**Functional abundance of species – a new concept in study of trait variability**

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**Conflict of interest statement**

All authors declare that they have no conflicts of interest.

**Author Contributions**

Evsey Kosman conceived the idea of functional abundances of species, designed formal methodology for measuring absolute and relative functional abundances, and wrote the original draft of the manuscript. Jukka Jokela contributed to the further refinement of ideas and metrics. All authors gave final approval for publication.

**Abstract**

1. A new concept of functional abundance of species is presented. The absolute and relative functional abundance is mainly aimed at analyzing functional variability of communities based on intraspecific trait variation.
2. Functional abundance of species in a given community was estimated for two models of proportional and nonproportional random sampling of individuals of each species for determining trait profiles of the selected individuals. The intraspecific trait variabilities obtained for each separate species were incorporated together with taxonomic abundance of those species to assess species functional abundance.
3. Two examples demonstrate the pipeline of calculations of the functional abundance for the two corresponding models. Possible applications of the functional abundance and related technical issues are briefly discussed.

**Keywords**

Diversity, dispersion, effective number of different individuals, Hill numbers, intrinsic functional variability, nonproportional random sampling, proportional random sampling, taxonomic abundance

**Introduction**

Numerous approaches and metrics for measuring functional variability have been developed assuming “identity” of individuals within a species or applying average estimates of trait values for each species, which is formally the same as the “identity” assumption because every species is represented by a single vector of traits. Thus, within species trait variation has not been taken into account, though the idea and necessity of incorporating intraspecific variability in study of functional diversity has been raised several times during the last decade (Bolnick et al., 2011; Carmona, de Bello, Mason, & Leps, 2016; Des Roches et al., 2018; Fontana, Petchey, & Pomati, 2016; Fontana, Thomas, Moldoveanu, Spaak, & Pomati, 2018; Olusoji et al., 2023). In several studies where functional variability at the individual level has been considered, the actual species composition of the community has usually been ignored. Instead, where a pool of individuals from different species has been considered, the commonly used methods for assessment of functional diversity for a community were simply applied to the whole set of individuals sampled from the community. However, such simplification of the situation actually leads to analyzing interindividual variability of communities rather than accounting for intraspecific variability (interindividual variation within a species) in a study of interspecific variability.

Most ecological processes that occur in populations of species are not representatively evaluated when species identity of individuals is ignored. Effects of different species, changes in species abundances, invasion and extinction of species, species turnover etc. will all have an effect on functional diversity and functional processes at the community level that can only be correctly evaluated if species identity and intraspecific individual level variability are taken into account. Ignoring the identity or individual level variation makes the predictions of functional changes less accurate than possible. Therefore, we suggest a new concept of species functional abundance that directly assumes that functional diversity depends on individual variability within a given species and applies this measure at the community level. Similar to the standard definitions of species absolute and relative abundances (AA and RA, respectively), we consider both the absolute and relative functional abundances and designate them FAA and FRA, respectively. If relevant, FAA and FRA can be utilized in a way like AA and RA. Utilizing the functional abundances instead of the taxonomic ones seems to be much more accurate and informative approach in many applications. We will consider an example aimed to support decision making of land use.

**Methods**

Our approach is based on the metric of functional-trait dispersion (Scheiner, Kosman, Presley, & Willig, 2017), which is determined by the dispersion of species in trait space and measures the effective number of functionally distinct species. Being applied to a set of several individuals of a given species, the effective number of different individuals (ENDI) in that set can be determined. Such obtained ENDIs for all species in a community can be employed for calculating FAA and FRA of every species. We further assume that taxonomic abundances of species in a community are known in advance (e. g. they were estimated using random community sampling). Sampling of individuals of all species in a given community for analyzing functional variability within each species can be performed in two different ways. The first one is so-called proportional sampling, when proportion of individuals of each species in the total sample for the studied trait is identical to the corresponding proportion of that species in the community in question. In particular, random sampling of individuals for analyzing functional variability independent of their species identity yields an example of proportional sampling. Otherwise, the sampling is nonproportional, i.e. for each species a number of individuals selected for the study of their traits is independent of the relative taxonomic abundance of that species in the community. This type of nonproportional sampling yields reliable estimates of intraspecies trait variance, but it doesn’t allow a simple transformation of the functional variability within each species into assessments of functional abundance of each species in the community. Both the models are considered in the next sections.

