What do functional diversity, redundancy, rarity, and originality actually measure?
A theoretical guide for ecologists and conservationists

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Abstract. Functional diversity, redundancy, rarity, and originality are fundamental concepts in ecology and conservation biology. Despite their frequent use, the precise meaning and relationships between these measures are often unclear. This paper aims to provide a comprehensive theoretical framework to elucidate what each of these measures captures and how they interrelate. By integrating traditional community-level diversity metrics with species-level specificity as used in fuzzy set theory, we bridge the gap between these concepts. Our framework reveals that while all four measures address distinct aspects of community-level and species-level functional resemblance, they can all be traced back to a common conceptual and formal framework. This theoretical guide is intended to aid ecologists and conservationists in applying these measures more effectively in their research and conservation strategies.

1. Introduction
Diversity measures are standard ecological tools for exploring community assembly at various spatial scales. Historically, community ecologist have linked the notion of diversity to species commonness and rarity. Therefore, classical diversity measures typically summarize community diversity based only on species abundances without considering other attributes such as phylogeny or functional characters. This assumption implies that all species are considered equally and maximally distinct from each other. However, it is commonly accepted that species are not interchangeable and their ecological strategies are connected to their functional traits (Díaz and Cabido 2001). By merging species abundances with their functional characters, a more comprehensive understanding of ecosystem functioning can be achieved. This has led to the development of various functional diversity measures that take into account the distinct traits of individual species (Rao 1982; Walker et al. 1999; Villéger et al. 2008; Schmera et al. 2009; Laliberté and Legendre 2010; Chao et al. 2014).

Unlike conventional abundance-based measures which summarize diversity in terms of species commonness and rarity, trait-based measures summarize the number of shared functional characters among species (Kondratyeva et al. 2019). Species that share many functional characters with other species in the community are generally said to be functionally redundant; species with distinctive functional characters that are not shared by many other species are said to be functionally unique (Kondratyeva et al. 2019; Ricotta et al. 2021).

At the same time, in conservation studies, the notion of functional (or phylogenetic) originality of species has been formulated to include the species functional characters (phylogenetic features) as a criterion in conservation strategies. Functionally original species with distinctive functional traits are often essential components of ecosystems, making their contributions to local-scale ecosystem

functioning disproportionately important (Cooke et al. 2020). Identifying functionally distinctive species facing extinction risk could then alert conservationists to consider these species and their habitats in conservation programs. The idea of prioritizing species based on their functional originality stems from the awareness that the assessment of conservation priorities should not exclusively rely on a species extinction probability (Steel et al. 2007). Among various possible criteria, the consideration of species with distinctive functional traits is also a viable option.

While functional diversity, redundancy, rarity, and originality are inherently interconnected (and are often used interchangeably without a clear distinction between them), they refer to distinct concepts, both in terms of what they measure and the type of uncertainty they address. The aim of this work is thus to establish a common reference framework that allows us to highlight the main analogies and differences among these concepts. The proposed framework is grounded on the integration of traditional community-level diversity with the notion of species-level specificity used in fuzzy set theory to represent the degree to which a fuzzy set contains one and only one element.

2. Methods
2.1. Diversity, rarity, and uncertainty

Given a species assemblage (sample site, community, plot, etc.) containing N species with relative abundances p_i $(i = 1, 2, ..., N)$ Patil and Taillie (1982) defined the diversity of the assemblage as the expected (i.e. average) rarity of their species relative abundances p_i:

$$D = \sum_{i=1}^{N} p_i \times \rho(p_i) \tag{1}$$

where the rarity $\rho(p_i)$ of species i is some decreasing function of its relative abundance p_i (with $0 < p_i \leq 1$ and $\sum_{i=1}^{N} p_i = 1$) such that for $p_i = 1$, $\rho(p_i) = 0$. This definition encompasses two of the most important diversity measures: the Shannon entropy (Shannon 1948) $H = -\sum_{i=1}^{N} p_i \log p_i$ with $\rho_H(p_i) = -\log p_i$, and the Simpson diversity (Simpson 1949) $S = 1 - \sum_{i=1}^{N} p_i^2$. A summary with definitions and formulas of all indices used in this paper can be found in Table 1.

