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# Can you trust comparative trait data based on singleton species?

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## Abstract

Trait measures are affected by intra- and interspecific variability. Most studies aggregate species-level data to averages to analyze patterns of interspecific variation. Reliable per-species averages require data for many individuals per species, which leads to insurmountable measuring effort when studying species-rich assemblages. Here we argue that across a large number of species, patterns and relationships can be precisely recovered even if they are based on measures from a single individual per species. While these deviate to an unknown degree from the true per-species averages, randomly distributed errors will level out across many species. We used subsamples of body size data along elevational gradients for moths and small mammals (dozens to several hundred species per dataset), as well as simulated species assemblages, to illustrate this effect and explore some of its consequences. Single-individual measures correlated well with “true” (i.e., full data) averages. Furthermore, single-individual measures recovered the same conclusions on elevation-body size relationships as true data. Randomly removing individuals per species recovered true elevation-body size relationships very well, while randomly dropping species quickly led to high random variability in relationships across subsampling runs. Simulated species assemblages illustrated how the ratio of intraspecific to interspecific variability affects the correlation between singleton-based and true data. We conclude that trait measures based on single individuals are a viable alternative to multi-individual averages when analyzing assemblages of medium to high species richness. Reducing study effort by limiting the measurement of individuals per species, while retaining all species, is a much more reliable approach than restricting the number of species included in a study.

## Highlights

- Interspecific trait comparisons across space and time are inherently important biogeographical analyses, but since many species in assemblages are rare and thus their trait averages less reliably measured, researchers face the decision to eliminate or retain rare species in interspecific comparisons.
- Here we demonstrate, using example datasets and simulations, that across species assemblages, trait patterns and relationships can be precisely recovered even if they are based on measures from a single individual per species.
- Contrary to common biogeographical practice, our subsampling analyses demonstrate that removing species from analyses (e.g., due to “limited data”) is more detrimental to recovering accurate interspecific patterns than retaining rare species.
- While our findings have limitations and we do not advocate using poor data in general, they provide strong arguments that trait patterns can be robustly studied in taxa and regions where measuring trait values for dozens of individuals per species is not feasible.

**Keywords:** body size, diversity, elevational gradient, interspecific, intraspecific, moths, rare species, sampling effort, simulations, small mammals

## Introduction

Analyses of species' traits are key to advancing a functional understanding of ecological and evolutionary patterns (Dawson et al. 2021). Such a functional understanding is a precondition, in particular, to make mechanistic predictions on biodiversity, species distributions and functional changes of ecosystem properties with global change (Cadotte et al. 2015). For most such approaches, researchers are primarily interested in the interspecific variability of species-wide averages, which are then analyzed as aggregates across time or localities (Wu et al. 2019), or in a comparative framework where each species is one sample point (Beck et al. 2016, Albert et al. 2010). However, traits typically also vary intraspecifically, sometimes in a non-random-manner across time and location (Sullivan and Miller 2007, Bolnick et al. 2011, Günter et al. 2019)—either genetically or due to phenotypic plasticity. To estimate true species averages, one therefore needs to measure data for a sufficient number of individuals per species. Having such data allows computing meaningful averages per species.

Acquiring trait data for many individuals per species increases the measuring effort by orders of magnitude. Researchers therefore face a trade-off between reducing data quality by measuring fewer individuals per species or by restricting the number of species in analysis, for example by excluding species too rare for sampling sufficient numbers of individuals. Empirical datasets often contain many rare species and singletons where traits can be measured in only one or a few individuals. This includes, for example, studies utilizing rare museum specimens (Beerli et al. 2017) or tropical field studies that may contain hundreds of singletons (Brehm et al. 2016).

If the aim of a study is a multi-species comparison of trait values, statistical sampling theory predicts that single-specimen measures of species traits are a valid approach (Box 1). However, with widespread skepticism and resistance to this apparently counterintuitive approach (e.g., by reviewers and editors), we feel it is useful to illustrate and explore this with empirical

data on body sizes and elevation, and with data simulations. For three different taxa, we examine (1) how body size data for singletons correlate with multi-individual averages, and (2) if body size data for singletons lead to equivalent conclusions on the link between body size and elevation. We also mimicked strategies of sampling effort reduction, by examining how (3) dropping individuals within species affects the inference error in comparison to dropping species from analysis. Furthermore, (4) we used simulated data to explore quantitatively how the ratio of intraspecific to interspecific variation affects the robustness of trait analyses based on data from single (or few) individuals per species.