***Functional abundance of species – proportional random sampling of species for determining functional traits.*** It is assumed here that proportion of functional profiles of each species among trait profiles of all sampled units (individuals) is identical to that in a community in question (i. e. identical to relative taxonomic abundances of species in the community). We start with a case when trait profiles exist for all individuals in a given community (generalization to any case of the proportional sampling of species is straightforward).

Let *S* be the number of species in a community sample, and are the absolute (AA; number of individuals, although any other sampling units can be used) and relative (RA) abundances of the *k*th species in the sample of all individuals with available trait profiles, respectively, so that there are individuals in the whole sample of functional profiles of *S* species. Within each species, let represents the standardized dissimilarity in trait space between the *i*th and *j*th individuals of species *k*, so that , , and (; ). Then the effective number of different individuals of *k*th species can be calculated according to the eqs. 5 or 6 in Scheiner et al. (2017) as follows.

First, we calculate a measure of variability among pairwise dissimilarities between individuals with the Hill function (Hill, 1973):

and

for , and , respectively, where is proportional contribution of into the total sum of the pairwise dissimilarities . From this quantity we calculate functional-trait individual diversity within *k*th species:

. (1)

This metric is in units of the effective number of equally-distant individuals (ENEDI) and has a range of ; minimum 1 is obtained when all individuals are identical, while maximum *Nk* is reached when all individuals are equidistant. As the evenness of the distribution of pairwise dissimilarities decreases, decreases. The greater (lesser) the value of, the more weight is given to pairs of individuals with large (small) dissimilarities, and for () effect of more (less) distant pairs of individuals is overestimated (with or without intention). If , all pairwise dissimilarities are equally weighted, and from this point provides the unbiased estimate of individual diversity.

Secondly, we determine a measure of individual dispersion *Mk* () in the trait space for the *k*th species. The mean of pairwise dissimilarities for all individuals (Kosman & Leonard, 2007) is the simplest metric of dispersion that provides a measure of the magnitude of dispersion. However, it has a range of and thus needs a correction to match interval. Therefore, the corresponding measure of dispersion is

. (2)

Note. any other dispersion estimates that range in interval can also be used (e.g. *KW* in Kosman & Leonard, 2007; see also Kosman, 1996; Gregorius & Kosman, 2017).

Finally, we combine functional-trait diversity of individuals (1) and dispersion *Mk* (2) into an integrated metric (functional-trait dispersion according to Scheiner et al., 2017) that provides the effective number of different individuals of the *k*th species

(3)

with a range of , where

(4)

is the evenness of distribution of individuals of *k*th species in the trait space, so that maximum evenness 1 is obtained if and only if all individuals are equally distant from each other.

Now we have all necessary attributes to define functional abundance of species of a given community. We call a quantity

(5)

the total effective number of different individuals within the community, where contribution of each species is predetermined by the effective number of different individuals (). Then the absolute () and relative () functional abundances of the *k*th species are defined as follows:

, (6)

. (7)

Obviously, . Yet, crucially to emphasize that values of and differ generally from each other, i. e. the functional and taxonomic presence of the *k*th species can be in considerable disagreement including a situation of different rank order, when , but for two species *k* and *m*. Another important note is that these functional abundances depend on parameter , and as was already mentioned, their unbiased versions are obtained for when all dissimilarities between individuals are equally weighted. In this particular case we further simplify designations of absolute and relative functional abundances of the *k*th species: and , respectively.

Finally, if a total number of individuals *NN* of all *S* species in a community is larger than proportionally sampled total number of individuals (*N*) for measuring trait variability within each species (which is usually the case) with (, then the absolute functional abundance of the *k*th species equals , whereas the estimate of relative functional abundance remains the same as in Eq. 7.

***Functional abundance of species – nonproportional random sampling of species for determining functional traits.*** In practice, species abundance can be evaluated in different ways of sampling by observations (e.g. number of animal or insect visits at monitoring stations), by evaluation of biomass of species or area covered by different plant species etc. Then several individuals (or other sampling units) of each species are sampled in so-called nonproportional mode independently of an estimate of its relative (taxonomic) abundance in a given community to evaluate variability of individual trait profiles of the corresponding species. Those sampled individuals of a selected species serve to assess so-called Intrinsic Functional Variability (IFV) of that species as it was done for the effective number of different individuals (Eqs, 1 – 3) with an additional need to normalize for the *k*th species (Eq. 3) to interval to make IFV of each species independent of a number of individuals of that species (sample size , ) used for estimating its IFA. Thus, IFV of the *k*th species is calculated as follows:

(8)

for (see Eq. 3 in Sun, Kosman, Sharon, Ezrati, & Sharon, (2020)). Note, the minimum 0 of IFV is obtained if all sampled individuals of species *k* have identical trait profiles, whereas the maximum 1 is reached when the individuals are absolutely different (maximum dissimilarity between all individual trait profiles), .