Specifically, the Simpson index is defined as the probability that two randomly selected individuals from a given assemblage are not of the same species. Therefore, the Simpson index aligns with Hurlbert's (1971) proposal to define diversity in terms of interspecific encounters (see also Patil and Taillie 1982). Note that the complement of the Simpson diversity, the Simpson dominance $1 - S = \sum_{i=1}^{N} p_i^2$, represents the probability that two randomly selected individuals belong to the same species. High dominance thus suggests that nearly all individuals in the assemblage belong to a single species that dominates in abundance.

In terms of average rarity, the Simpson index can be formulated as:

$$S = \sum_{i=1}^{N} p_i (1 - p_i) \tag{2}$$

where the rarity function $\rho_S(p_i) = (1 - p_i)$ is linearly decreasing with the relative abundance of species.

Although the Shannon entropy and the Simpson index have very distinct origins (for a brief history of such measures, see Good 1982), they have both been used in community ecology to capture the uncertainty in predicting the relative abundance of species in a given assemblage. In both cases, for

a non-empty assemblage, diversity is zero if the assemblage contains only one species and progressively increases with increasing species richness and evenness such that, for an assemblage composed of N species, diversity is maximal if all N species occur in equal abundance (i.e., $p_i = 1/N$ for all $i = 1, 2, ..., N$). Accordingly, both indices can be considered community-level indicators of probabilistic uncertainty or conflict, summarizing the disagreement in choosing among several mutually exclusive alternatives (Klir and Wierman 1999). Indeed, high values of Shannon entropy and Simpson diversity have both been associated with elevated conflict in species abundance distribution. These values correspond to high equality in species abundances and high species richness, indicating a considerable level of informational uncertainty about the identity of an individual randomly sampled from the assemblage.

The main difference between the Shannon entropy and the Simpson index is how their rarity functions weight rare and common species. While the Shannon entropy is more sensitive to changes in the abundance of the rarest species, the Simpson index responds more strongly to changes in the abundance of common species, becoming less sensitive to changes in abundance as rarer species are considered (Hill 1973; Peet 1974).

To make clear the type of uncertainty measured by diversity indices, take for example the Simpson diversity $S = \sum_{i=1}^{N} p_i (1 - p_i)$, where the term $(1 - p_i) = \sum_{j \neq i}^{N} p_j$ summarizes the relative abundance of all species that differ from species i in the range $[0, 1]$. That is, the probabilities of all events that conflict with i or, in other words, the probability that an individual randomly drawn from the assemblage does not belong to i. Likewise, the rarity function of the Shannon entropy $-\log\left(1 - \sum_{j \neq i}^{N} p_j\right)$ summarizes the conflict of all species that differ from i in the range $[0, \infty]$.

Accordingly, the Shannon and the Simpson diversity can be both considered as measures of expected conflict among the distinct species in the assemblage (Ricotta and Szeidl 2006). However, while the Shannon entropy offers a complex, logarithmic measure of diversity/uncertainty, the Simpson index provides a more readily interpretable approach in ecological contexts (see Hurlbert 1971). Therefore, in this paper we will use the Simpson index as the cornerstone of our work.

2.2. Functional diversity, uniqueness, and redundancy

While conventional diversity measures focus solely on species richness and abundance, it is widely recognized that a more comprehensive ecological characterization of ecosystem functioning is achieved by considering the range and distribution of the species functional traits (Díaz and Cabido 2001; Mouchet et al. 2010). Therefore, various measures of functional diversity have been developed that incorporate species abundance and functional traits into a single metric.

Typically, the information available for summarizing the functional organization of a specific community consists of a list of functional attributes for each species. Since most diversity indices rely on functional dissimilarities, these traits are usually converted into a square matrix of multivariate functional dissimilarities between pairs of species (Villéger et al. 2008). Given species abundance and dissimilarity data, several authors have shown that the quadratic diversity measure proposed by Rao (1982) can be effectively used for calculating the functional diversity of species.

Quadratic diversity is defined as the expected dissimilarity between two individuals drawn randomly with replacement from the community:

$$Q = \sum_{i,j}^{N} p_i p_j d_{ij} \tag{3a}$$

where d_{ij} is the symmetric dissimilarity among species i and j such that $d_{ij} = d_{ji}$ and $d_{ii} = 0$.