We explore this topic here in an exemplary setting of body size variation along an ecological gradient. However, we note that analogous issues of hierarchically structured data variability exist in many other disciplines, among others, any other quantitative trait variability across temporal or geographic gradients in multi-species assemblages, or within- and between-individual variability of behavioral measurements in psychology or behavioral genetics.

## Material & Methods

### Empirical data

We used published body size data for Neotropical moths from Brehm et al. (2019). These data consist of forewing length measures (in *mm*, henceforth called size) for quantitative samples of two species-rich moth taxa (Lepidoptera: Geometridae, Arctiinae) along an elevational gradient. The two families are not closely related and differ substantially in their ecology, so we treat them as independent datasets. Furthermore, we used unpublished small mammal (rodents and shrews, Appendix S1) body mass data (in *g*; henceforth called size) from elevational transects in the Colorado Rocky Mountains (McCain et al. 2018; data pooled for the present analyses).

### Box 1: Random sampling of traits for interspecific comparisons

The mean of a trait of a random sample of  $n$  individuals for a species is an unbiased estimator of the true mean of the species (*population mean*). A sample of the size  $n = 1$  (one individual) is a random draw from the underlying frequency distribution of trait values for the species (Gaussian for body sizes; Gouws et al. 2011). It is therefore also an unbiased estimator of the population mean, although it cannot be assessed how close the sample is to the population mean (i.e., there is no variance or confidence interval). While this implies that an  $n = 1$  sample is not a reliable absolute estimator for a species' mean trait, the random error would be equally distributed around the mean if the same draw was repeated  $N$  times. If  $N$  is large, the *average* error would approach zero. In an interspecific analysis with  $N'$  species, we argue analogously that the average error from  $n = 1$  samples per species will be small across the dataset of  $N'$  species. Correlation analyses involving many species will therefore recover true effects even if measures for any particular species may not be reliably near the true species mean (see Fig. 1 for illustration). We tentatively call this effect "higher order correlation robustness".

We removed all data that were not actually measured on individuals (Brehm et al. 2019). We furthermore removed all data measured on <5 specimens per species (and, in an alternative analysis, <20 specimens). Table 1 summarizes species and individual numbers for each dataset. For the remaining species we calculated mean sizes, which we treat as the ‘truth’ for further analyses (i.e., these are averages of 5, respectively 20, up to many hundreds of specimens per species). Note that, conservatively, we kept males and females pooled in the dataset. For dimorphic species this will increase random error for single individuals-measures.

### Subsampling empirical data

We randomly sampled the body size of one individual per species. To mimic maximum sampling bias, we also extracted data for the smallest and the largest individual of each species (i.e., pretending a researcher had always chosen the smallest or the largest available specimen for measuring). We used Pearson’s  $r$  to quantify how well these single-individual measures predict mean size.

We calculated the mean elevation at which each species occurred (always using the full data), and correlated this to the size of species (mean of all specimens, and subsamples). We ignored all issues of spatial or phylogenetic non-independence, which are not the topic of this paper. We compare the recovered conclusions on these eco-geographic patterns.

To simulate the trade-off between measuring traits for many species vs. measuring traits on many individuals per species, we first subsampled each dataset so that it contained exactly 20 individuals per species (i.e., we randomly selected those among all available individuals, while dropping species that did not have data for 20 or more specimens (last row in Table 1). We used these to fit regressions of size vs. mean elevation (as described above) and considered these as ‘true’ values for the following comparisons. We then mimicked situations as if we had only 80%, 60%, 40%, 20%, 10% and 5% of resources to measure individual sizes –either by reducing the number of individuals per species, or by reducing the number of species in analysis (in both cases: random draws). We calculated Pearson’s  $r$  for the size vs. mean elevation correlation and compared them to the ‘true’ data.

