

DRAFT: Harmonized and trait aggregation paper

Introduction

Explaining and predicting how communities are shaped by environmental factors is one of the main goals of ecology. Species traits, defined as measurable properties of an organism [1], might be beneficial in achieving this goal [2]. Traits evolve through adaptations (e.g., physiological, behavioural, etc.) of organisms to their environment and indicate direct or indirect linkages between the biological response of an organism or a population and its environment [3, 4]. Besides providing a mechanistic explanation of species-environment relationships, trait-based approaches might be suitable for large scale analysis because the variability in trait responses is lower than in taxonomic responses [5, 6]. Traits of freshwater invertebrate individuals are difficult to determine because - unlike plant traits - they often can not be measured directly. For example, to gain knowledge on feeding habits requires evaluating mouthpart morphology, consumed food, and the organisms function within its community [7]. Nevertheless, invertebrate traits have been increasingly used in freshwater ecology, e.g. by relating macroinvertebrate trait composition to environmental factors and as trait metrics in biomonitoring [8–11].

In the last decades, freshwater ecologists have compiled comprehensive invertebrate trait databases for various continents [12–17]. The availability of invertebrate trait data from different continents enables comparisons of trait variation and analyses of their relation to environmental factors across large scales. However, such analyses have been carried out mostly within continents, using information from one or two trait databases. For example, Bonada et al. [5] compared trait composition for Mediterranean and temperate regions in Europe using traits from Usseglio-Polatera et al. [12] (typically referred to as Tachet database); Poff et al. [8] characterized trait composition across sites in the Western US using traits from Poff et al. [18], and Botwe et al. [19] investigated the effect of salinity on invertebrate traits in different sites in South Australia using trait data from Poff et al. [18] and Schäfer et al. [20]. Analyses of invertebrate traits that synthesize information on invertebrate grouping features from more than two different continents are rare.

In this study, we follow the terminology proposed by Schmera et al., where a grouping feature is defined as a general property (e.g. feeding mode) that comprises a "group of related traits (e.g., predator, shredder, etc.) that vary among species or among individuals within a species" [21]. Thus, we use the term grouping feature in place of which many studies use the term "trait", and the term trait instead of "trait state", "modality" or "trait category". Traits can be described using different codings (binary, fuzzy) that represent the prevalence of a characteristic in an organism.

To our knowledge, only Brown et al. [22] harmonized grouping features from more than two geographically distant invertebrate trait databases, for a limited set of grouping features (8) and taxa (112), in a study on the influence of decreasing glacier cover on functional diversity and community assembly of invertebrates.

We suspect that the heterogeneity of information in freshwater invertebrate trait databases,

besides the diversity of taxa across regions, is likely a major reason for the lack of studies across continents. To harmonize grouping features from different regions, first commonly accepted and unambiguous trait definitions are required [23]. In the best case, grouping features would be classified into the same traits across databases or they could easily be harmonized using standardized terminology. However, a lack of standardized terminology of trait definitions and poor metadata quality in many trait databases are common issues throughout the field of trait-based ecology [6, 23]. Secondly, consistent coding of traits facilitates the compatibility of trait data from different databases.

Traits can be described in a binary fashion, or with multiple categories, ignoring uncertainty how the trait is expressed in any particular organism (e.g. adult terrestrial stage, presence of gills) or continuous (e.g. tolerance of pollution, body size). One approach for dealing with uncertainty is the use of fuzzy coded variables, where the traits are assigned probabilistic values. Fuzzy codes are used to account for plasticity in traits, variability in traits within taxonomic groups above species, and incomplete knowledge and are usually converted to proportions.

However, invertebrate trait databases are heterogeneous regarding the coding they use for their traits [24]. Brown et al. [22] harmonized grouping features based on trait databases from Europe, North America, and New Zealand because in these trait databases identical grouping features are classified differently into traits. As the traits from North America were coded binary in contrast to the traits from Europe and New Zealand which have been established using affinity scores, the authors consulted experts to assign fuzzy coded traits to North American taxa or inferred them from the European trait database. Thus, it becomes apparent that using invertebrate trait data from several regions requires extensive data processing prior to the actual data analysis. A centralized database with standardized and unambiguous traits and a consistent coding of traits would minimize data processing effort. Discrepancies in the taxonomic resolutions (e.g. species, genus or family) when linking observational taxonomic data to trait database represents another challenge. When observations are on a more precise taxonomic level than data available in the trait databases (e.g. observations on species-level, trait data on genus-level) trait information of the less precise taxonomic level is often assigned (e.g. [9, 25]). Conversely, if trait information is only available on more precise taxonomic levels than the observed taxa, traits are aggregated to a less precise taxonomic level, e.g. [9, 18, 26, 27]. Studies have used different methods of trait aggregation, e.g. the mean [28], median [9] or the mode [26]. Up to now, studies on how and to which extent different trait aggregation methods influence trait-based analysis are missing. However, related knowledge would inform future studies regarding the choice of the aggregation method.

We studied the influence of grouping feature harmonization and trait aggregation on trait-environment relationships. In particular, we aimed to (1) determine the effect of different harmonization methods using 4 invertebrate trait database for 7 grouping features from Europe, North America, New Zealand, and Australia. Furthermore, we (2) compared trait affinities obtained through different trait aggregation methods to trait affinities assigned at family-level by experts. We (3) re-analysed data on the effect of anthropogenic salinisation on biological traits by Szöcs et al. [9] using harmonized grouping features and aggregated traits. By comparison with the original analysis, we investigated how harmonizing and aggregating trait data can modify the outcome of trait-environment relationships. Finally, we (4) present an overview of discrepancies in trait definition between the used invertebrate trait datasets and discuss challenges of trait data synthesis.

Methods

Selection of traits and harmonization of trait databases

We extracted information from 6 trait databases from Europe, North America, Australia, and New Zealand and harmonized 7 grouping features. Trait information for Europe was obtained from the [freshwaterecology.info](#) database [13] and the Tachet database [12]. The [freshwaterecology.info](#) contains taxa on species-level, while taxa recorded in the Tachet database are on species, genus and family-level. Trait information for North America was obtained from Twardochleb et al. [29] and complemented by Vieira et al. [14]. Data on body form for European and North American taxa was based on expert knowledge [30]. For Australia and New Zealand, we used trait databases from Kefford et al. [16] and Philips and Smith respectively [15]. To increase readability we refer to the databases as well as the datasets we extracted from them by the name of the continent they originate from, except for European databases, which we refer to by their commonly used names ([freshwaterecology.info](#) and Tachet database).

We selected traits of seven grouping features that were available in all databases, are commonly applied in trait-based ecological studies, and describe different parts of the biology of a species: life history (Voltnism), morphology (Respiration, Body form, Size), ecology (Locomotion, Feeding mode) and reproduction (Oviposition). We omitted ecological traits that describe habitat preferences (e.g. temperature preference) because these traits are missing in the New Zealand trait database. The grouping features were differently classified across the databases, we therefore harmonized them into 26 traits (Table 1). Harmonization was undertaken by amalgamating similar traits into one trait (e.g. crawlers and sprawlers into crawlers). Thereby, for a particular taxa the highest trait affinity score among the amalgamated traits was taken.

We used fuzzy coded traits for establishing our harmonized datasets unless data quality prohibited. In the latter case we used binary traits, i.e. categorical and continuous traits were converted into binary traits. For example, in the [freshwaterecology.info](#) database, the classification of the trait voltnism accounts for different faunistic regions. Hence, the entries such as "arctic" or "boreal" of the e.g. the trait univoltine were substituted with a value of 1. Implicitly, we assumed for binary traits that a value of 1 and 0 corresponds to the highest and no affinity for a particular trait. Fuzzy codes are reported with different ranges in the trait databases (e.g. [freshwaterecology.info](#) 0 to 10, Tachet database 0 to 3 or 0 to 5). We standardized these to a range between 0 and 1 and converted trait affinities to percentages. Thus, fuzzy coded and binary traits were in the same range.

Prior to harmonization we consolidated duplicate taxa on species, genus or family-level if present within a dataset, by either applying the median for fuzzy coded traits, or the maximum for binary traits. We omitted taxa with a lower taxonomic precision than family-level.

Table 1: Traits of the harmonized grouping features. The last column indicates traits that were amalgamated for harmonization (no amalgamation needed if empty).

