval =  $[-6.75, -1.33]$ ). This model predicted that species with lower morphPC2 values (i.e., broader but less serrated/rugose lacinia mobilis; Fig. 4d, e) respond positively to PCoA1, and are thus more likely to be found in forests containing high proportions of plantation- and disturbance-associated tree species (Fig. 4a). Conversely, species with higher morphPC2 values (i.e., narrower but more serrated/rugose lacinia mobilis; Fig. 4h, i) respond negatively to PCoA1, and are thus more likely to be found in forests containing high proportions of late-successional tree species (Fig. 4c). The trait–environment interaction estimated by a Bayesian generalized linear latent variable model (which was analogous to the top GLMM

**Fig. 2** Principal coordinates analysis (PCoA) ordination of the 58 forest plots used in this study. The first axis (PCoA1) captured tree compositional changes along a forest recovery gradient, with more disturbed, abandoned rubber (*Hevea brasiliensis*) plantation-type forests having more positive PCoA1 scores, and more recovered or pristine, native species-dominated forests having more negative PCoA1 scores. Points represent plot-level tree communities; texts denote average species loadings on PCoA axes, and are sized proportionately to the number of plots each is found in. Points located closer to species names are more likely to contain large proportions of these species





**Fig. 3** Principal components analyses (PCAs) of all (a), morphological mouthpart (b), mechanical mouthpart (c), and body size-locomotory functional traits of the six isopod species. Points represent the trait values of individual isopods, while polygons about the points represent the functional trait space occupied by that species. Arrows indicate the loadings of individual traits on PCA axes, and are colored or dashed according to the class (body size, locomotory, morphologi-

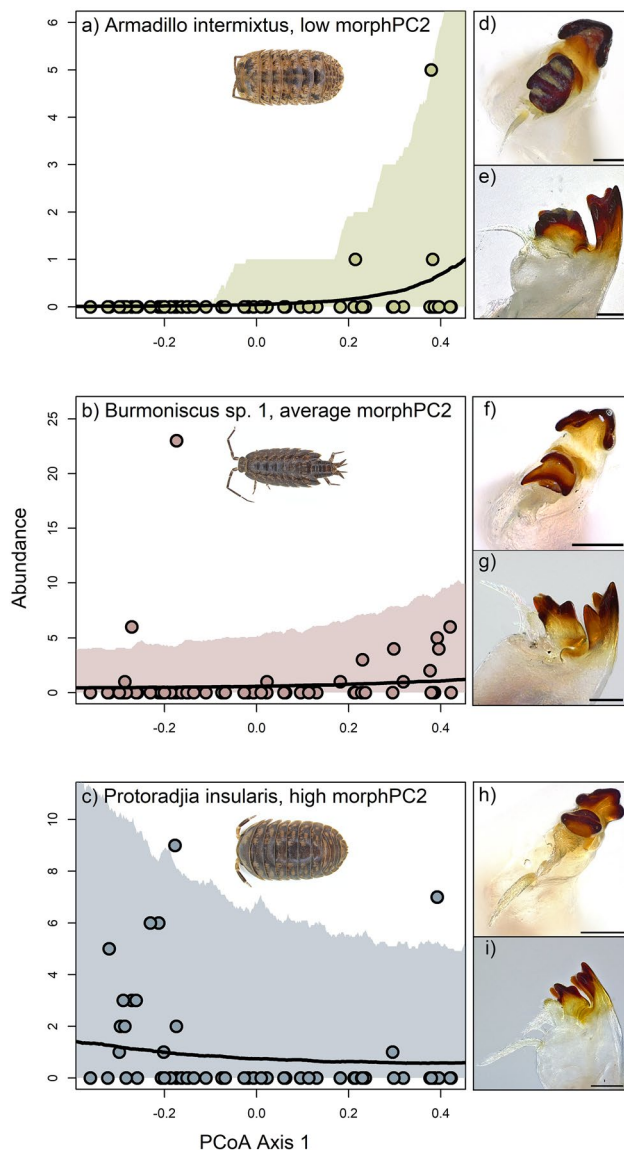
cal mouthpart or mechanical mouthpart) each trait belongs to. Trait abbreviations: *IP\_e* incisor process edge length, *IP\_r* incisor process rugosity, *LM\_a* contact area of lacinia mobilis, *LM\_r* lacinia mobilis rugosity, *CL\_a* side profile area of ciliated lobe, *IP\_f* incisor process biting force, *IP\_ma* incisor process mechanical advantage, *Mpro\_f* molar process biting force