We ran 500 iterations of all subsampling routines and report averages and their spread where appropriate.

### Simulated data

To investigate how the variability of traits within species affects our conclusions, we simulated a species community of 100 species with a species-specific trait following a lognormal distribution (as was often recorded, e.g., for body sizes: Novotny and Kindlmann 1996; we used distribution parameters so that the histogram resembled empirical data as commonly seen:  $m = 100$ ,  $s = 50$ ;

location =  $\log\left(\frac{m^2}{\sqrt{m^2 + s^2}}\right)$ , shape =  $\sqrt{\log\left(1 + \frac{s^2}{m^2}\right)}$ ; Sagalnik 2017).

We then simulated individuals within each species, sampling from a normal distribution with a mean equaling the species-specific trait simulated above. The standard deviation of this normal distribution was set in comparison to the standard deviation of the interspecific data (moment matching of normal and lognormal parameters; Sagalnik 2017), so that we could express intraspecific variability (standard deviation, SD) as a proportion of interspecific variability ( $s = \text{SD}$ ).

We simulated situations for intraspecific variabilities between 10 and 120 percent of interspecific variability. For each of 100 random draws, we correlated single-individual data to species means and summarized data for Pearson’s  $r$ . We repeated this simulation while varying the number of individuals drawn, from one individual to ten individuals per species. All data manipulation, subsampling and analyses were carried out in R (v. 4.1.2; R-scripts for subsampling and simulations are available in Appendix S2 and S3).

## Results

### Empirical data: $n = 1$ subsamples correlate well with average species values

Subsamples with only one individual per species correlate well with ‘true’ data (averages of all individuals per species), for the two moth taxa (Table 2, most  $r^2 > 0.95$ ) in particular. For small mammals and the restricted dataset of Arctiinae  $\geq 20$  individuals we observed more spread and deviation of values, probably due to the smaller number of species. Utilizing only the smallest, respectively the largest individual of each species, led to the same conclusion (Table 2).

**Table 1.** Species and individual numbers as used for analyses (i.e., after exclusion of missing size data and rare species, see main text). Species numbers represent the  $N'$  for correlation analyses below. The last row gives individual numbers for a data subset where each species was represented by exactly 20 randomly selected individuals (this was used for “dropping species vs. dropping individuals”-analyses).

	Geometrid moths	Arctiine moths	Small mammals
Species ( $\geq 5$ individuals)	429	137	32
Individuals (for species $\geq 5$ individuals)	13,057	3,510	5,928
Species ( $\geq 20$ individuals)	157	42	21
Individuals (for species $\geq 20$ individuals)	10,361	2,617	5,822
Species x 20 individuals (for species $\geq 20$ individuals)	3,140	840	420

**Table 2.** Pearson  $r$  between ‘true’ species mean size and subsamples of  $n = 1$  individual per species for empirical data sets (Table 1). All data refer to 500 random subsampling runs, averages are presented with standard deviations (SD).

	Geometrid moths		Arctiine moths		Small mammals	
	Spec. $\geq 5$ individ.	Spec. $\geq 20$ individ.	Spec. $\geq 5$ individ.	Spec. $\geq 20$ individ.	Spec. $\geq 5$ individ.	Spec. $\geq 20$ individ.
average $r \pm SD$	0.990 $\pm$ 0.001	0.990 $\pm$ 0.002	0.98 $\pm$ 0.003	0.985 $\pm$ 0.007	0.925 $\pm$ 0.039	0.935 $\pm$ 0.059
minimum $r$	0.98	0.98	0.97	0.91	0.78	0.65
$r_{\text{smallest individ.}}$	0.99	0.99	0.98	0.97	0.86	0.83
$r_{\text{largest individ.}}$	0.99	0.99	0.99	0.99	0.89	0.98

**Table 3.** Pearson correlations between elevation and body size for ‘true’ size and subsampling of  $n = 1$  individual per species, for data sets containing all species with 5 or more individuals, and data sets containing only species with 20 or more individuals. All data are based on 500 subsampling runs, averages are given with standard deviations (SD). “% significant” (last row) refers to significance assessments from Pearson correlations of individual simulated datasets (e.g., all (100%) of the subsampling correlations for Arctiinae would have been considered significant). \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ 