In this case, an assessment of FAA is obtained by incorporating both the IFV and taxonomic abundance (in terms of numbers of individuals, area covered, biomass etc.) of all species in a given community into calculations as follows.

1. Taxonomic abundance of species in terms of conditional units.

Assuming relative taxonomic abundances of all species in a given community are known (, ; ), which is usually the case, one can calculate an ‘absolute’ taxonomic abundance of each species in terms of ‘conditional units’ AACU that are integers from to with , if values of () have *nd* digits after the decimal point:

, . (9)

For example, if , , , and (, then , , and for , but could also be 220, 630 and 150, respectively, for and so on.

1. Functional absolute abundance of species in terms of conditional units.

One can consider an effective number of different individuals in terms of conditional units ENDICU along with the AACU for each separate species. Calculation of ENDICU is performed assuming that the intrinsic functional variability (IFV) is an inherent property of a species in a fixed community environment, and thus its estimate is invariant for that species, i. e. of the *k*th species (Eq. 8) is independent of the sample size . In other words, Eq. 8 holds also for and when they replace and , respectively:

(10)

for . Values of can be interpreted as functional absolute abundances of species in terms of conditional units (FAACU), and Eq. 10 immediately results in the following estimates of FAACU:

(11)

for . ranges from 1 to when the intrinsic functional variability and , respectively.

1. Functional relative and absolute abundance of species.

In a given community, the total functional absolute abundance of species in terms of conditional units equals

.

Then the functional relative abundance of the *k*th species is defined as a limit of

when *n* tends to infinity:

(12)

for .

The total (taxonomic) absolute abundance of species () and absolute abundances of all species () in a given community are usually known in terms of number of individuals, biomass, area covered by plants etc. Then the functional absolute abundance of species , , is defined as a limit of

when *n* tends to infinity:

(13)

for . Then the total functional absolute abundance of species () in that community equals

. (14)

As was already explained, all mentioned metrics will be used for parameter , and designations of absolute and relative functional abundances of the *k*th species will then be simplified: and , respectively.

**Examples and Discussion**

***Example 1 (proportional sampling of species for determining individual trait profiles)*.** Let a sample of community C1 consists of 60 individuals of species , with six individuals of and (), nine individuals of and (), and fifteen individuals of and (). All individuals were characterized by 10 binary traits so that for each species values (0 or 1) of a fixed number of traits were variable and randomly generated for every individual: four such polymorphic traits were in species and , three – in and , and two – in and . The obtained binary profiles of all 60 individuals are shown in Table S1 separately for each species. We also considered community C2 that comprised 30 individuals of the first three species , and .

Estimates of the species functional abundances obtained according to Eqs. 1 - 7 are shown in Table 1. All calculations were based on the simple mismatch dissimilarity (*m*) between the binary individual profiles (). The effective number of equally-distant individuals (ENEDI; functional-trait individual diversity) within each species was calculated based on the Hill numbers of order 1 (; Eq. 1). Dispersion of individuals (*M*; Eq. 2) was measured with the metric of the mean pairwise *m*-dissimilarities between all individuals (*ADW*) within each species. The obtained values of diversity and dispersion were combined to get the effective number of different individuals (ENDI) of each species (Eq. 3) and the estimates of the functional abundances (FAA and FRA; Eq. 6 and 7, respectively).

In community C1 of 6 species (60 individuals), the functional relative abundance differed considerably from the (taxonomic) relative abundance for species ( vs. ) and ( vs. ) with larger FRA for and smaller for . Two pairs of equally abundant species and (), and and () were of highly different values of the FRA: vs. , and vs. . The total functional absolute abundance of community C1 (TFAA, sum of the effective numbers of functionally different individuals of all species) was 13.71 that is much smaller than the total number of 60 individuals in C1.