The mathematical properties of quadratic diversity have been thoroughly explored by several

authors (Shimatani 2001; Champely and Chessel 2002; Rao 2010; Pavoine 2012; Ricotta et al. 2022) and for a detailed understanding of Rao's index the reader is referred to these papers. Here, it is sufficient to mention that if the functional dissimilarities d_{ij} are in the range $[0,1]$, a condition maintained throughout this paper, quadratic diversity is always lower than the Simpson diversity: $Q \leq S$. Accordingly, the Simpson diversity can be also interpreted as the expected dissimilarity between two individuals drawn at random from a Boolean community where all species are considered maximally distinct from each other (i.e. with $d_{ii} = 0$ and $d_{ij} = 1$ for all $i \neq j$).

Since by definition $d_{ii} = 0$, for the purposes of this paper, it is convenient to express Rao's quadratic diversity as the mean functional dissimilarity between individuals of distinct species (Ricotta et al. 2023):

$$Q = \sum_{i \neq j}^{N} p_i p_j d_{ij} \tag{3b}$$

Q increases with increasing functional dissimilarity among species. Therefore, Ricotta et al. (2021) proposed this index as a measure of community-level functional uniqueness (*U*). In the same way, the difference between Simpson diversity and Rao's quadratic diversity (i.e., the mean functional similarity between individuals of distinct species)

$$S - Q = \sum_{i \neq j}^{N} p_i p_j s_{ij} \tag{4}$$

can be considered a suitable measure of functional redundancy (*R*), a relevant component of the community functional structure which is thought to play a crucial role in providing insurance against the potential loss of ecosystem processes due to nonrandom species extinctions (Loreau 2004; Ricotta et al. 2016).

Two species are considered functionally redundant if they perform similar functions within an ecosystem (Carmona et al. 2016). If redundant species are similar in their ecosystem functions but differ in their environmental preferences, redundancy may enhance community functioning and stability after environmental perturbations. For example, if a nitrogen-fixing species is lost due to environmental perturbations, its role can be partially compensated by the presence of other nitrogen fixers, which are more tolerant to perturbation. To this end, the presence of multiple redundant species that maintain similar ecosystem functions increases the likelihood that they will not share the same sensitivity to perturbations, thereby strengthening this compensatory effect (Fischer and de Bello 2023).

Unlike functional rarity, functional redundancy (i.e., the degree of interspecies functional similarity) does not increase functional diversity. In cases of high redundancy, as in cases of high species dominance, functional diversity is generally low. However, with high dominance, the decrease in functional diversity is primarily driven by a decrease in species diversity (one or a few species dominate in abundance). In contrast, high functional redundancy can occur even with high abundance-based diversity.

Based on the assumption that ecological differences between species are related to their functional dissimilarities, such that functionally similar species have similar ecological roles, Leinster and Cobbold (2012) defined the ordinariness of species *i* as the abundance of all species that are functionally similar to *i* (including *i* itself):

$$\omega_i = \sum_{j=1}^{N} p_j s_{ij} \tag{5}$$

where $s_{ij} = 1 - d_{ij}$ is the functional *similarity* between species i and j. ω_i thus embodies the commonness of all individuals that support the functions associated with species i. For $0 \le s_{ij} \le 1$, ω_i ranges from p_i if all species j ($j \ne i$) are maximally dissimilar from i, to 1 if all species j are functionally identical to i. Combining Eq. 3 and 5 it is easily shown that quadratic diversity can be expressed as the expected functional rarity of the species ordinariness ω_i (Ricotta and Szeidl 2006):

$$Q = \sum_{i=1}^{N} p_i(1 - \omega_i) = \sum_{i=1}^{N} p_i \times \rho_S(\omega_i) \tag{6}$$

In terms of uncertainty, Rao's Q can be interpreted as a measure of expected rarity or conflict among functionally overlapping species, thus relaxing the mutually exclusive nature of the conflicting alternatives. Q is high when the most abundant species are also the most functionally rare, and is low when the most abundant species are the least functionally rare (Kondratyeva et al. 2019).