Grouping feature	Trait	Amalgamated traits
Voltnism	Semivoltine	<1 generation per year
	Univoltine	1 generation per year
	Bi/multivoltine	>1 generation per year
Body Form	Cylindrical	Cylindrical, tubular
	Flattenend	Flattenend, dorsoventrally flattened ^a
	Spherical	Spherical, round (humped)
	Streamlined	Streamlined, fusiform
Size	Small	<9 mm, <10 mm ^b
	Medium	9 - 16 mm, 10 - 20 mm
	Large	>16 mm, >20 mm
Respiration	Gills	Tracheal gills, gills
	Plastron/Spiracle	Temporary air store, Spiracular gills, atmospheric breathers, plant breathers, functional spiracles, air (plants), aerial, plastron/spiracle
	Tegument	Cutaneous, tegument
Locomotion	Burrower	Interstitial, boring, burrowing
	Crawler	Sprawler, walking, climber, clinger, crawler
	Sessile	Attached, sessile
	Swimmer	Skating, diving, planctonic, swimming
Feeding mode	Filterer	Active/passive filterer, absorber, filter-feeder, collector-filterer, filterer
	Gatherer	Deposit-feeder, collector-gatherer, detivore, gatherer
	Herbivore	Grazer, scraper, piercer herbivore, herbivore, algal piercer, piercer (plants) ^c
	Parasite	Piercer (animals) ^c , predator
	Predator	Miner, xylophagus, shredder, shredder detivore
	Shredder	
Oviposition	Aquatic eggs	Eggs attached to substrate/plants/stones, free/fixed eggs/clutches
	Ovoviparity	
	Terrestrial eggs	Terrestrial clutches, terrestrial

a The trait "bluff (blocky)" occurred in the Vieira et al. [14] database and was newly classified by expert knowledge into cylindrical and flattened [30].

b Reflects the different size classifications by the North American trait databases and the other trait databases.

c The trait piercer was defined in the Tachet database for piercing plants and animals, in contrast to the other databases [12]. Taxa exhibiting this trait have been assigned to predators or herbivores based on expert knowledge [31].

Trait aggregation

Traits of the harmonized grouping feature datasets were aggregated to family-level using three approaches. I) Direct aggregation of taxa to family-level giving equal weight to every taxon using the mean or median, denoted *direct_agg_mean* and *direct_agg_median*, respectively. II) Stepwise aggregation, i.e. first to the genus-level and subsequently to the family-level using the mean or median. This approach gives equal weights to each genus. Hereafter, we denote this aggregation type as *stepwise_aggmean* or *stepwise_aggmedian*, respectively. III) Aggregation using a weighted mean approach, denoted as *weighted_agg*. This method weights the genera according to the number of their species in the trait datasets regardless if for every used grouping feature information was available (Figure 1).

To examine the influence of the taxonomic hierarchy and the trait variability on the outcome of the different trait aggregation methods we created three hypothetical examples of different taxonomic hierarchies. 1) A family with an equal number of genera and species (5 genera each with 5 species respectively), denoted as *sim_base*. 2) A family where one genus has a much larger number of species than the other 4 genera (1 genus with 13 species, 4 genera with 3 species respectively), denoted as *sim_extreme*. 3) A family where all genera have a different number of species (8, 2, 7, 3, 5), denoted as *sim_variation*. In total every family consisted of 25 species. To each hypothetical taxonomic hierarchy a hypothetical grouping feature with 3 traits was assigned. The 25 affinities for each trait were simulated by sampling from a truncated normal distribution with a mean value of 0.5 and 5 levels of standard deviations (0.2, 0.4, 0.6, 0.8, and 1) respectively to simulate different levels of trait variability. The truncated normal distribution was bound to 0 and 1. Simulated trait affinities were converted to percentages, similar to the data processing of the trait databases. The sampling was repeated 100 times for each standard deviation. Hence, in total 12500 ($25 * 5 * 100$) trait affinities were simulated. All trait aggregation methods were applied to each simulated dataset. The results were compared based on the produced range of aggregated trait affinities between levels of trait variability and hypothetical taxonomic hierarchies. We also compared for each simulated dataset the differences in trait affinities obtained by each aggregation method.

Comparison of family-level aggregated traits with family-level assigned traits

Aggregated trait affinities of the five trait aggregation methods (*direct_aggmedian*, *direct_aggmean*, *stepwise_aggmedian*, *stepwise_aggmean*, and *weighted_agg*) were compared to trait affinities assigned at family-level by experts, which were available for Australia and North America for a subset of grouping features and taxa. For the Australian dataset, we compared aggregated trait affinities with assigned trait affinities resolved at family-level for the grouping features feeding mode and size using data from Chessman et al. [32]. In Chessman et al. [32] feeding mode is classified similarly as in the Australian dataset except that the trait parasite is missing. We conducted the comparison for the 220 families available in Chessman et al. [32]. Considering each factor combination of family and trait (in total 8) this amounts to 1760 cases.

For the North American dataset, we compared aggregated trait affinities with assigned trait affinities on family-level for the grouping features feeding mode, respiration, size, voltinism, and locomotion. The assigned trait affinities at family-level are part of the North American database (Twardochleb et al.) [29] and originate from expert knowledge. Trait information was available for 94 families of which all were present in the North American dataset (total number of cases 1598).

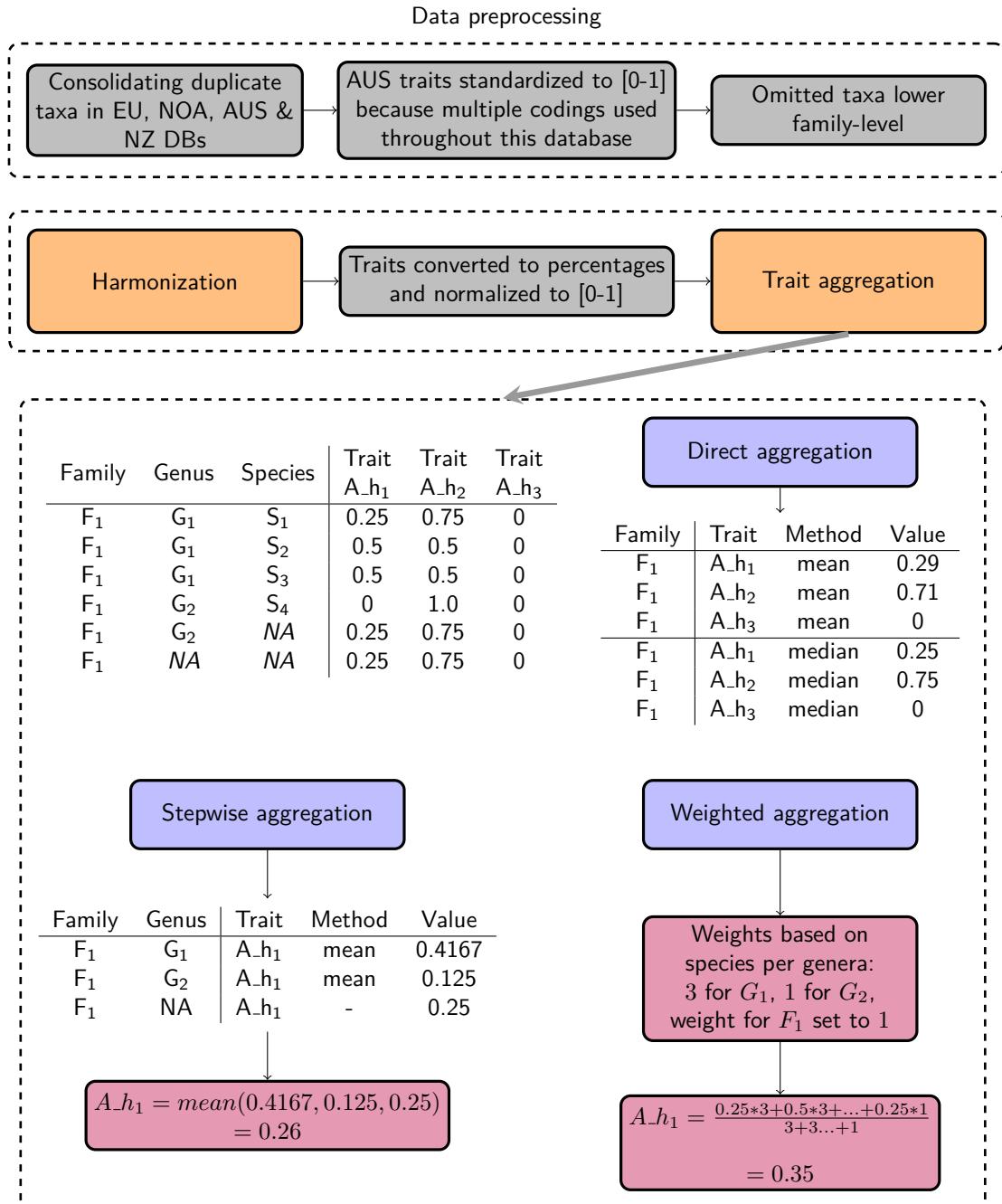


Figure 1: Data processing steps of the selected traits. Intermediate (gray) and main (orange) steps of data preparation are depicted. The dashed bottom box illustrates the different trait aggregation methods using a small made-up example (data in the upper left corner). The aggregation methods (blue) and intermediate steps of the aggregation methods (purple) are displayed. Abbreviations: EU: Europe, NOA: North America, AUS: Australia, NZ: New Zealand, DB: Database.

The traits were on the categorical scale and were converted to binary traits prior to the comparison with aggregated trait affinities.

As mentioned above, trait affinities ranged from 0 to 1. Hence, the maximum difference possible in trait affinities is 1 or -1 (corresponds to 100 %). For convenience and to improve interpretation, we report absolute trait differences.

Analysis of the effect of harmonization and trait aggregation on trait-environment relationships

We repeated the analysis of Szöcs et al. [9] who studied the effect of anthropogenic salinization on invertebrates in the River Werra in Germany. For the re-analysis we used the established harmonized grouping features for Europe and additionally aggregated traits using the aforementioned aggregation methods.