	Geometrid moths		Arctiine moths		Small mammals	
	Spec. $\geq 5$ individ.	Spec. $\geq 20$ individ.	Spec. $\geq 5$ individ.	Spec. $\geq 20$ individ.	Spec. $\geq 5$ individ.	Spec. $\geq 20$ individ.
‘True’ data:	$r = 0.091$ $p = 0.06$	$r = 0.147$ $p = 0.07$	$r = 0.520$ $p < 0.0001$	$r = 0.486$ $p = 0.001$	$r = -0.011$ $p = 0.95$	$r = -0.028$ $p = 0.90$
$n = 1$ sample:						
average $r \pm SD$	0.090 $\pm$ 0.007	0.145 $\pm$ 0.012	0.513 $\pm$ 0.014	0.478 $\pm$ 0.024	-0.013 $\pm$ 0.076	-0.030 $\pm$ 0.074
minimum $r$	-0.068	0.104	0.470	0.411	-0.272	-0.214
maximum $r$	0.113	0.181	0.558	0.573	0.154	0.185
% significant	29% *	18% *	100% ***	100% **	0% *	0% *

### Empirical data: $n = 1$ subsamples recover the same relationships as full data

For two taxa, ‘true’ elevation-body size relationships are clearly positive (Arctiinae) or nonexistent (small mammals), and single-individual subsamples recover these findings well (Table 3). For geometrid moths, the ‘true’ elevation-body size relationship is unclear (i.e., weak and marginally significant), and single-individual subsamples also recover weak effects ( $r$ -values; sometimes significant, more often not; Table 3).

### Empirical data: Dropping individuals per species precisely recovers ‘true’ body size-elevation relationships, but dropping species introduces high random variability.

Elevation-body size correlations were quite precisely recovered if many or most individuals per species were dropped from analyses (Fig. 2, left panels). Contrary to this, removing species from analyses quickly leads to a wide variability of  $r$ -values (Fig. 2, right panels).

### Simulated data: The ratio of intraspecific to interspecific variability matters, but relatively small samples can still yield reliable results.

In our empirical body size data (using only species  $\geq 20$  specimens) the intraspecific SD was estimated as 15.4% of interspecific SD for Geometridae, 16.2% for Arctiinae and 26.6% for small mammals. It is reasonable to expect that these variability ratios depend on both

the taxon and the trait involved, and that the ratio of intraspecific to interspecific variability affects the degree to which small subsamples per species can recover ‘true’ relationships. We explored this with simulated data.

Trait data based on one or few individuals correlate better with true species means if intraspecific variability is small in comparison to interspecific variability of the dataset (Fig. 3). For example, for a variability ratio of 25 percent, most  $n = 1$  simulation runs still yield  $r > 0.9$ . The relationship weakens with higher intraspecific variability, but this can be compensated by drawing not only one but a few individuals per species. For example, drawing 5 individuals per species yields reliable data (most runs  $r > 0.9$ ) for a variability ratio of 60 percent. A sample of 10 individuals per species is quite reliable (95 percent of runs  $r > 0.87$ ) for an intraspecific variability equal to the interspecific variability of the dataset (i.e., 100 percent).