Expanding on Eq. 6, Ricotta and Szeidl (2006) further proposed a general class of functional diversity measures expressed as the expected functional rarity of the species ordinariness ω_i:

$$FD = \sum_{i=1}^{N} p_i \times \rho(\omega_i) \tag{7a}$$

where $\rho(\omega_i)$ is any rarity function of choice. This general formula allows rare and abundant species to be weighted differently for the calculation of functional diversity, such that, for practical purposes, one uses the type of rarity measure which is most adequate to solve the specific problem at hand (Ricotta and Szeidl 2006).

Likewise, since $p_i \le \omega_i$ and hence $\rho(p_i) \ge \rho(\omega_i)$, we can define a general class of functional redundancy measures expressed in terms of rarity as:

$$R = D - FD = \sum_{i=1}^{N} p_i \left(\rho(p_i) - \rho(\omega_i) \right) \tag{7b}$$

2.3. Functional originality and specificity

To incorporate functional (or phylogenetic) information into conservation efforts, a number of indices that summarize the originality or distinctiveness of individual species have been proposed. When original species are threatened, there is a concern that a disproportionate amount of unique functional characters (phylogenetic history) is lost. Therefore, identifying these endangered original species could prompt conservation practitioners to prioritize them in their programs (Pavoine and Ricotta 2022, 2023). The idea of prioritizing species based on their functional originality stems from the awareness that the assessment of conservation priorities should not exclusively rely on a species extinction probability (Steel et al. 2007). Among various possible criteria, the consideration of species with distinctive functional traits is also a viable option.

In global conservation studies, species originality is commonly evaluated using presence and absence data, without considering species abundance. Conversely, local studies more frequently utilize abundance data, which can provide valuable insights into ecosystem functioning at smaller

scales (e.g., Enquist et al. 2019).

When dealing with functional traits, a common approach to summarize the functional distinctiveness of a focal species i based on presence and absence data is to compute the mean functional dissimilarity of i from all other species in the assemblage (Grenié et al. 2017; Violle et al. 2017; Cooke et al. 2020; Pavoine and Ricotta 2022).

$$D_i = \frac{\sum_{j=1, j \neq i}^{N} d_{ij}}{N-1} \tag{8}$$

In fuzzy set theory, this index corresponds to a classical measure of specificity introduced by Yager (1992, p. 285), a non-probabilistic kind of uncertainty, which summarizes the degree of having just one element in a fuzzy set (Yager 1982; Klir and Wierman 1999). Indeed, species functional (dis)similarity can be interpreted in terms of fuzzy set theory. The similarity between two species represents the degree to which one species belongs to the set defined by the other species (Roberts 1986; Feoli and Zuccarello 1986; Feoli and Orlóci 2011). Therefore, the higher the dissimilarity between a focal species i and any other species j in the assemblage, the lower the possibility that species j belongs to the same functional group as i (*sensu* Fischer and de Bello 2023), and hence the higher the specificity of i. A brief overview of specificity and specificity measures is provided in Appendix 1 of this paper.

If we generalize Eq. 8 to include species abundance, we obtain a well-known measure of species-level originality/specificity, expressed as the weighted functional dissimilarity of species i from all other species in the assemblage (Ricotta et al. 2016; Violle et al. 2017):

$$D_i = \sum_{j=1, j \neq i}^{N} \frac{p_j}{1-p_i} d_{ij} \tag{9}$$

Where the term $\dfrac{p_j}{1-p_i}$ is the relative abundance of species j ($j \neq i$) such that $\sum_{j=1, j \neq i}^{N} \dfrac{p_j}{1-p_i} = 1$ (Pavoine and Ricotta 2021).

3. Synthesis: Bridging the gap between functional rarity, and originality

A relevant relationship between functional rarity and originality was highlighted by Pavoine and Ricotta (2021). Since $d_{ii} = 0$ we have: $1 - \omega_i = \sum_{j=1, j \neq i}^{N} p_j d_{ij}$. Therefore, Eq. 9 can be expressed in terms of functional rarity as:

$$D_i = \frac{1-\omega_i}{1-p_i} \tag{10}$$

Expanding on Pavoine and Ricotta (2021), the same approach can be used to define the complement of Eq. 9 in terms of functional rarity:

$$1 - D_i = \sum_{j=1, j \neq i}^{N} \frac{p_j}{1-p_i} s_{ij} = 1 - \frac{1-\omega_i}{1-p_i} = \frac{\omega_i - p_i}{1-p_i} \tag{11}$$

This gives rise to an index of nonspecificity (*NSp*), which measures the uncertainty regarding the number of elements that belong to a fuzzy set to a certain degree (Klir and Wierman 1999). Since

$\omega_i - p_i = \sum_{j=1, j \neq i}^{N} p_j s_{ij}$ is the commonness of all species j ($j \neq i$) that are functionally similar to i, Eq. 11 shows the direct relationship between nonspecificity and the functional resemblance among the distinct species in the assemblage.