The river Werra has been subject to effluents from the potash industry since the mid of the 20th century and allows to study responses of invertebrates and their trait compositions to salinization [33]. Sites downstream, upstream, and close to the salt discharge (transition) were compared regarding their trait composition. Further details can be found in Szöcs et al. [9].

We substituted 6 of the grouping features from the original data with harmonized grouping features from the European trait dataset. We compared the results of the redundancy analysis (RDA) from the original study to the case when using harmonized grouping features. Specifically, the trait composition expressed as community weighted mean (CWM) traits was ordinated along an electric conductivity gradient. We compared the species scores obtained from the RDA, i.e. the coordinates of the tips of the vectors representing the CWM traits in the bi- or triplots. Following the original study, we identified traits associated with high or low salinity based on their distance to the ordination axis median using the mahalanobis distance. Traits with a mahalanobis distance greater than the 97.5% -quantile of the Chi-square distribution (5.02) were regarded as traits responding to either low or high salinity. For our analysis, we used the same 21 grouping features that Szöcs et al. [9] used. The 6 harmonized grouping features used were *Size*, *Feeding mode*, *Locomotion*, *Oviposition*, *Respiration*, and *Voltinism*. Additionally, for testing the effect of aggregated traits we assigned to each taxon in Szöcs et al. [9] the aggregated trait value for its corresponding family and repeated the RDA.

Data analysis

The data processing and aforementioned analyses were carried out using R (Version 3.6.1). Raw data and the R code for data processing and grouping feature harmonization is located in the Github repository: https://github.com/KunzstLD/Invertebrate_traits. Scripts and data to reproduce the trait aggregation and analysis with aggregated traits are located in the Github repository <https://github.com/KunzstLD/Trait-aggregation>.

Results

Taxonomic coverage of the harmonized trait datasets

Regarding the taxonomic coverage, the New Zealand dataset has the smallest taxon pool (478 taxa, Table 2). By contrast, the European trait dataset has the largest taxon pool with 4601 taxa followed by the North American trait dataset that contained trait information on 3753 taxa. The Australian dataset contains 1402 taxa. The European, New Zealand, and North American datasets have most taxa on the species-level whereas the Australian dataset has a similar number of taxa on species and genus-level.

Table 2: Number of taxa per harmonized dataset and per taxonomic level. Numbers in parenthesis show rounded relative frequencies in percentage.

Database	Nr. of taxa	Species	Genus	Family	Nr. aquatic insects
EU	4601	3739 (81)	704 (15)	158 (3)	3942 (86)
NOA	3753	2414 (64)	1163 (31)	176 (5)	3305 (88)
AUS	1402	564 (40)	578 (41)	260 (19)	1016 (72)
NZ	478	404 (85)	47 (10)	27 (6)	443 (93)

Completeness of trait information

The amount of entries with available information for the selected grouping features varied strongly for the preprocessed European, North American, and Australian datasets (Table 3). By contrast, the New Zealand dataset contained complete trait information for most of the investigated grouping features (between 94 % and 100 %).

Table 3: Rounded percentage of entries that have information for the individual grouping features shown per trait dataset.

Database	Body form	Oviposition	Voltinism	Locomotion	Size	Respiration	Feeding mode
EU	8	15	23	36	11	57	76
NOA	28	13	47	52	73	44	63
AUS	4	46	49	39	75	68	99
NZ	100	94	100	99	100	100	99

Simulation of varying taxonomic hierarchies

We evaluate the simulation results based on the range of produced aggregated trait affinities and by comparing results of every simulated dataset.

The trait aggregation methods *direct_agg_{mean}*, *direct_agg_{median}* and *weighted_agg* yielded similar ranges of aggregated trait affinities within each level of trait variability for the *sim_base* scenario.

Aggregation methods using the median yielded greater ranges of aggregated trait affinities than methods using the mean. Thereby, the (*stepwise_agg median*) yielded the greatest range of aggregated trait affinities (Figure S2).

By contrast, the ranges of trait affinities differed for all aggregation methods for the simulation scenarios *sim_extreme* and *sim_variation*. *Weighted_agg* and *stepwise_agg_{mean}* produced a wider range of values than the *direct_agg_{mean}* in the *sim_extreme* scenario. For most levels of trait variability the *stepwise_agg median* resulted in the largest range of trait affinities in both scenarios

Analysing the individual simulation runs showed that differences between the results of the aggregation methods increased with increasing trait variability. Most differences occurred for the *sim_extreme* scenario. Differences greater than an absolute trait affinity of 0.1 occurred between methods using the median and the mean. Thereby, the most frequent differences above 0.1 were found between the aggregation methods *direct_agg_{mean}* and *stepwise_agg_{median}*, *direct_agg_{median}* and *stepwise_agg_{median}*, and *stepwise_agg_{median}* and *weighted_agg* (Figure S3).

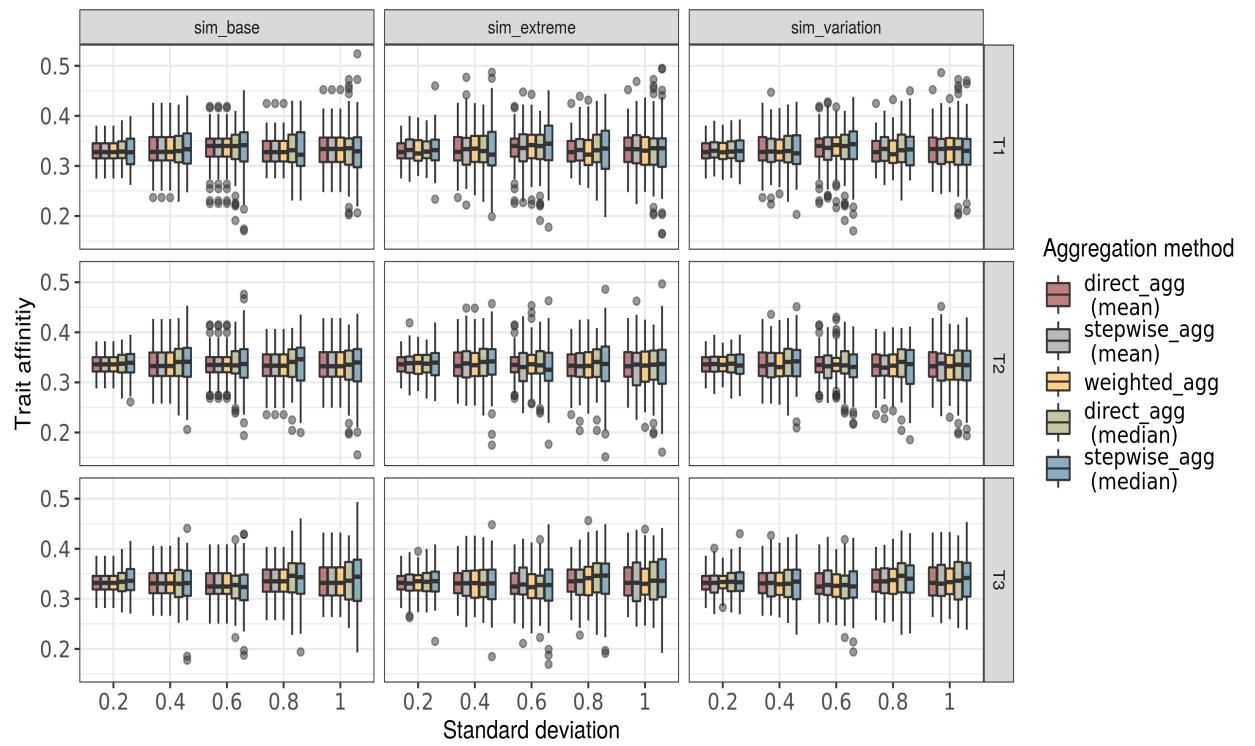


Figure 2: Ranges of aggregated trait affinities for the three examples of taxonomic hierarchies and simulated levels of trait variability. Boxplots depict results for each trait aggregation method of 100 simulations. T1, T2, and T3 are the simulated traits.