A bit different story was with community C2 of 3 species (30 individuals). The considerably uneven distribution of species based on their taxonomy (, and ) was dissimilar to the almost even distribution of species based on the trait data (, and ). Like for community C1, the TFAA of community C2 was much smaller than the total number of individuals in C2, 6.33 vs. 30. However, the relative number (TFAA/AA) for C1 was a bit larger than for C2 (0.23=13.71/60 vs. 0.21=6.33/30).

***Example 2 (nonproportional sampling of species for determining individual trait profiles)*.** Let community of grasses C3 covers an area of 5000 m2 and consists of species with relative abundances , , , and . Each species was independently sampled ( plants, and ), and trait profiles of the sampled individuals are shown in Table S1 separately for each species (see explanations in Example 1).

Estimates of the species functional abundances obtained according to Eqs. 8 - 14 are shown in Table 2. Calculations for the sampled individuals of each species were performed as explained in Example 1. Then the intrinsic functional variability (IFV) was obtained according to Eq. 8. Based on the relative (taxonomic) abundances of species and the invariance of IFV values (Eq. 10), the functional relative and absolute abundances of each species were calculated (FRA and FAA; Eq. 12 and 13, respectively).

In community C3 of 6 species, the functional relative abundance differed considerably from the (taxonomic) relative abundance for species ( vs. ), ( vs. ), ( vs. ), and ( vs. ) with much larger FRA for and and much smaller ones for and . Two species and were of nearly the same FRA as their taxonomic RA. The functional relative abundances of and were larger than that of ( and vs. ), although the (taxonomic) relative abundance was larger for ( vs. ). The total functional absolute abundance of community C3 (TFAA) can be interpreted as the total functionally effective area (TFEA, sum of the functionally effective areas of all species). The TFEA was 786 m2 that is about 16% of the area covered by the six species of grasses of this community (5000 m2).

***Conceptual and technical issues***. The suggested concept of species functional abundance is relevant when data on functional variability within a species are available. Values of the functional absolute abundances of species are smaller than the taxonomic absolute abundances of the corresponding species. However, not much can be, or should be, stated in advance about the relation between the functional relative abundance and the taxonomic relative abundance of a species within a given community. For a selected species, a value of FRA could be similar, smaller or greater than the corresponding value of AA as was clearly shown in the examples above for two different models of study functional variability of species community (community sample and independent sampling of species). Nevertheless, distributions of functional and taxonomic relative abundances of species are generally different.

The species functional abundances (FAA and FRA) are predetermined by trait variation among individuals within a species in question and depend on the taxonomic abundances of that species (AA and RA) in a given community. The variation within species was defined by combining two facets of variability – diversity and dispersion of individuals, whereas each of these components can be determined using several approaches based, in turn, on different estimates of dissimilarity between individuals. Therefore, dozens of scores of functional abundances can be obtained with the same data, and a valid analysis of a given system needs selection of proper tools and estimates of all the mentioned attributes of variability.

A proper assessment of dissimilarity between trait profiles of individuals is a key issue because it predetermines estimates of all components of functional variability to a large extent. The ‘proper’ refers to the biological relevance rather than mathematical properties of the metric. We do not intend to deeply address this issue here, but it is worthy to mention that there is a large number of dissimilarity indices for dichotomous, qualitative and quantitative data (e.g. Lesot, Rifqi, & Benhadda, 2009). Selecting the right dissimilarity measure is one of the challenges encountered by researchers because the measures may perform differently for same datasets (Shirkhorshidi, Aghabozorgi, & Wah, 2015; Wijaya et al., 2016; Kosman & Jokela 2019); the proper metric results in a more accurate data analysis, and in particular, a more precise assessment of functional abundance of species.

***Applications of functional abundances***. Species (taxonomic) abundances are among the basic tools and components to describe and measure biological diversity. Knowing the abundance of different species can serve conservation efforts and provide insight into how a community functions. Trait variability within species is rarely considered in community ecology. However, if such functional data are available for all species in a community in question, utilizing the functional abundances instead of taxonomic ones sounds more suitable especially in studies of functional diversity. To realize this, taxonomic abundances need to be formally replaced by the corresponding estimates of functional abundances in relevant metrics and approaches.

One can imagine using the functional absolute abundance in a choice of a ‘more appropriate’ community for a declared goal. For instance, if grazing lands need to be reduced, an optimal decision could be to preserve plots with high total functional absolute abundances (TFAA) of communities of grasses, forbs and legumes growing there based on relevant functional traits of the plants. In Example 2, the community TFAA (the total functionally effective area, TFEA) was 786 m2, whereas the total (taxonomic) absolute abundance (TAA) in terms of area covered by this community was 5000 m2. The ratio could serve a criterion for making the decision: the plot is preferable, if an estimate of its community is larger.