Expanding the horizon, the above formulation allows us to conjecture a general class of abundance-based originality/specificity measures of the form:

$$Sp_i = \frac{\rho(\omega_i)}{\rho(p_i)} \qquad (12)$$

with

$$NSp_i = 1 - Sp_i = \frac{\rho(p_i) - \rho(\omega_i)}{\rho(p_i)} \qquad (13)$$

That is, the functional originality/specificity of species i can be expressed as the ratio of its functional rarity $\rho(\omega_i)$ and its abundance rarity $\rho(p_i)$. Since $p_i \leq \omega_i \leq 1$, we have $\rho(p_i) \geq \rho(\omega_i) \geq 0$, and hence $0 \leq Sp_i \leq 1$.

4. Discussion

In this paper, we have attempted to unify the concepts of functional diversity, redundancy, rarity, and originality within a single framework. While the Simpson-Rao family of diversity measures has been used extensively throughout this work, the same approach can be generalized to any diversity measure that can be additively decomposed into distinct species-level contributions. Our approach is based on the observation that by relaxing the mutually exclusive nature of species, which is typical of classical abundance-based diversity (Eq. 1), functional rarity and originality can both be traced back to the same formal and conceptual framework. Furthermore, to the best of our knowledge, this is the first time that the concept of species originality is explicitly linked to fuzzy uncertainty and specificity (see Appendix 1), demonstrating that its measurement has a more solid theoretical foundation than one might imagine.

While rarity and originality are both species-level indicators of functional resemblance, Pavoine and Ricotta (2021) noted that a community-level measure of expected originality/specificity, defined as:

$$Sp = \sum_{i=1}^{N} p_i \times D_i \qquad (14)$$

would not serve as a suitable index of diversity, as it does not necessarily reflect the functional (or phylogenetic) variability of all species in the assemblage (see Gregorius and Kosman 2017).

Indeed, in the most extreme scenario, Sp can reach its maximum value when a very abundant species i (with p_i tending to one) is also maximally dissimilar from all other species in the assemblage. Therefore, unless we are dealing with presence and absence data, Sp is generally not a suitable index of diversity (Pavoine and Ricotta 2021). For species presence and absence data, Sp reduces to the average dissimilarity between any two species in the assemblage (excluding comparisons of a species with itself). In a phylogenetic context, this index is commonly referred to as the Mean Pairwise Distance (Webb 2000): $MPD = \sum_{i \neq j}^{N} \frac{d_{ij}}{N(N-1)} = \sum_{i=1}^{N} \frac{1}{N} D_i$. Hence, if species abundances are either unknown or irrelevant, such as in large-scale studies, we can use expected specificity/originality as an appropriate proxy for functional diversity.

In contrast, when dealing with species abundances, to formulate a suitable index of community-level functional diversity based on species originality/specificity, we first need to convert functional originality into functional rarity:

$$FD = \sum_{i=1}^{N} p_i \left(Sp_i \times \rho(p_i) \right) = \sum_{i=1}^{N} p_i \times \rho(\omega_i) \tag{15}$$

with $\rho(\omega_i) = Sp_i \times \rho(p_i)$. Note that the quantity $\rho(\omega_i)$ in Eq. 15 is equivalent to the 'effective originality' of Pavoine and Ricotta (2021) i.e., the product of originality and abundance-based rarity. The same approach can be used to express functional redundancy in terms of non-specificity:

$$R = \sum_{i=1}^{N} p_i \left(NSp_i \times \rho(p_i) \right) = \sum_{i=1}^{N} p_i \left(\rho(p_i) - \rho(\omega_i) \right) \tag{16}$$

For an alternative formulation of the relationship between functional diversity and specificity, refer to Appendix 2.