**Table 2** Model selection table comparing the top models of isopod abundance, as ranked by Akaike's information criterion with correction for small sample sizes (AICc)

Model rank	Fixed effects formula	df	AICc	ΔAICc	Weight	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>
1	~ PCoA1 × morphPC2	10	493.21	0.00	0.64	12.3	25.3
2	~ PCoA1 × mechPC1	10	494.71	1.50	0.30	9.7	27.9
...							
4	~ null	5	499.67	6.46	0.03	0.0	10.1
...							
6	~ PCoA1	8	499.70	6.49	0.03	1.4	23.9

df degrees of freedom, weight Akaike weight = weight of evidence in favor of a model being the best model in the candidate set, R<sup>2</sup><sub>m</sub> marginal R<sup>2</sup> of fixed effects only, R<sup>2</sup><sub>c</sub> conditional R<sup>2</sup>, of fixed and random effects of the model, PCoA1 first principal coordinate axis of plot tree composition, representing the forest recovery gradient, morphPC2 second principal component of isopod morphological mouthpart traits, mechPC1 first principal component of isopod mechanical mouthpart traits





**Fig. 4** Top model predicted responses of three isopod species to a forest recovery gradient (gradient of PCoA1 values). *Armadillo intermixtus* (Armadillidae), which has a low morphPC2 value (large [d] but flat [e] lacinia mobilis), responds positively to the forest recovery gradient (a), *Burmoniscus* sp. 1 (Philosciidae), which has an average morphPC2 value, does not respond to the gradient (b) while *Protoradja insularis* (Scleropactidae), which has a high morphPC2 value (narrow [h] but highly serrated/rugose [i] lacinia mobilis), responds negatively. In a–c, points represent raw data; black lines represent model predictions, and shaded regions represent 95% confidence intervals of predictions; in d–i, scale bars represent 100  $\mu$ m

except for the inclusion of two latent variables in the model) estimated a very similar  $PCoA1 \times morphPC2$  value, and thus validated the findings presented above (Appendix S1).

In comparison to the top model, the second-ranked model containing PCoA1, mechPC1, and their interaction had a  $\Delta AICc$  of 1.50, but a trait–environment interaction coefficient ( $\beta_2$  in Eq. 2) whose 95% confidence interval

$[-0.37, 5.05]$  intercepted zero. The global null model, which contained neither environmental variables nor traits, was ranked fourth and had a  $\Delta AICc$  of 6.45, while the environment-only null model which contained PCoA1 but not traits was ranked sixth with a  $\Delta AICc$  of 6.48 (Table 2).

We supplemented our findings with observations from two additional isopod species known from the study area but not collected in our sample, and for which environment associations are well known. As predicted, the species strongly associated with undisturbed forests (*Adinda* sp.; Scleropactidae) had high morphPC2 values, and the one associated with highly disturbed vegetation types (*Venezillo parvus*; Armadillidae) had low morphPC2 values (Fig. S6).

## Discussion

In this study, we examined the functional traits of leaf litter isopods from 58 plots across primary and secondary forests in Singapore. Tree communities in the 58 plots fell along a continuous gradient of forest recovery that was reflected in the first axis of a principal coordinates analysis (PCoA1), with communities containing high proportions of plantation- and disturbance-associated tree species at one end, and communities containing high proportions of later successional native tree species at the other. We examined if isopod body size, locomotory, mechanical mouthpart, and morphological mouthpart traits of isopods responded to this forest recovery gradient, as well as to variation among the plots in tree diversity, basal area, and litter amount. Morphological mouthpart traits were found to respond to PCoA1 (the forest recovery gradient), with species with broader but less serrated/rugose lacinia mobilis (LM) that are likely to cut/crush food fragments more efficiently being more abundant in forests which experienced more intensive and/or recent agricultural and logging impacts. This finding supports our hypothesis that differences across tropical forest gradients in resource availabilities explain differences in isopod—and possibly other leaf litter detritivore—distributions. Isopod species in less disturbed and more mature tropical forests may have more fungivorous feeding habits or rely more on microbial conditioning of litter, while those in more disturbed forests may more often feed directly on leaf litter material and rely less on microbial conditioning of litter. Since morphological mouthpart traits likely also predict consumption and excretion rates of isopods (and thus potentially their effects on litter decomposition and nutrient cycling), it is possible that these traits would assist predictions of the ecosystem functions provided by isopods and other detritivorous litter invertebrates.