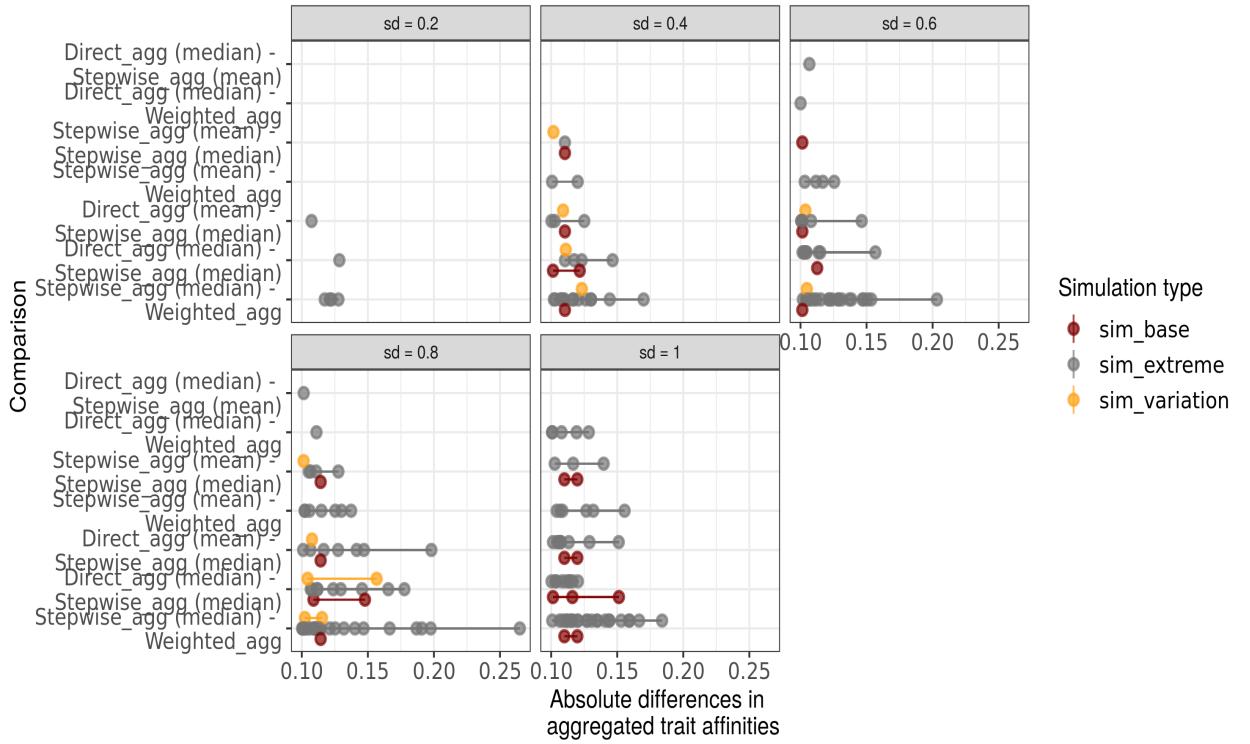


Figure 3: Comparison of the results of the trait aggregation methods for every simulated dataset. Simulated datasets where absolute differences between aggregated trait affinities were greater than 0.1 are depicted. Only the comparisons are shown where differences greater than 0.1 occurred.

Differences in trait affinities obtained by trait aggregation methods compared to traits assigned at family-level

The percentage of differing cases of trait affinities obtained by the trait aggregation methods compared to trait affinities originally assigned at family-level varied between 16.2 % and 22.9 % for the Australian dataset. For the North American dataset, comparison of the trait aggregation methods to trait affinities assigned at family-level yielded between 15.3 % and 47 % differing cases (Table 4).

In general, trait aggregation methods using the median yielded fewer cases with differences compared to approaches using the mean. However, aggregation methods using the median produced greater differences for both datasets. Standard deviations of absolute differences were similar for all tested aggregation methods. For both datasets maximum differences of 1 occurred for all investigated grouping features (Figure 4 and Figure 5).

A comparison of the aggregation methods with each other for the 4 datasets revealed that differences in aggregated trait affinities were largest between the *stepwise-agg_{median}* and *direct-agg_{median}* (Figure S1).

Table 4: Amount of differing cases, the minimum and maximum, and means and standard deviations of absolute differences between trait affinities assigned at family-level and aggregated trait affinities.

Database	Comparison to traits at fam.-lvl.	Differing cases [%]	Min. differences	Max. differences	Mean abs. differences	SD abs. differences
Australia (Chessman)	direct_agg (median)	16.53	0.01	1.00	0.45	0.27
	direct_agg (mean)	23.24	< 0.01	0.99	0.34	0.23
	stepwise_agg (median)	17.90	0.01	1.00	0.42	0.26
	stepwise_agg (mean)	23.24	< 0.01	0.99	0.33	0.22
	weighted_agg	23.24	< 0.01	1.00	0.34	0.24
North America	direct_agg (median)	15.33	0.17	1.00	0.70	0.26
	direct_agg (mean)	47.00	< 0.01	1.00	0.30	0.26
	stepwise_agg (median)	18.00	0.08	1.00	0.63	0.28
	stepwise_agg (mean)	47.00	< 0.01	1.00	0.30	0.27
	weighted_agg	47.00	< 0.01	1.00	0.31	0.28

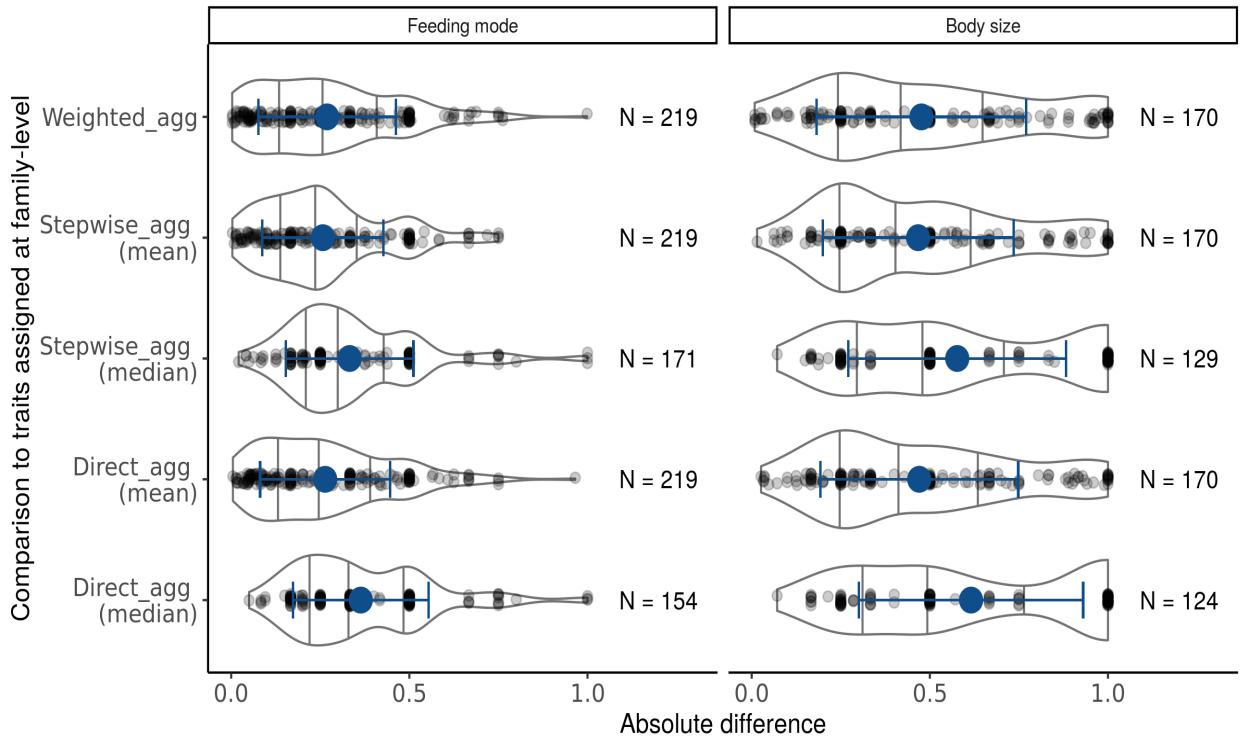


Figure 4: Display of the cases where differences occurred between aggregated traits and traits assigned at family-level. Violin plots - a mirrored density plot - show the density of the absolute trait affinity differences for the Australian dataset for the grouping features feeding mode and body size. Absolute differences in trait affinities are depicted as gray dots. N denotes the number of cases per comparison where differences occurred. The blue dot indicates the mean of absolute differences and the error bars the standard deviation. The gray vertical lines show the 25th, 50th and 75th quantile of the density estimate.