To clarify the distinction between functional rarity and originality, it is worth remembering that both indicators were developed independently of each other in separate research fields, each addressing different facets of functional resemblance among species. Functional rarity is not an independent concept *per se*. It is a (species-level) component of functional diversity that refers to the total number of individuals that perform the functions associated with a particular species, including the individuals of that species. For example, if the focal species is a nitrogen-fixing species, functional rarity is determined by the abundance of the functional group of all nitrogen-fixing individuals in the observed community. Functional rarity thus mirrors the perspective of an external observer who considers all individuals in the community that perform the functions associated with a particular species. Therefore, it can also be defined as the rarity of a species' functional characteristics, such as the state of a specific trait (Kondratyeva et al. 2019).

Conversely, in a conservation context, functional originality, pertains to the degree of functional (or evolutionary) differentiation of a particular species from the other species in the community (Scheiner 2019). Therefore, the abundance of the focal species is not considered when calculating functional originality. Using the previous metaphor, functional originality mirrors the perspective of an internal observer (the focal species) who considers all individuals from other species in the community that are functionally similar to itself.

In summary, standard abundance rarity $\rho(p_i)$ represents the low probability of encountering the species, functional rarity $\rho(\omega_i)$ represents the low probability of encountering the species functional characteristics, and functional originality $\rho(\omega_i)/\rho(p_i)$ represents the low probability of encountering the species functional characteristics in individuals of different species.

The differences between functional rarity and originality lead to distinct mathematical formulations for each measure. However, this distinction lies primarily in how the measures are scaled, not in what they measure. Functional rarity $\rho(\omega_i)$ ranges between its theoretical (i.e., global) minimum and maximum values, which correspond to zero and one, respectively. For a given species, functional rarity approaches one if the total number of community individuals displaying the traits of the focal species is very low. Conversely, functional rarity equals zero if all community individuals exhibit the same traits of the focal species.

On the other hand, for the calculation of functional originality, the quantity $\rho(\omega_i)$ is normalized by its local maximum $\rho(p_i)$. This means, it is scaled by the maximum value that functional rarity can achieve when the relative abundance of the focal species is equal to p_i. In essence, functional

originality measures the extent to which rarity decreases when taking into account all individuals that are functionally similar to the focal species in the calculation of rarity.

Which properties $\rho(p_i)$ and $\rho(\omega_i)$ must possess to obtain appropriate measures of functional diversity and originality remains an open question, and its answer may enrich the ecological toolbox with new instruments, allowing us to integrate more effectively community assembly processes into conservation strategies and vice versa.

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CRediT authorship contribution statement

Carlo Ricotta: Writing – original draft, Methodology, Formal analysis, Conceptualization.
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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 1. Definitions and formulas of all indices used in this paper. The notation is the same as in the main text.

Species-level measures	General formula	Simpson-Rao family
Abundance-based Rarity A decreasing function of the species relative abundances p_i. In terms of encounter theory, abundance-based rarity represents the low probability of encountering the individuals of species *i*.	$\rho(p_i)$	$\rho_S(p_i) = (1 - p_i)$
Species ordinariness The abundance of all species that are functionally similar to species *i* (including *i* itself).	$\omega_i = \sum_{j=1}^{N} p_j s_{ij}$	
Functional Rarity A decreasing function of the species ordinariness ω_i. Functional rarity represents the low probability of encountering the species functional characteristics.	$\rho(\omega_i)$	$\rho_S(\omega_i) = (1 - \omega_i)$
Functional originality/specificity Functional originality represents the low probability of encountering the functional characteristics of species *i* in individuals of different species. In fuzzy set theory, the concept of specificity represents the degree to which a fuzzy set contains one and only one element.	$Sp_i = \dfrac{\rho(\omega_i)}{\rho(p_i)}$	$D_i = \sum_{j=1, j \neq i}^{N} \dfrac{p_j}{1 - p_i} d_{ij} = \dfrac{1 - \omega_i}{1 - p_i}$ For presence and absence data functional originality reduces to $D_i = \left(\sum_{j=1, j \neq i}^{N} d_{ij} \right) \Big/ (N - 1)$
Nonspecificity The complement of functional originality/specificity.	$NSp_i = 1 - Sp_i = \dfrac{\rho(p_i) - \rho(\omega_i)}{\rho(p_i)}$	$1 - D_i = \sum_{j=1, j \neq i}^{N} \dfrac{p_j}{1 - p_i} s_{ij} = 1 - \dfrac{1 - \omega_i}{1 - p_i} = \dfrac{\omega_i - p_i}{1 - p_i}$
Community-level measures		
Abundance-based Diversity Expected rarity of the species relative abundances p_i. In terms of probabilistic uncertainty, abundance-based diversity summarizes the conflict or disagreement in choosing among several mutually exclusive alternatives.	$D = \sum_{i=1}^{N} p_i \times \rho(p_i)$	$S = \sum_{i=1}^{N} p_i (1 - p_i)$