## Discussion

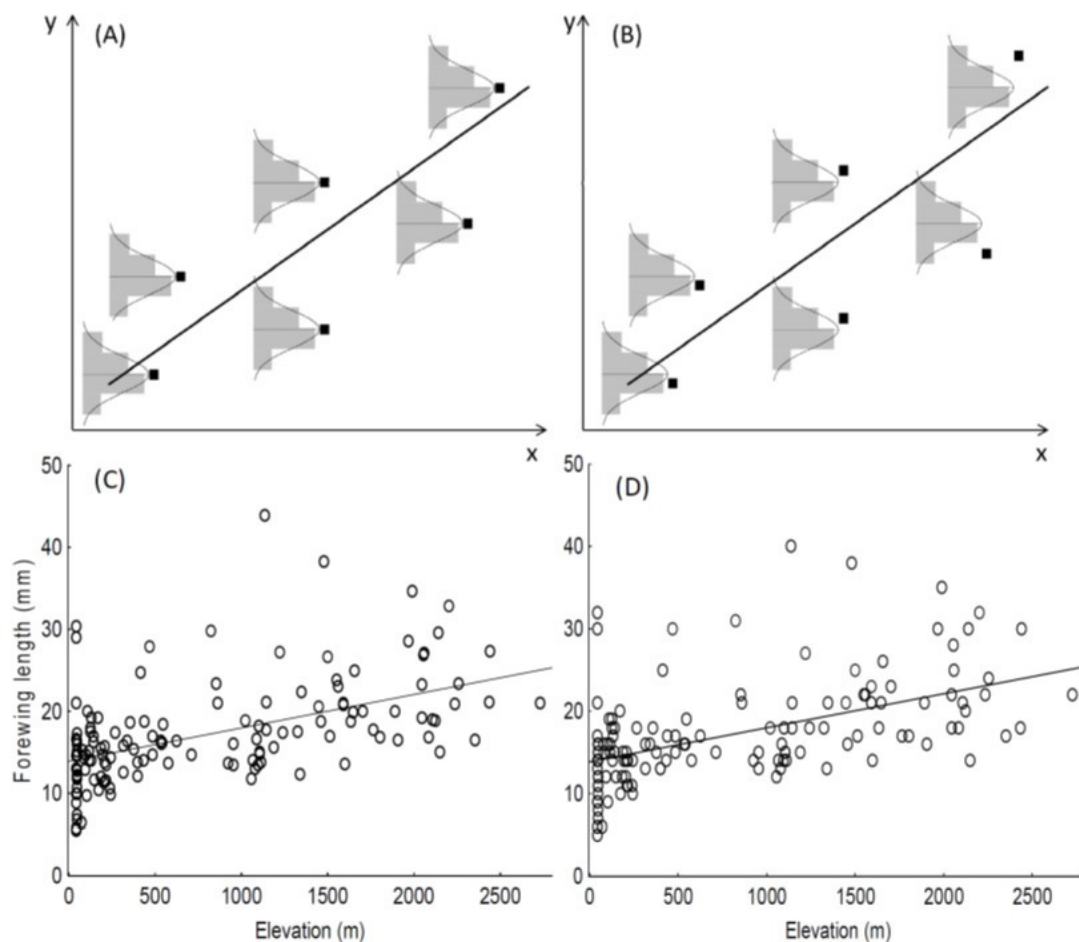
Subsampling analyses of three empirical datasets showed that species trait data based on randomly chosen singletons correlate very well with “true” data, i.e., species averages based on all available data. Furthermore, singleton data lead to equal conclusions on a trait vs. environment correlation (here: body size vs. elevation). Under the conditions of these example datasets (in particular, a moderate to high species richness (32 sp. to several hundreds), a rather low ratio

of intra- to interspecific variability (see below) and an aggregate analysis on assemblage level) singleton data were an adequate proxy for multi-individual averages. This would have allowed a substantial reduction of measurement effort in an empirical study.