## Morphological mouthpart traits respond to a forest recovery gradient

Morphological mouthpart traits, particularly those associated with the lacinia mobilis (LM), responded to the forest recovery gradient identified in our study (Fig. 4). Species more often found in disturbed forest types in our study tended to have LMs that were larger in area (Fig. 4d), but less serrated in their edges (Fig. 4e). These structures appear to be adapted to further crushing and masticating food particles that have been fragmented by the incisor processes and are indicative of a diet that contains a high proportion of fibrous leafy and/or woody litter. In contrast, the LMs of species that were associated with more recovered forest habitats were more serrated, having more pointed edges (Fig. 4i) and smaller cross-sectional areas (Fig. 4h), suggesting a diet that contains a high proportion of fungi. These results are similar to those of a comparative study of Oribatid mite mouthpart morphology (Xavier and Haq 2007), which found that fungal feeders (described as “microphytophages”) had “elongated and narrow chelicerae with small sharp teeth suitable for nibbling fungal cushions” and less developed rutellae, while species which grazed directly on leaves and wood had chelicerae bearing thicker teeth, and rutellae which were more developed (i.e., larger and more sclerotized) and that contained a concave vestibule that was used to collect scraped food particles for further mastication.

Our findings support observations from other studies that suggest that trophic niches of leaf litter detritivore communities appear to shift toward “fast energy channels” in more disturbed forests (Zhou et al. 2022; Wildermuth et al. 2023)—that is, in more disturbed forests, canopy tree species tend to have higher quality (more nutritious and less chemically defended) leaves, and more litter invertebrate species are primary litter consumers which feed on freshly fixed plant carbon, such as living plant material, fresh leaf litter, or bacteria, while in more recovered or pristine forests, canopy tree species tend to have lower quality leaves, and more litter invertebrate species are secondary litter consumers which graze on fungi (Frouz 2018). Many studies have shown that fungi comprise a significant proportion of isopod diets (Kayang et al. 1996; Crowther et al. 2013) and that isopods often prefer microbe-conditioned (i.e., partially decomposed) leaf litter over freshly fallen leaves (Rushton and Hassall 1983; Zimmer et al. 2003; Ihnen and Zimmer 2008). It is likely that most isopod species feed on both fungi and leaf litter (Potapov et al. 2022), but that the higher volumes of recalcitrant litters and greater diversities of saprotrophic fungi communities in more pristine tropical forests (Tomao et al. 2020) increasingly favor secondary (fungivorous) rather than primary (direct detritivory) feeding strategies.

The role of mouthpart traits of isopods and other detritivorous taxa in moderating species environmental responses

and ecosystem functioning should be a key focus of future studies. Our study is based on a relatively small sample size of only 174 isopod individuals from six species (although see Fig. S6 for confirmation of our results with additional species from outside the study sites). These species include both roller species (isopod species that are able to roll into a ball [a.k.a. conglobate] for physical protection; from the families Armadillidae and Scleropactidae in our study) and runner species (isopod species that are unable to do so; from the family Philosciidae in our study). Systematic differences in the morphologies between these two functional groups could potentially confound inferences of trait–environment interactions. This is, however, unlikely to have been a problem in our study, since negative (e.g., *Protoradja insularis*, a roller, and *Burmoniscus* sp. 2, a runner) and intermediate-positive (e.g., *Armadillidae* sp., a roller, and *Burmoniscus* sp. 4, a runner) species responses to PCoA1 were exhibited by species in both functional groups. While the low total number of individuals sampled in this study may give rise to relatively large error margins in model parameter estimates (i.e., low statistical precision), the main findings of the study are nevertheless reliable because of the strong differences in habitat associations between the isopod species in the study. For example, despite only being represented by seven individuals in the sample, there is no doubt that *Armadillo intermixtus* is associated with less recovered forests, both from the data obtained (Fig. 4a), as well as from many observations we have made while working in these habitats (Table S1). Future studies should aim to investigate mouthpart traits of isopods and other detritivorous taxa using more comprehensive samples with larger numbers of species and individuals from each functional group.