Functional Diversity Expected rarity of the species ordinariness ω_i. Since *FD* increases with increasing functional dissimilarity among species, *FD* is also a measure of community-level functional uniqueness. In terms of probabilistic uncertainty, functional diversity summarizes the conflict among functionally overlapping species	$$FD = \sum_{i=1}^{N} p_i \times \rho(\omega_i) = \sum_{i=1}^{N} p_i \left(Sp_i \times \rho(p_i) \right)$$	$$Q = \sum_{i,j}^{N} p_i p_j d_{ij}$$
Functional Redundancy The degree of functional similarity among distinct species. Redundancy is thought to play a crucial role in providing insurance against the potential loss of ecosystem processes due to nonrandom species extinctions.	$$R = D - FD = \sum_{i=1}^{N} p_i \left(\rho(p_i) - \rho(\omega_i) \right)$$ $$= \sum_{i=1}^{N} p_i \left(NSp_i \times \rho(p_i) \right)$$	$$R = S - Q = \sum_{i \neq j}^{N} p_i p_j s_{ij}$$
Expected Specificity Mean abundance-weighted species originality/specificity. *Sp* is generally not a suitable index of diversity, as it does not reflect the functional variability of all species in the assemblage.	$$Sp = \sum_{i=1}^{N} p_i \times Sp_i$$	$$Sp = \sum_{i=1}^{N} p_i \times D_i$$ For presence and absence data, expected specificity reduces to the average dissimilarity between any two community species $$Sp = \sum_{i \neq j}^{N} d_{ij} \Big/ N(N-1)$$

Appendix 1

A brief overview of specificity and specificity measures

Fuzzy sets are sets whose elements have a continuum of grades of membership ranging between zero and one (Zadeh 1965). The basic principles of fuzzy set theory have been thoroughly described elsewhere (Dubois and Prade 1980; Klir and Yuan 1995), and for additional details, the reader is addressed to these papers. In short, let X be a crisp set composed of N elements $x_1, x_2, ..., x_N$, and A be a fuzzy subset on X for which $\mu_i (0 \le \mu_i \le 1)$ represents the membership degree of x_i to A such that $0 \le \sum_{i=1}^{N} \mu_i \le N$. In other words, μ_i represents the degree of compatibility of the i-th element with the concept represented by the fuzzy set A (Klir and Wierman 1998).

Two types of uncertainty can be associated to fuzzy sets: fuzziness, which measures the extent to which a fuzzy set is not crisp, and specificity, which measures the degree of having just one element in a fuzzy set (Klir and Wierman 1998). The concept of specificity was introduced by Yager (1982) to measure the extent to which the distribution μ_i $(\mu_1, \mu_2, ..., \mu_N)$ restricts the possibility that the i-th element belongs to A to a small number of elements (for simplicity, here we assume the distribution is ranked such that $\mu_i \ge \mu_{i+1}$). In community ecology, a number of authors noted that the functional (or phylogenetic) dissimilarity matrices of species can be interpreted in terms of fuzzy set theory. Indeed, the similarity between two species represents the degree of belonging of one species to the set defined by the other species (Roberts 1986; Feoli and Zuccarello 1986; Feoli and Orlóci 2011). Therefore, the higher the dissimilarity between species i and any other species j in the assemblage, the lower the possibility that species j belongs to the set defined species i, and hence the higher the specificity of i.