As a closing remark we note that alike to the functional abundance, one can introduce a notion of “genetic abundance” of a population in a given metapopulation based on genetic profiles of individuals. All explanations and metrics are obtained from the corresponding ones for functional abundances by changing terminology. The following are chief necessary substitutions: metapopulation instead of community, population instead of species, and genotypes instead of trait profiles. Such measure would allow ranking of populations in a metapopulation, for example, for their genetic conservation value.

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**Box 1. Acronyms.**

AA – Absolute Abundance

*AAk* – Absolute Abundance of species *k*

RA – Relative Abundance

*RAk* – Relative Abundance of species *k*

IFV – Intrinsic Functional Variability

*IFVk* – Intrinsic Functional Variability of species *k*

FAA – Functional Absolute Abundance

*FAAk* – Functional Absolute Abundance of species *k*

FRA – Functional Relative Abundance

*FRAk* – Functional Relative Abundance of species *k*

ENDI - Effective Number of Different Individuals

Table 1. Pipeline of calculations of functional abundances in the case of proportional random sampling of individuals for analyzing trait variability within each species (Example 1).

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | AAa | RAb | | Dispersion | Diversity | FAAe | | FRAg | |
| Species | # ind | 6 sp | 3 sp | ADWc | ENEDId | ENDIf | | 6 sp | 3 sp |
| S1 | 6 | 0.1 | 0.2 | 0.167 | 5.58 | 1.93 | 1.93 | 0.141 | 0.305 |
| S2 | 9 | 0.15 | 0.3 | 0.143 | 8.33 | 2.19 | 2.19 | 0.160 | 0.347 |
| S3 | 15 | 0.25 | 0.5 | 0.094 | 12.79 | 2.21 | 2.21 | 0.161 | 0.349 |
| S4 | 6 | 0.1 |  | 0.094 | 5.48 | 1.52 |  | 0.111 |  |
| S5 | 9 | 0.15 |  | 0.138 | 8.33 | 2.15 |  | 0.157 |  |
| S6 | 15 | 0.25 |  | 0.194 | 14.01 | 3.71 |  | 0.271 |  |
| Total | 60 |  |  |  |  | 13.71 | 6.33 |  |  |

a AA – Absolute taxonomic Abundance

b RA – Relative taxonomic Abundance

c ADW – Average Difference between individuals Within a species

d ENEDI – Effective Number of Equally Distant Individuals

e FAA – Functional Absolute Abundance

f ENDI – Effective Number of Different Individuals

g FRA – Functional Relative Abundance

Table 2. Pipeline of calculations of functional abundances in the case of nonproportional random sampling of individuals for analyzing trait variability within each species (Example 2).

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | RAa | AAb |  | Sample | | |  | IFVf | FRAg | FAAh |
| Species |  | (m2) | # ind | Mc | Ed | | ENDIe |  |  | FEAi |
| S1 | 0.25 | 1250 | 6 | 0.200 | 0.929 | | 1.93 | 0.186 | 0.295 | 232.3 |
| S2 | 0.10 | 500 | 9 | 0.161 | 0.925 | | 2.19 | 0.149 | 0.095 | 74.5 |
| S3 | 0.15 | 750 | 15 | 0.101 | 0.853 | | 2.21 | 0.086 | 0.082 | 64.6 |
| S4 | 0.10 | 500 | 6 | 0.113 | 0.913 | | 1.52 | 0.104 | 0.066 | 51.7 |
| S5 | 0.10 | 500 | 9 | 0.156 | 0.926 | | 2.15 | 0.144 | 0.092 | 72.0 |
| S6 | 0.30 | 1500 | 15 | 0.208 | 0.934 | | 3.71 | 0.194 | 0.370 | 290.9 |
| Total |  | 5000 | 60 |  | |  |  |  |  | 786.0 |

a RA – Relative taxonomic Abundance

b AA – Absolute taxonomic Abundance

c M – dispersion of individuals within a species,

d E – evenness of distribution of individuals within a species,

e ENDI – Effective Number of Different Individuals

f IFV – Intrinsic Functional Variability of a species,

g FRA – Functional Relative Abundance

h FAA – Functional Absolute Abundance

i FEA – Functionally Effective Area