## A subset of traits may capture key axes of variation in isopod functional ecology

Contrary to expectations, mechanical mouthpart traits did not respond strongly to the environmental gradients investigated in this study. Mechanically stronger mouthparts facilitate direct feeding on tougher, more recalcitrant leaf litter in springtails (Raymond-Léonard et al. 2019) and mites (Perdomo et al. 2012). However, larger-sized isopods may not be limited by biting force, which may be why mandible mechanical traits do not appear to respond to environmental (resource) gradients in our study. Nevertheless, it is noteworthy that incisor process (IP) biting force was weakly correlated with the lacinia mobilis (LM) traits that characterized the morphPC2 gradient (between IP\_f and LM\_r, Pearson's  $\rho = -0.52$ , false discovery rate-corrected  $p$ -value = 0.277; Fig. S5; note also the loadings of opposite directions on all PC1 in Fig. 3a). That is, our data suggested that species that are likely fungivorous with narrow, serrated LM tended to have lower biting strength than those that are likely directly

detritivorous with broader, less serrated LMs. This covariation in mechanical strength and morphology is also noted by Xavier and Haq (2007) for Oribatid mites, and should be further explored using larger datasets of isopod species.

Our data also showed that body size and locomotory traits tend to be coupled across isopod species (Fig. 3d). The relative lengths of pereopods and antennae were strongly positively correlated among the six species examined in this study (Fig. S5), suggesting that faster running isopods with longer relative pereopod lengths also require relatively longer antennae to provide a wider sensory radius (Schmalz 1998). Furthermore, body size traits (i.e., body length and width) were weakly negatively correlated with locomotory traits (Fig. 3d), meaning that smaller-bodied species tended to have relatively longer appendages and presumably rely more on running than rolling for defense (Tuf and Ďurajková 2022).

### Morphological mouthpart traits may enable bottom-up predictions of ecosystem function

A key goal of functional trait ecology is to enable the prediction of ecosystem function across different environments using traits, but this goal can only be achieved if appropriate traits (i.e., those which both respond to the environment and have an effect on ecosystem function) are measured. Our findings reinforce existing studies in suggesting that mouthpart traits measured from the mandibles in isopods (Brousseau et al. 2019) and collembolans (Raymond-Léonard et al. 2019), and from the chelicerae or rutellae in oribatid mites (Xavier and Haq 2007; Perdomo et al. 2012), may qualify as such traits. Our study found that morphological mouthpart traits in detritivorous litter isopods respond to variation among tropical forest tree communities across an environmental gradient. If these same traits can also act as good predictors of resource consumption and nutrient excretion rates of litter isopods (a reasonable albeit unproven assumption), an unbroken chain of causality would be established between the environment, detritivore traits, and the ecosystem functions they facilitate (such as decomposition and nutrient cycling). Establishing parameters for such a mechanistic pathway would allow robust predictions of the effects of isopod communities on nutrient cycling rates in any forest patch whose forest recovery status is known. Further research should thus focus on quantifying the effect of morphological mouthpart traits on decomposition and nutrient cycling and extending the use and generalizability of mouthpart trait measurements across other detritivorous invertebrate taxa.

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**Author contributions** WNL, SBHA and EMS conceived the study. GKP, SKBT, WNL and SBHA carried out the fieldwork. SBHA measured the traits. WNL and SBHA performed the analysis and wrote the first manuscript draft. All other authors contributed to revisions, and approved of the final version of the manuscript for submission.

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**Data accessibility** Data supporting this article will be made available via Figshare upon publication. Mean ( $\pm$  SE) values of measured traits are presented in Table S2 of the online supporting information.