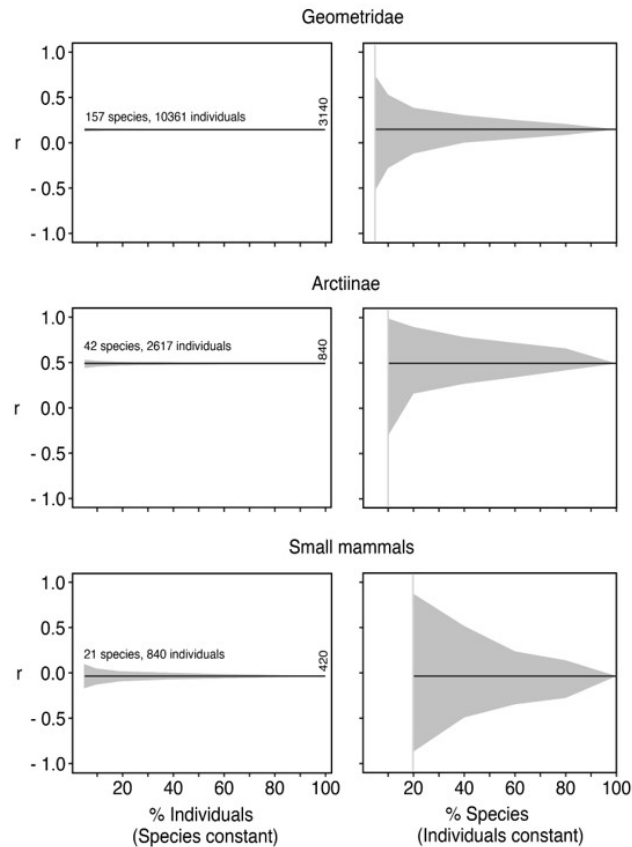
Our empirical analyses were based on elevation-body size correlations for three distinct taxonomic groups from two major ecological and phylogenetic lineages (mammals and moths). While these cannot prove generality (taxonomical or with regards to environment-trait correlations), there is no good reason why theoretical predictions of sampling theory, which were illustrated here, should be limited to a particular trait and environmental gradient, or a particular taxon (but see discussion of intra- vs. interspecific variability below). In line with theoretical expectations, the sample size of correlation analyses (i.e., number of

species) contributed strongly to its robustness, with small mammals (only 32 species) exhibiting highest fluctuations (lowest  $r$ , Table 2). Note that this is not due to a less completely sampled community for Rocky Mountain small mammals compared to the Ecuadorian moths (rather, the opposite is true).

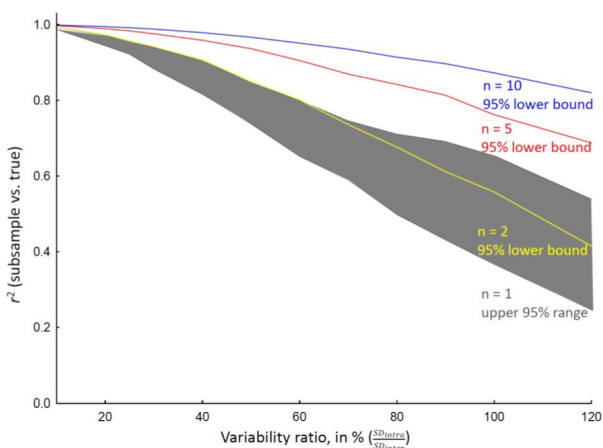
Rare species comprise (almost) always a significant part of samples from species assemblages, but particularly so in tropical regions (Novotny and Basset 2000). For example, in a dataset of 1857 geometrid moth species from southern Ecuador, 545 species (29%) were represented by just one individual (Brehm et al. 2016). Because no reliable average can be calculated from singletons, or from species represented by just a few individuals, there is a temptation to omit such species from analyses – among other reasons, because they invite hard-to-refute criticism of data quality.



**Figure 1.** (A and B) show fictive correlations of a species trait  $y$  with a variable  $x$ . Black squares represent measured data, drawn from an underlying frequency distribution (symbolized by the Gaussian curve). (A) Measured data are true species means, based on averages from a large number of individuals. (B) Measured data deviate randomly from true species means (e.g., from single-specimen measures; the variance of the sampling distribution (i.e., the expected deviation of the sample (black square) from the true mean) is inversely proportional to the sample size within each species). Crucially to our study, scenario B leads to the same regression of  $x$  and  $y$  as recovered in scenario A. (C and D) Example of an empirical elevation-body size correlations (137 species of Arctiine moths from Ecuador, see below) for mean body sizes of all available individuals (C) and for a random single-individual sample (D). Correlations and regression lines are almost identical (slopes: 13.88 vs. 13.84).