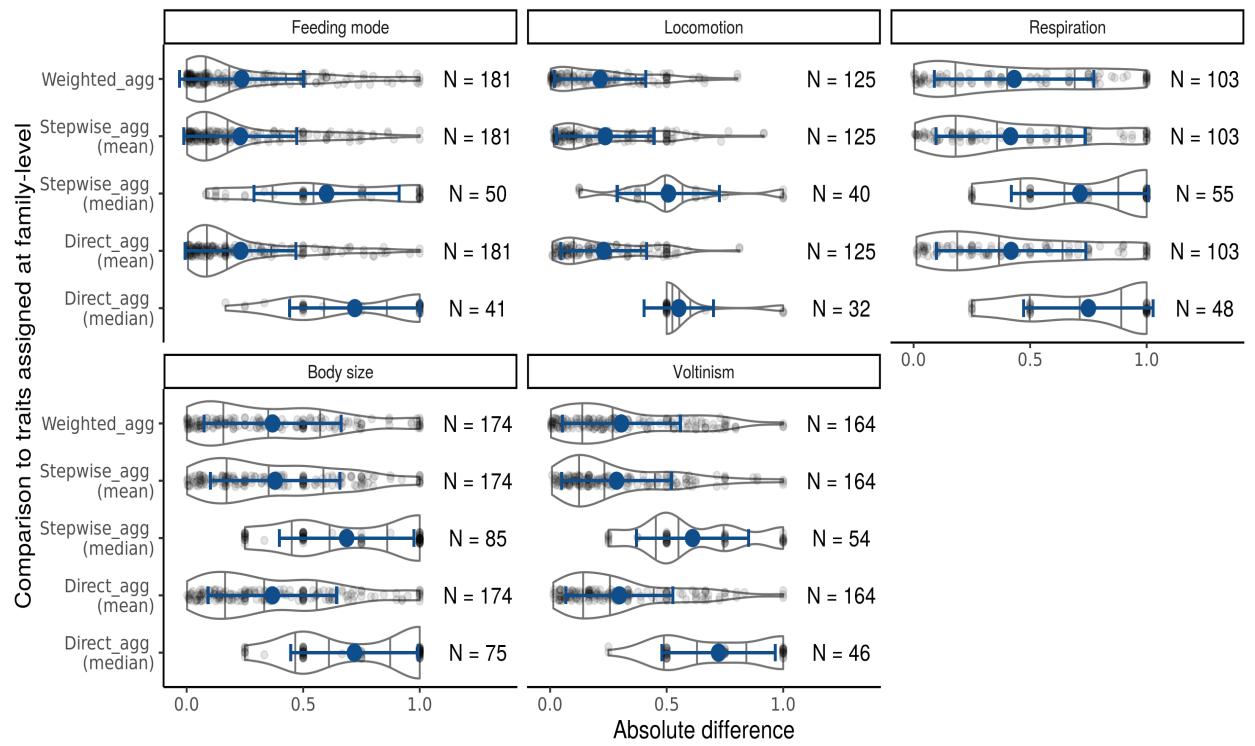


Figure 5: Display of the cases where differences occurred between aggregated traits and traits assigned at family-level. Violin plots - a mirrored density plot - show the density of the absolute trait affinity differences for the North America dataset for the grouping features feeding mode, locomotion, respiration, body size and voltinism. Absolute differences in trait affinities are depicted as gray dots. N denotes the number of cases per comparison where differences occurred. The black dot indicates the mean of absolute differences and the error bars the standard deviation. The gray vertical lines show the 25th, 50th and 75th quantile of the density estimate.

Re-analysis of Szöcs et al. using harmonized and aggregated grouping features

The original RDA in Szöcs et al. [9] indicated that downstream sites (high salinity) were characterised by the traits shredder, ovoviparity, multivoltinism, long life cycle (> 1 year), and gill respiration and upstream sites (low salinity) were characterized by univoltinism, oviposition in clutches and short life cycle duration (< 1 year).

Using harmonized grouping features resulted in fewer traits that distinguish upstream and downstream sites in comparison to the original analysis (Figure and Figure). According to the RDA of the trait composition, downstream sites were characterised by taxa with the traits multivoltinism and ovoviparity and upstream sites were characterised by univoltine taxa that lay their eggs in an aquatic environment (aquatic eggs). The traits shredder, gill respiration and long life cycle duration did not characterise sites with high salinisation. Also, the trait short life cycle duration did not characterise upstream sites with low salinity.

Using at family-level aggregated traits from the harmonized dataset showed results similar to the original analysis (Figure and Figure). The *direct_aggmean*, *direct_aggmedian*, and *weighted_agg* characterised the downstream sites with the same traits as the original analysis except that downstream sites were not characterised by the trait shredder. Upstream sites were characterised by the traits univoltinism, aquatic eggs and short life cycle duration. The trait aquatic eggs of the harmonized grouping feature oviposition has been derived by amalgamating the trait oviposition in clutches and other related traits (Table 1). The same results were obtained when re-analysing the data with traits aggregated by the *stepwise_aggmean* and *stepwise_aggmedian*, with the exception that none of the life cycle traits characterised upstream or downstream sites. Thus, in our comparison the direct and weighted family-level aggregation methods yielded to the least change in species scores of all methods compared to the original results.

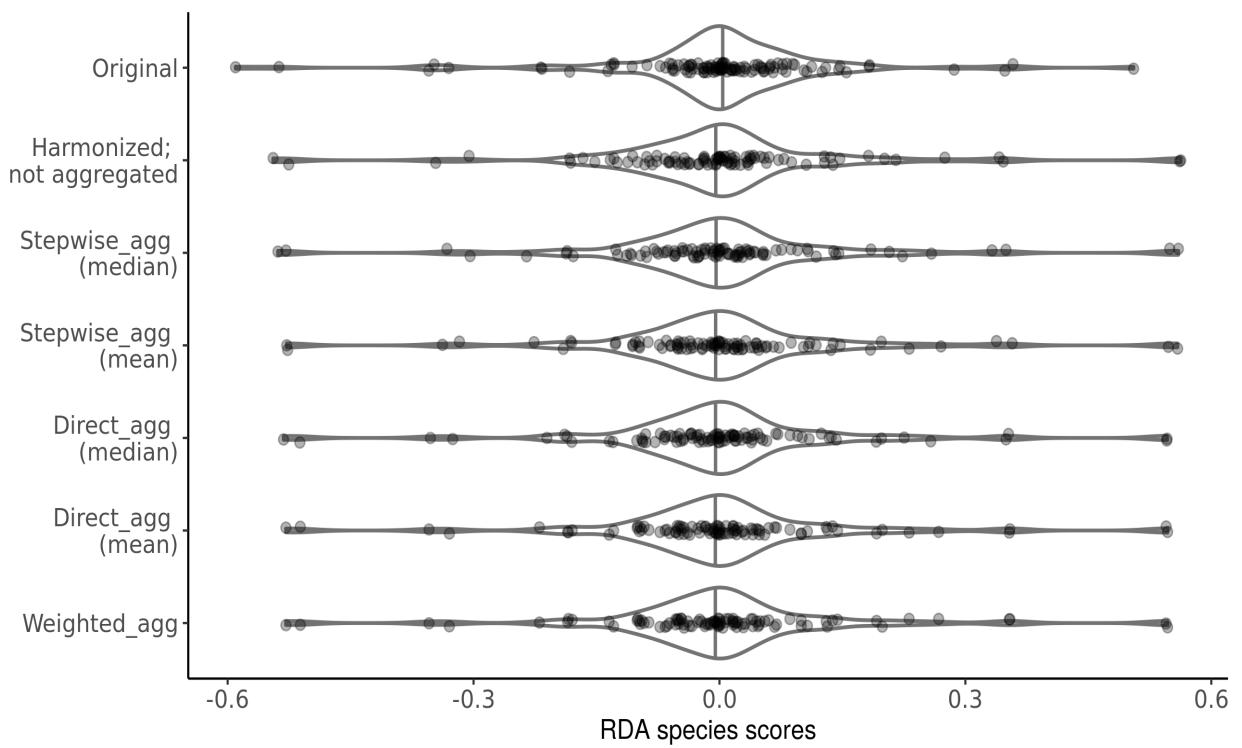


Figure 6: Species scores obtained by RDA from the original analysis [9], using harmonized grouping features, and using harmonized grouping features with traits aggregated to family-level. The dots represent the individual species scores for each analysed trait. The violin plot shows the density estimate of the species scores. Gray vertical lines indicate the median of the obtained species scores.