### Declarations

**Conflict of interest** We declare we have no competing interests.

### References

- Auclerc A, Beaumelle L, Barantal S, Chauvat M, Cortet J, De Almeida T, Dulaurent AM, Dutoit T, Joimel S, Séré G, Blight O (2022) Fostering the use of soil invertebrate traits to restore ecosystem functioning. *Geoderma* 424:116019. <https://doi.org/10.1016/j.geoderma.2022.116019>
- Barton K (2022) MuMIn: multi-model inference. R package version 1.46.0. <https://CRAN.R-project.org/package=MuMIn>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc Ser B Stat Methodol* 57:289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Brousseau P-M, Gravel D, Handa IT (2018) On the development of a predictive functional trait approach for studying terrestrial arthropods. *J Anim Ecol* 87:1209–1220. <https://doi.org/10.1111/1365-2656.12834>
- Brousseau P, Gravel D, Handa IT (2019) Traits of litter-dwelling forest arthropod predators and detritivores covary spatially with traits of their resources. *Ecology* 100:e02815. <https://doi.org/10.1002/ecy.2815>
- Buckingham S, Murphy N, Gibb H (2019) Effects of fire severity on the composition and functional traits of litter-dwelling macroinvertebrates in a temperate forest. *For Ecol Manag* 434:279–288. <https://doi.org/10.1016/j.foreco.2018.12.030>

- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York
- Crowther TW, Stanton DWG, Thomas SM et al (2013) Top-down control of soil fungal community composition by a globally distributed keystone consumer. *Ecology* 94:2518–2528. <https://doi.org/10.1890/13-0197.1>
- Csonka D, Halasy K, Buczkó K, Hornung E (2018) Morphological traits—desiccation resistance—habitat characteristics: a possible key for distribution in woodlice (Isopoda, Oniscidea). *Zookeys* 801:481–499. <https://doi.org/10.3897/zookeys.801.23088>
- deCastro-Arrazola I, Andrew NR, Berg MP, Curtsdotter A, Lumaret JP, Menéndez R, Moretti M, Nervo B, Nichols ES, Sánchez-Piñero F, Santos AMC, Sheldon KS, Slade EM, Hortal J (2023) A trait-based framework for dung beetle functional ecology. *J Anim Ecol* 92:44–65. <https://doi.org/10.1111/1365-2656.13829>
- Dias ATC, Krab EJ, Mariën J et al (2013) Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. *Oecologia* 172:667–677. <https://doi.org/10.1007/s00442-012-2541-3>
- Dudgeon D, Ma HHT, Lam PKS (1990) Differential palatability of leaf litter to four sympatric isopods in a Hong Kong forest. *Oecologia* 84:398–403
- Ellers J, Berg MP, Dias ATC et al (2018) Diversity in form and function: vertical distribution of soil fauna mediates multidimensional trait variation. *J Anim Ecol* 87:933–944. <https://doi.org/10.1111/1365-2656.12838>
- Ferrara F, Meli C, Taiti S (1995) Taxonomic revision of the subfamily Toradjiinae (Crustacea: Oniscidea: Scleropactidae). *Zool J Linn Soc* 113:351–459. <https://doi.org/10.1111/j.1096-3642.1995.tb00938.x>
- Frouz J (2018) Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma* 332:161–172
- Funk JL, Larson JE, Ames GM et al (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol Rev* 92:1156–1173. <https://doi.org/10.1111/brv.12275>
- Gravel D, Poisot T, Albouy C et al (2013) Inferring food web structure from predator-prey body size relationships. *Methods Ecol Evol* 4:1083–1090. <https://doi.org/10.1111/2041-210X.12103>
- Hassall M (1977) The functional morphology of the mouthparts and foregut in the terrestrial Isopod *Philoscia muscorum* (Scopoli, 1763). *Crustaceana* 33:225–236
- Hessler RR (1982) The structural morphology of walking mechanisms in eumalacostracan crustaceans. *Philos Trans Royal Soc* 296:245–298. <https://doi.org/10.1098/rstb.1982.0005>
- Hishi T, Urakawa R, Saitoh S et al (2022) Topography is more important than forest type as a determinant for functional trait composition of Collembola community. *Pedobiologia* 90:150776. <https://doi.org/10.1016/j.pedobi.2021.150776>
- Huberty AF, Denno RF (2006) Trade-off in investment between dispersal and ingestion capability in phytophagous insects and its ecological implications. *Oecologia* 148:226–234. <https://doi.org/10.1007/s00442-006-0371-x>
- Hui FKC (2016) boral—Bayesian ordination and regression analysis of multivariate abundance data in R. *Methods Ecol Evol* 7:744–750. <https://doi.org/10.1111/2041-210X.12514>
- Ihnen K, Zimmer M (2008) Selective consumption and digestion of litter microbes by *Porcellio scaber* (Isopoda: Oniscidea). *Pedobiologia (Jena)* 51:335–342. <https://doi.org/10.1016/j.pedobi.2007.06.001>
- Kayang H, Sharma GD, Mishra RR (1996) The influence of isopod grazing on microbial dynamics in decomposing leaf litter of *Alnus nepalensis* D. Don *Eur J Soil Biol* 32:35–39
- Koehler H-R, Alberti G (1990) Morphology of the mandibles in the millipedes (Diplopoda, Arthropoda). *Zool Scr* 19:195–202. <https://doi.org/10.1111/j.1463-6409.1990.tb00255.x>
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16:545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Malcicka M, Berg MP, Ellers J (2017) Ecomorphological adaptations in Collembola in relation to feeding strategies and microhabitat. *Eur J Soil Biol* 78:82–91. <https://doi.org/10.1016/j.ejsobi.2016.12.004>
- McCary MA, Schmitz OJ (2021) Invertebrate functional traits and terrestrial nutrient cycling: Insights from a global meta-analysis. *J Anim Ecol* 90:1714–1726. <https://doi.org/10.1111/1365-2656.13489>
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Moretti M, Dias ATC, Bello F et al (2017) Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Funct Ecol* 31:558–567. <https://doi.org/10.1111/1365-2435.12776>
- Oksanen J, Blanchet FG, Friendly M et al (2016) vegan: community ecology package. R package version 24-1
- Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35:526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Parr CL, Dunn RR, Sanders NJ et al (2017) *GlobalAnts*: a new database on the geography of ant traits (Hymenoptera: Formicidae). *Insect Conserv Divers* 10:5–20. <https://doi.org/10.1111/icad.12211>
- Pekár S, Wolff JO, Černecká L et al (2021) The World Spider Trait database: a centralized global open repository for curated data on spider traits. *Database* 2021:baab064. <https://doi.org/10.1093/database/baab064>
- Perdomo G, Evans A, Maraun M et al (2012) Mouthpart morphology and trophic position of microarthropods from soils and mosses are strongly correlated. *Soil Biol Biochem* 53:56–63. <https://doi.org/10.1016/j.soilbio.2012.05.002>
- Pey B, Nahmani J, Auclerc A et al (2014) Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic Appl Ecol* 15:194–206. <https://doi.org/10.1016/j.baae.2014.03.007>
- Potapov AM (2022) Multifunctionality of belowground food webs: resource, size and spatial energy channels. *Biol Rev*. <https://doi.org/10.1111/brv.12857>
- Potapov AM, Beaulieu F, Birkhofer K et al (2022) Feeding habits and multifunctional classification of soil-associated consumers from protists to vertebrates. *Biol Rev* 97:1057–1117. <https://doi.org/10.1111/brv.12832>
- R Core Team (2020) R: a language and environment for statistical computing. Austria, Vienna
- Raymond-Léonard LJ, Gravel D, Handa IT (2019) A novel set of traits to describe Collembola mouthparts: taking a bite out of the broad chewing mandible classification. *Soil Biol Biochem* 138:107608. <https://doi.org/10.1016/j.soilbio.2019.107608>
- Richter S, Edgecombe GD, Wilson GDF (2002) The lacinia mobilis and similar structures—a valuable character in arthropod phylogenetics? *Zoologischer Anzeiger J Comp Zool* 241:339–361. <https://doi.org/10.1078/0044-5231-00083>
- Rousseau L, Venier L, Aubin I et al (2019) Woody biomass removal in harvested boreal forest leads to a partial functional homogenization of soil mesofaunal communities relative to unharvested forest. *Soil Biol Biochem* 133:129–136. <https://doi.org/10.1016/j.soilbio.2019.02.021>