**Figure 2.** Effects of dropping individuals (within species; left), or of dropping species (right), on reliability of trait-environment correlations. Percent of used data (x-axis) are plotted against Pearson’s  $r$  of empirical body size-elevation correlations (95% CI: grey). Left panel: The number of individuals per species varied between 5% (one individual per species) and 100% (20 individuals per species). Right panel: The number of species is varied whereas the number of individuals per species is kept constant at 20. All data refer to 500 subsampling runs.



**Figure 3.** Variability ratio (x-axis) plotted against  $r^2$  (y-axis) of a correlation between subsampled trait values and true population means (based on a simulated assemblage of  $N' = 100$  species). The grey-shaded area indicates the upper 95 percentiles of subsampling runs for singleton measures ( $n = 1$ ), whereas the colored lines show the lower bounds of 95 percentiles for  $n = 2$ ,  $n = 5$  and  $n = 10$  sampled individuals per species. 95% of simulation runs had an  $r^2$  equal or higher than these values.

Our subsampling simulations clearly show that such species should be included in trait analyses. Reducing individual numbers per species retained reliable eco-geographical correlations, while omitting species led to wide random fluctuation of recovered correlations (Fig. 2). Singleton data are unbiased estimators of the mean and represent an essential part of the analyzed communities (Zhang et al. 2021). Our subsampling analyses corroborated the effect outlined in Box 1.

Without question there is value in obtaining large amounts of trait data on different hierarchical levels (individual, population, assemblage) where this is feasible (e.g., fine root density or leaf size in a tree; Petruzzellis et al. 2017). These allow analytical approaches that partition the variability of the different levels (Bolker et al. 2009), as well as providing data suitable for species-level studies (Chardon et al. 2020). Towards this end, we also recommend detailed reporting of new trait data, ideally for each individual, to facilitate future combined analyses (Jetz et al. 2019). However, our subsampling simulations show that many conclusions on interspecific patterns can also be retained from more austere data collections, even if random sampling error on species-level data remains unknown. Crucially, with limited resources, priority should be given to include

more species even if this means more uncertain species averages from few or even single measurements. Our data simulations based on, but not necessarily restricted to, elevation-body size relationships, confirm expectations based on general sampling theory on an interspecific level.

### *Intra- vs. interspecific variability*

Intraspecific variability is of high ecological and evolutionary relevance, and it can be of similar magnitude as interspecific variability (Violle et al. 2012). In no way do we advocate ignoring it as a matter of principle. However, apart from measurement effort discussed above, published trait data are often aggregated per species, often without transparent metadata on sample size and data spread. Consequently, interspecific variability is *de facto* the only subject of many ecogeographic studies. Our analyses generally support the reliability of this approach. We have shown (Fig. 3) that the singleton data-approach works best where intraspecific variability is relatively low compared to interspecific variability, as was the case for our three body size datasets. Depending on taxa and traits analyzed, intraspecific variability could potentially be much higher. Where pre-study data suggest high intraspecific variability (Des Roches et al. 2018), even a slight increase of individual numbers (e.g., from singletons to a few individuals per species; Fig. 3) can substantially increase the reliability of data. Our simulations (Fig. 3) may offer some guidance on how the intraspecific variability affects the robustness of singleton-analyses.

## Conclusions

Our simulations confirm the suggested “higher order correlation robustness” (Box 1): Data with high species-level uncertainty due to small sample size (e.g., singleton trait measures) yield robust ecological patterns on the higher level of assemblage-wide patterns. These findings are a justification for singleton analyses where practical constraints make other approaches not feasible. Furthermore, we showed clearly that dropping species from analyses because of low sample size (i.e., uncertainty of averages) is inferior to including such purportedly “poor” data as it greatly diminishes the robustness of higher-order pattern recovery.

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## Author Contributions

JB & GB designed the study, GB & CMcC supplied data, JB analyzed data, all authors contributed to writing the manuscript.

## Data Availability Statement

Moth data were published with Brehm et al. (2019). Small mammal data are available as Supplementary Appendix S1, with species identities and sites anonymized (full data will be published later elsewhere). R-scripts are available as Appendices S2 and S3.

## Supplemental Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

**Appendix S1.** Small mammal data

**Appendix S2.** R-script: subsampling analyses

**Appendix S3.** R-script: data simulations

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