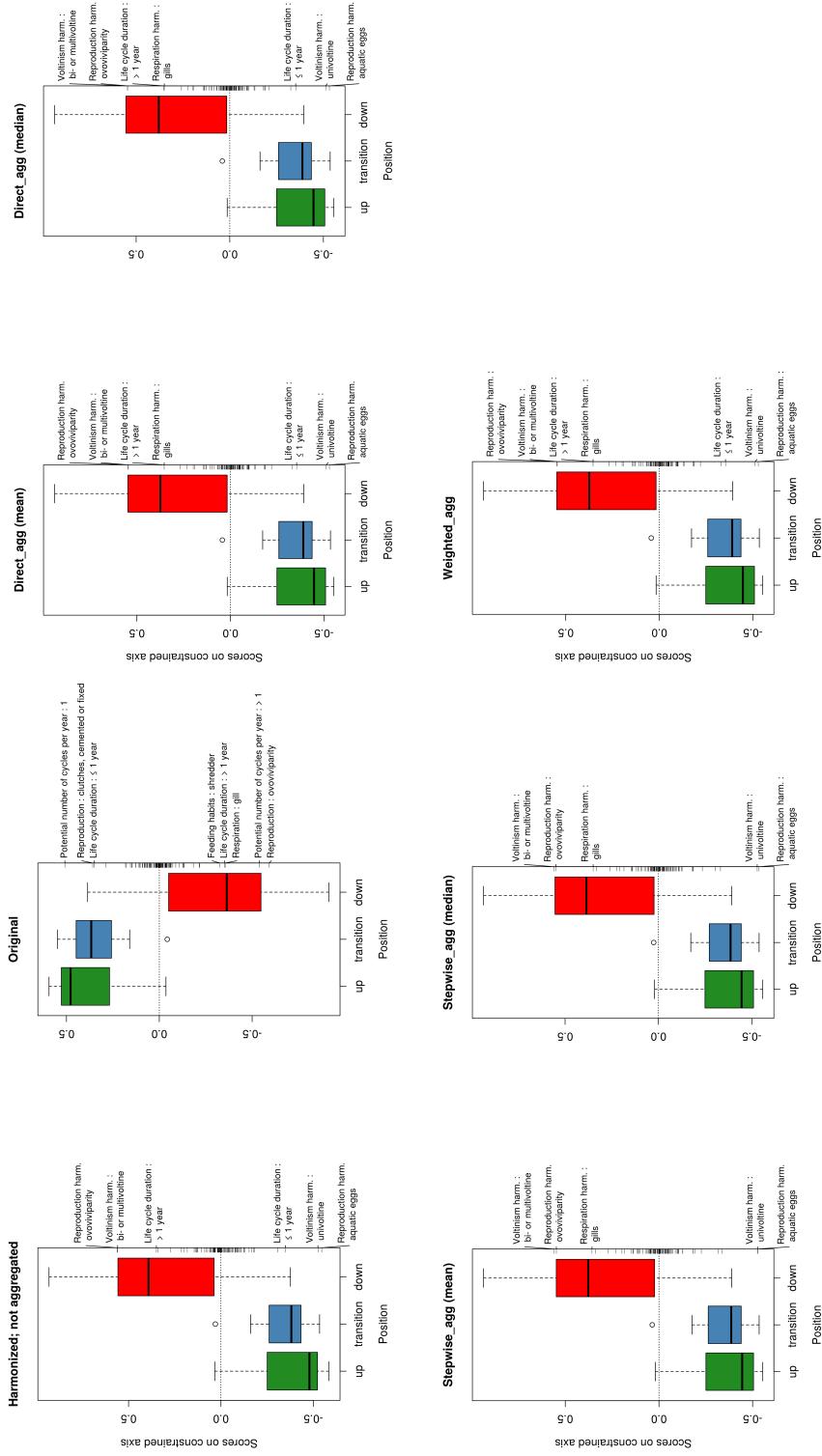


Figure 7: RDA of traits constrained by electric conductivity for the tested methods and the original study. Shown are boxplots of the site scores along the conductivity axis. The rug on the right side of each plot indicates species scores of the traits on the conductivity axis. Only traits with a mahalanobis distance greater than the 97.5% quantile of the Chi-square distribution (5.02) were labelled.

Discrepancies of invertebrate trait definitions

Definitions of grouping features and traits varied in their level of detail in the original trait databases. The *freshwaterecology.info* database, the Tachet database and the North American database (Twardochleb et al.) provided more detailed descriptions of their trait information compared to the North American (Vieira et al.) and New Zealand database. An exception is the Australian trait database which is a collection of seven specific trait datasets [16]. Thus, grouping features occur multiple times with varying differentiation into traits. Depending on the dataset trait information is described with more or less detail.

The definition of grouping features varied across databases mainly concerning their differentiation into traits but also in their scope. We provide a summary of discrepancies in trait definitions in the appendix (Table S1). Both, differences in differentiation and scope can lead to discrepancies in trait definitions. For example, for the grouping feature feeding mode discrepancies arise because traits are assigned in different ways. The Tachet database defines predators as carvers, engulfers and swallowers. By contrast, in the North American (Twardochleb et al.) database predators are defined as engulfers and carnivorous piercers. In turn, in the Tachet database, piercers are defined as a separate trait encompassing herbivorous and carnivorous piercers. Furthermore, the scope in the *freshwaterecology.info* database for feeding mode is primarily on the food source of a species (except for filterers), while the other databases focus on the strategies of food acquisition. Therefore, the *freshwaterecology.info* database defines e.g. predator as "eating from prey", while the other databases use the mouthpart morphology as basis of their definition. The Tachet database captures the food source in an additional grouping feature. Varying levels of differentiation are also present in all other investigated grouping features between the trait databases (Table 5 and Table S1). Locomotion definitions differ also in scope between databases. *Freshwaterecology.info* and New Zealand databases describe locomotion as the way of movement of an organism, Tachet as substrate relation and locomotion, the North American (Vieira et al.) as how organisms deal with flow, Australia as attachment, and the North American (Twardochleb et al.) database includes not only the way of movement, but also the location of movement. Similarly, regarding the reproduction traits, databases differ in their scope. Reproduction is captured in one grouping feature and defined as location of oviposit clutches and mode of reproduction in the *freshwaterecology.info* and Tachet databases. North America (Vieira et al.) provides information on the oviposition location but not on reproductive behavior. The Australian database report traits for reproductive behavior but also on oviposition site. The New Zealand database distinguishes three grouping features related to reproduction: reproductive technique, oviposition site (e.g. water surface, terrestrial), and egg/egg mass (e.g. free, cemented).

Various codings of traits are used throughout the databases (e.g. binary, fuzzy, continuous). The *freshwaterecology.info* and Australian use different codings in their databases. Tachet and the New Zealand database exclusively use fuzzy coding. Both North American trait databases contain categorical grouping features that can be converted into traits using a binary coding (Table 5). Binary coding represents a simple approach in which a taxon either expresses a trait or not. Fuzzy coding characterizes the affinity of an organism to exert a certain trait. It is used to account for plasticity in traits, e.g. taking into account that traits can change over the development time of an organism. Usually, fuzzy coded affinities are converted into proportional values. Continuous coding is used for traits like body size.

Table 5: Number of traits per grouping feature and type of coding of the traits for the respective grouping feature per database.

Database	Feeding Mode	Voltinism	Locomotion	Respiration	Reproduction	Size	Body Form
Freshwater-ecology.info	10	6	6	7	9	-	-
	10 point assignment system	single category assignment system	10 point assignment system	binary	-	-	-
	7	3	8	5	8	7	-
Tachet	fuzzy [0 – 3]	fuzzy [0 – 5]		fuzzy [0 – 3]		-	-
North America (Twardochleb)	6	3	10	3	10	3	-
North America (Vieira)	8	3	9	8	10	3	5
	16 ^a	7	9	10	13 ^b	9	4
Australia	binary; proportional [0 – 1]; fuzzy [0 – 3]	binary; fuzzy [0 – 3]	binary; proportional scale [0 – 1]; fuzzy [0 – 3]	categorical	binary; continuous; fuzzy [0 – 3]	fuzzy codes [0 – 3]	
New Zealand	6	3	4	4	4	5	4

^a Some of the traits were similar (e.g. trait *Shredder*, *Shredder*, *Detrivore*, and *Collector*, *Shredder*).

^b Many traits were rather comments than traits in the original database and were not considered.

Discussion

- **aggregated vs assigned traits**

- In general, differences produced by the aggregation methods seem to arise by using mean or median, not so much driven by the different weighting approaches (direct vs. stepwise vs. weighted)
- Approaches that used the median resulted in fewer differences to the assigned traits, albeit if differences occurred to the assigned traits, they were greater.
- Simulation shows that approaches using the median generally produce a larger range of values → Especially with higher trait variability for situations where one genus has a lot more species than the other genera within the family
- Differences greater for the NOA dataset because of the binary coding → differences are greater between traits
- Taxonomic hierarchy in the investigated datasets?
 - In every investigated dataset families have only 1 to few genera. 76 (North America) to 93 % (New Zealand) of the families have 5 or less genera (see SI).
- There is no "true" value to compare to, i.e. assigned traits at genus or family level can be biased as well (i.e. the person who assigned the trait was thinking about particular species within a genus not all). Comparison of species-level traits in fwe and traits on genus-level in tachet would be interesting in this context?
- Suggestions from Co-Authors:
 - should include where the classifications come from
 - what do we really know because someone has watched the animals and published their behaviour; what is extrapolated knowledge?
 - are the differences between continents because of evolution or only because scientists have done more research in one of the continents?

- **Influence of aggregation methods on trait-environment relationships**

- We re-analysed only a small-scale study, what would be different when applying a large-scale study?

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Supporting Information

Differences in trait affinities obtained by trait aggregation methods compared to traits assigned at family-level