- Rushton SP, Hassall M (1983) Food and feeding rates of the terrestrial Isopod *Armadillidium vulgare* (Latreille). *Oecologia* 57:415–419
- Schindelin J, Arganda-Carreras I, Frise E et al (2012) Fiji: an open-source platform for biological-image analysis. *Nat Methods* 9:676–682. <https://doi.org/10.1038/nmeth.2019>
- Schmalfuss H (1998) Evolutionary strategies of the antennae in terrestrial isopods. *J Crustac Biol* 18:10–24. <https://doi.org/10.1163/193724098X00025>
- Sfendourakis S, Taiti S (2015) Patterns of taxonomic diversity among terrestrial isopods. *Zookeys* 515:13–25. <https://doi.org/10.3897/zookeys.515.9332>
- Suding KN, Lavorel S, Chapin FS et al (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Glob Change Biol* 14:1125–1140. <https://doi.org/10.1111/j.1365-2486.2008.01557.x>
- Taiti S, Ferrara F (1986) Terrestrial isopods from the oriental region. *Monitore Zoologico Italiano Supplemento* 21:185–195. <https://doi.org/10.1080/03749444.1986.10736714>
- Taiti S, Paoli P, Ferrara F (1998) Morphology, biogeography, and ecology of the family Armadillidae (Crustacea, Oniscidea). *Isr J Zool* 44:291–301
- Tomao A, Antonio Bonet J, Castaño C, de-Miguel S (2020) How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. *For Ecol Manag* 457:117678. <https://doi.org/10.1016/j.foreco.2019.117678>
- Tuf IH, Ďurajková B (2022) Antipredatory strategies of terrestrial isopods. *Zookeys* 1101:109–129. <https://doi.org/10.3897/zookeys.1101.76266>
- Vandel A (1960) Les isopodes terrestres de l'archipel maderien. Éditions du Muséum, Paris
- Violle C, Navas ML, Vile D et al (2007) Let the concept of trait be functional! *Oikos* 116:882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Wildermuth B, Riko F, Dragan M et al (2023) Conifers and non-native tree species shift trophic niches of generalist arthropod predators in Central European beech forests. *BMC Ecol Evol* 23:3. <https://doi.org/10.1186/s12862-023-02105-1>
- Williamson J, Teh E, Jucker T et al (2022) Local-scale temperature gradients driven by human disturbance shape the physiological and morphological traits of dung beetle communities in a Bornean oil palm–forest mosaic. *Funct Ecol* 36:1655–1667. <https://doi.org/10.1111/1365-2435.14062>
- Wong MKL, Guénard B, Lewis OT (2019) Trait-based ecology of terrestrial arthropods. *Biol Rev* 94:999–1022. <https://doi.org/10.1111/brv.12488>
- Xavier A, Haq MA (2007) A study on the feeding habits and gnathal appendages in Oribatid mites (Acarina: Cryptostigmata). *Zoos Print J* 22:2671–2674
- Yee ATK, Chong KY, Seah WW et al (2019) Vegetation of Singapore. *Flora Singap* 1:47–70. <https://doi.org/10.26492/fof1.2019-05>
- Zhou Z, Krashevskaya V, Widyastuti R et al (2022) Tropical land use alters functional diversity of soil food webs and leads to monopolization of the detrital energy channel. *Elife* 11:e75428. <https://doi.org/10.7554/eLife.75428>
- Zimmer M (2002) Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. *Biol Rev Camb Philos Soc* 77:S1464793102005912. <https://doi.org/10.1017/S1464793102005912>
- Zimmer M, Kautz G, Topp W (2003) Leaf litter-colonizing microbiota: supplementary food source or indicator of food quality for *Porcellio scaber* (Isopoda: Oniscidea)? *Eur J Soil Biol* 39:209–216. <https://doi.org/10.1016/j.ejsobi.2003.07.001>

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