Comparison of the trait aggregation methods with each other

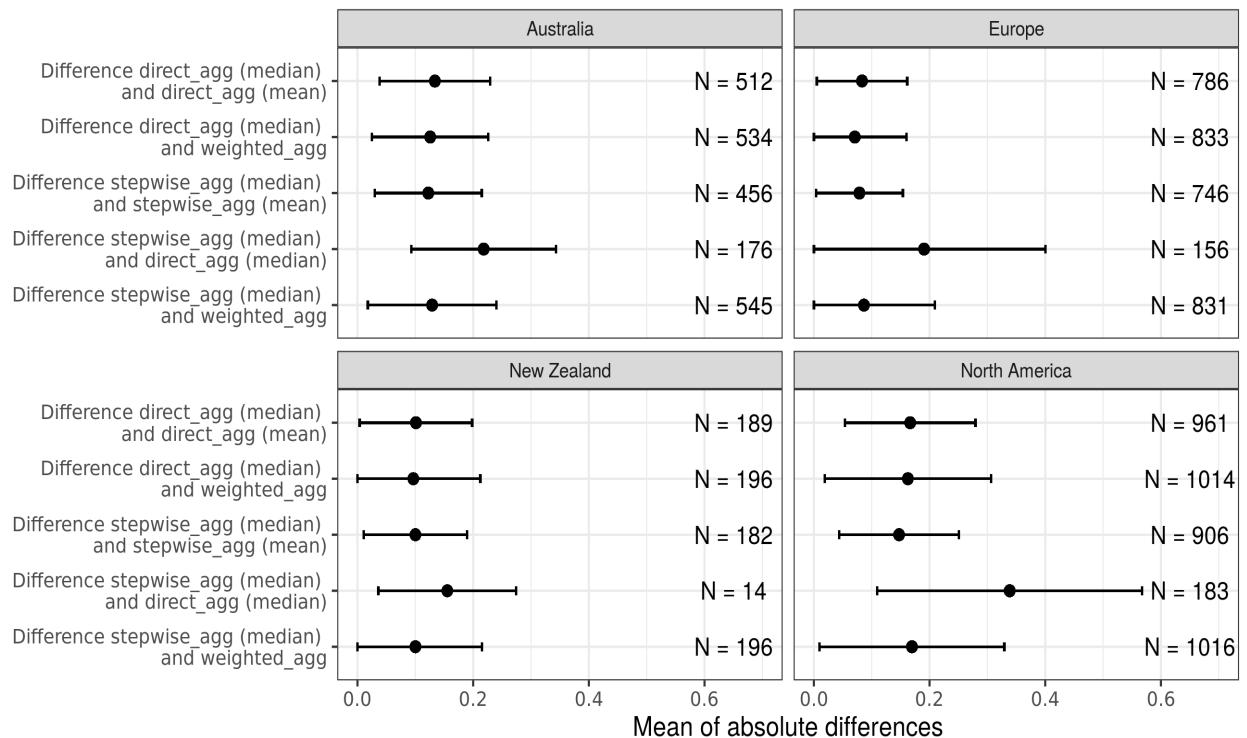


Figure 1: Comparison of trait aggregation methods when aggregating over all traits for all datasets. Displayed are means of absolute differences in trait affinities with standard deviations (truncated at 0). Compared aggregation methods are displayed on the y-axis. N indicates the number of cases where differences occurred. Total number of cases: Australia 2223, Europe 3352, New Zealand 777, and North America 4080.

Taxonomic hierarchy in the analysed trait datasets

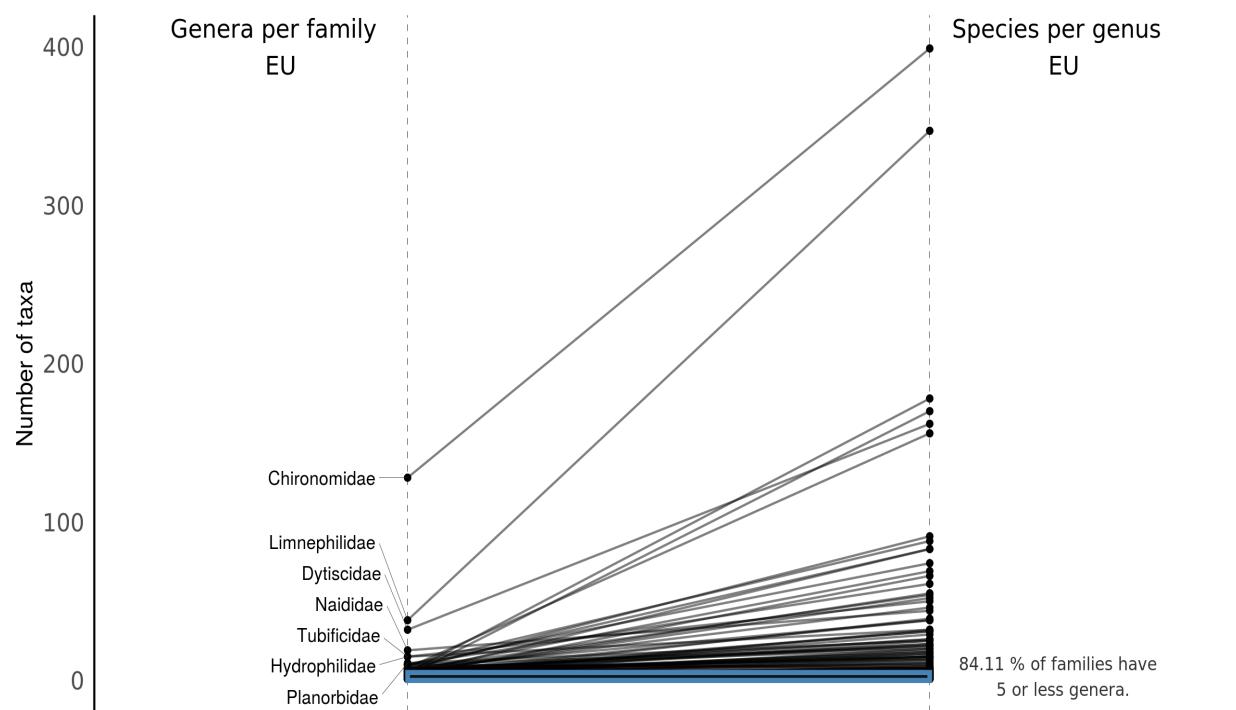


Figure 2: Number of genera per family and species per genus for the European trait dataset. For better visual display only families with more than 10 genera are displayed.

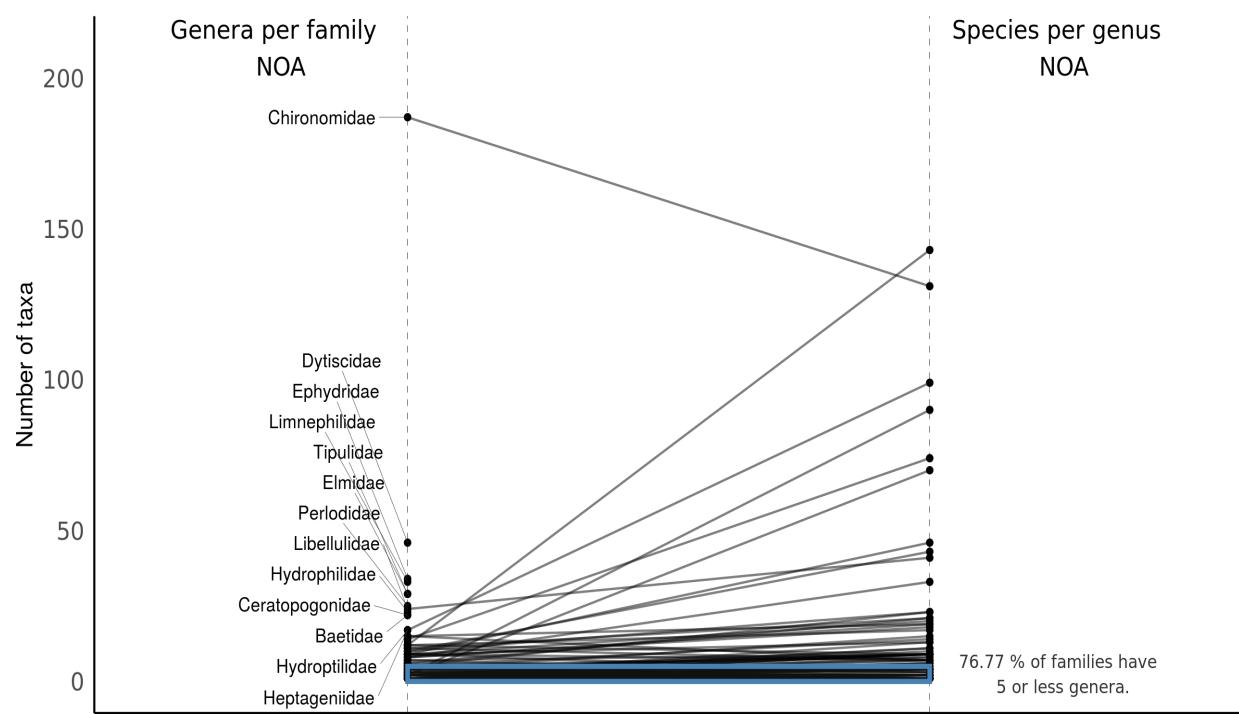


Figure 3: Number of genera per family and species per genus for the North American trait dataset. For better visual display only families with more than 15 genera are displayed.

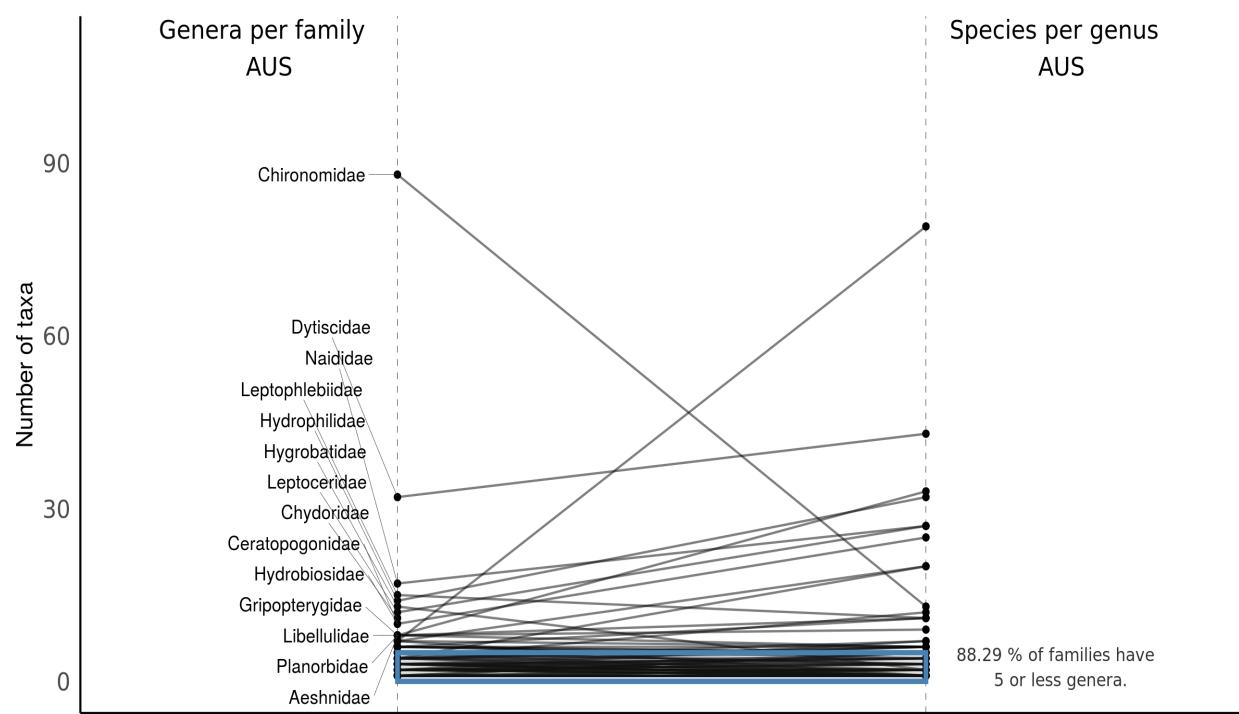


Figure 4: Number of genera per family and species per genus for the Australian trait dataset. For better visual display only families with more than 7 genera are displayed.

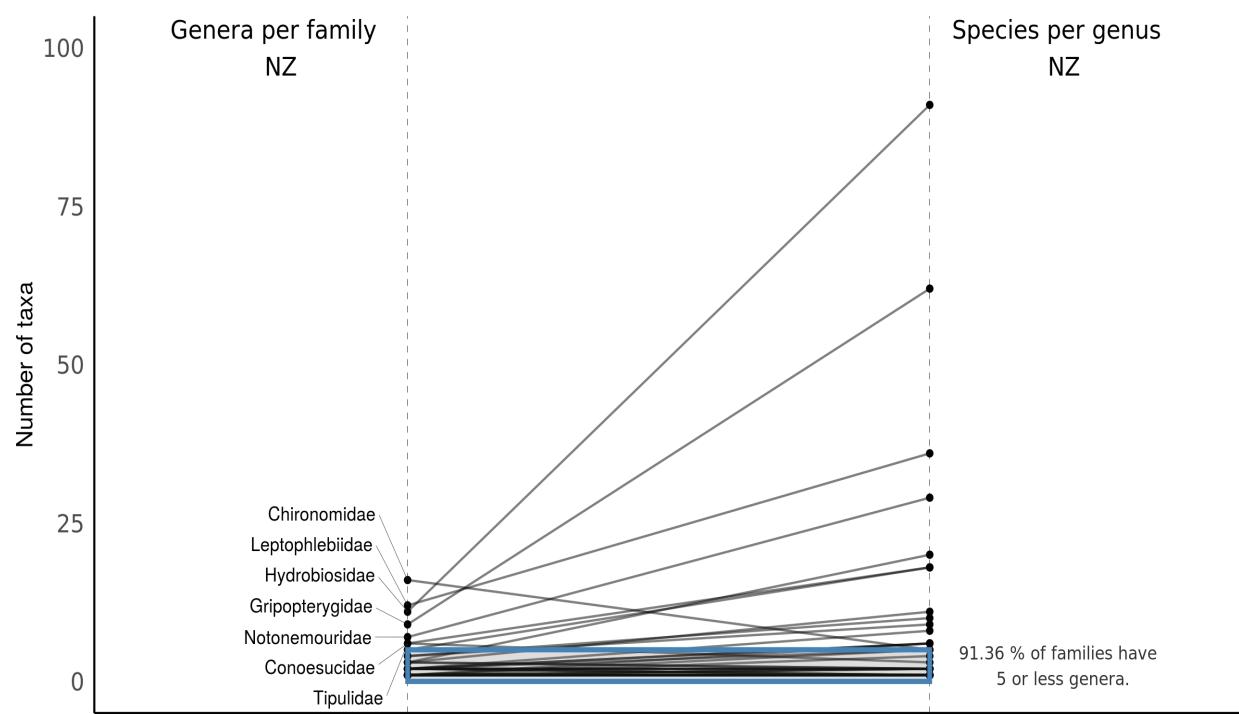


Figure 5: Number of genera per family and species per genus for the New Zealand trait dataset. For better visual display only families with more than 5 genera are displayed.

Discrepancies in trait definitions

Table 1: Comparison of trait definitions between invertebrate trait databases. Only traits that are differently described across databases are listed. The definition is quoted if it enables differences to be identified, otherwise the differences are described. The hyphen indicates a missing trait. Reproduction was captured in multiple grouping features per database. Hence, differences for reproduction have been described in the paper. Body form traits are not different between databases, except that the North America (Vieira) database contains the trait Bluff (blocky) which does not appear in the other databases.

Trait	Freshwater-ecology.info	Tachet	North America (Twardochleb)	North America (Vieira)	Australia	New Zealand
Feeding shredder	"Feed from fallen leaves, plant tissues, CPOM"		<ul style="list-style-type: none"> • "Shred decomposing vascular plant tissue" 	<ul style="list-style-type: none"> • "Eat coarse detritus, plants or animal material" 	<ul style="list-style-type: none"> • Trait herbivore includes among others insect that shred <i>living aquatic plants</i> 	<ul style="list-style-type: none"> • Detrivore ^a • Trait herbivore includes among others the shredder

		Carvers, engulfers & swallowers	Engulfers ("ingest prey whole or in parts") & piercers ("prey tissues and suck fluids")	Piercer & engulfer	Predator
Feeding predator	"Eating from prey"	• Piercers (plants & animals) are an additional trait.			
Feeding filter-feeder	Distinguishes between active and passive	No distinction be- tween active and passive	No distinction be- tween active and passive	No distinction be- tween active and passive	No distinction be- tween active and passive
Semivoltine	"One generation in two years"	"Life cycle lasts <i>at least</i> two years"	"< 1 generation per year"	"< 1 generation per year"	"< 1 reproductive cycle per year"
Multivoltine	" <i>Three</i> or more gen- erations per year" ^b	"Able to complete <i>at least</i> two suc- cessive generations per year"	"> 1 generations per year"	"> 1 generations per year"	<ul style="list-style-type: none"> • bi/multivoltine • up to 5 gen- erations per year • up to 10 generations per year

			Distinguishes swimmer skater	Swimmers and column)	(water
Locomotion swimming	<ul style="list-style-type: none"> • Passive movement like floating or drifting (trait swimming/skating) • Active movement (trait swimming/diving) 	<ul style="list-style-type: none"> • Surface swimmers (over and under the water surface) "Adapted for "fish-like" swimming" • Full water swimmers (e.g. Baetidae). 			
Locomotion burrowing		<ul style="list-style-type: none"> • Burrowing "within the first centimeters of the benthic fine sediment" • "Inhabiting fine sediment of streams and lakes" • Differentiates also the trait interstitial (endobenthic) 	Burrower	"Moving deep into the substrate and thus avoiding flow"	Burrowers (in-fauna)
Locomotion sprawling & walking		<ul style="list-style-type: none"> • "Sprawling or walking actively with legs, pseudopods or on a mucus" 	Sprawler	"inhabiting the surface of floating leaves of vascular hydrophytes or fine sediments"	-

Locomotion	-	"Crawling over the bottom substrate"	Defined as crawling on the surface of floating leaves or fine sediments on the bottom	Does traits sprawner, crawler, climber and clinger.	Database contains crawler, climber	Crawlers (epibenthic)
Locomotion	Does not distinguish and permanently attached	Distinguishes temporarily and permanently attached	Does not distinguish temporarily and permanently attached	Does not distinguish temporarily and permanently attached	Distinguishes temporarily and permanently attached	Does not distinguish temporarily and permanently attached
Respiration	Plastron and spiracle (aerial) are two separate traits	Definition includes respiration using air stores of aquatic plants	Plastron and spiracle combined into one trait	Distinguishes spiracular gills, plastron, atmospheric breathers and plant breathers	Plastron and spiracle (termed aerial) occur as separate and combined traits. Contains also traits: air (plants), atmospheric, and functional spiracles	Distinguishes plastron and spiracle (termed aerial)
Body size	-	Multiple size classifications ^d	< 9 mm 9 - 16 mm > 16 mm	< 9 mm 9 - 16 mm > 16 mm	< 9 mm ^{a;c} 9 - 16 mm > 16 mm	Multiple size classifications ^e

^a Traits from Botwe et al.

^b Contains also bivoltine (two generations per year), trivoltine (three generations per year) and flexible.

^c Contains a size trait with numeric size values. Contains also traits classifying size like Tachet and like the North American trait databases.

^d Size classifications: <= 0.25 cm, > 0.25 – 0.5 cm, 0.5 – 1 cm, 1 – 2 cm, 2 – 4 cm, 4 – 8 cm, > 8 cm. No distinction into small, medium and large.

^e Size classifications: > 0.25 – 0.5 cm, 0.5 – 1 cm, 1 – 2 cm, 2 – 4 cm, 4 – 8 cm. No distinction into small, medium and large.