A measure of specificity Sp of a normal fuzzy set A in the range $[0,1]$ should satisfy the following basic conditions (a fuzzy set A is said to be normal if $\max \mu_i = 1$. That is, if the fuzzy set has at least one element with membership degree one):

1. $Sp_A = 1$ iff there exists one and only one element x_i with $\mu_i = 1$ and $\mu_j = 0$ for all other elements j ($j \ge 2$) where μ_j is the j-th largest membership grade in A.

2. $Sp_A = \min$ iff $\mu_i = 1 \forall i \in N$

3. Sp_A is strictly decreasing with respect to $\mu_j \forall j \ge 2$,

The first and second requirement provide boundary conditions for specificity. Condition 1 shows that specificity is maximal if the fuzzy set contains only one element. Condition 2 shows that for a normal fuzzy set composed of N elements, minimal specificity is attained if all N elements have maximal membership degree in A. The last condition shows that for a normal fuzzy set, any increase in the membership degree of the j-th element ($j \ge 2$) reduces the specificity of the fuzzy set (Yager 1982). Note that the reason for limiting our discussion to normal fuzzy sets is that we assume that the degree of belonging of one species i to the set defined by species i itself is always equal to one.

Yager (1992) introduced a family of specificity measures which he called linear specificity measures. For a normal fuzzy set, these measures take the form:

$$Sp_A = \mu_1 - \sum_{j=2}^{N} \mu_j \times w_j \tag{1}$$

where w_j $(j \geq 2)$ is a set of weights satisfying the following basic conditions (Yager 1992):

1. $0 \leq w_j \leq 1$

2. $\sum_{j=2}^{N} w_j \leq 1$

If we assume that i) the degree of belonging of species j to the set defined by species i equals the (functional) similarity between i and j, such that $\mu_j = s_{ij}$ with $0 \leq s_{ij} \leq 1$ and $\mu_i = s_{ii} = 1$, and ii) $w_j = 1/(N-1)$ for all $j \geq 2$, Eq. 1 can be expressed as:

$$Sp_i = \mu_i - \sum_{j=2}^{N} \mu_j \times w_j = 1 - \frac{1}{N-1} \sum_{j=2}^{N} s_{ij} \tag{2}$$

which is simply the difference between the largest membership degree $s_{ii} = 1$ and the mean of the remaining membership values s_{ij}. In terms of functional *dis*similarities, since $d_{ij} = 1 - s_{ij}$, Eq. 2 can be also formulated as:

$$Sp_i = \frac{1}{N-1} \sum_{j=2}^{N} d_{ij} \tag{3}$$

Thus recovering Eq. 8 of the main text. This shows that the measurement of species-level originality has a more solid theoretical basis that one might imagine.
In the same way, assuming that the weights of individual species j $(j \geq 2)$ are equal to their relative abundances: $w_j = p_j / (1 - p_i)$, we recover Eq. 9 of the main text:

$$Sp_i = 1 - \sum_{j=2}^{N} \frac{p_j}{1-p_i} s_{ij} = \sum_{j=2}^{N} \frac{p_j}{1-p_i} d_{ij} \tag{4}$$

Finally note that, assuming $w_j = 1$ for $j = 2$, and $w_j = 0$ for all $j > 2$, we obtain:

$$Sp_i = \mu_1 - (\mu_2 \times w_2) = \mu_1 - \mu_2 = 1 - \max s_{ij} = \min d_{ij} \tag{5}$$

which is simply the functional distance of a focal species i to its functional nearest neighbor j within the regional species pool. Violle et al. (2017) called this measure the functional uniqueness of i.

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Appendix 2

An alternative formulation of the relationship between functional diversity and specificity

Using the same notation of the main text, let

$$FD = \sum_{i=1}^{N} p_i \times \rho(\omega_i) \tag{1}$$

be a generalized measure of functional diversity, of which Rao's quadratic diversity index $Q = \sum_{i \neq j}^{N} p_i p_j d_{ij}$ is one of the main examples, and

$$D = \sum_{i=1}^{N} p_i \times \rho(p_i) \tag{2}$$

be the corresponding measure of abundance-based diversity. For the Rao index, this corresponds to the Simpson diversity $S = 1 - \sum_{i=1}^{N} p_i^2$.

Pavoine and Ricotta (2021) argued that, unlike Eq. 1, a community-level measure of expected species-level originality/specificity, defined as:

$$Sp = \sum_{i=1}^{N} p_i \times Sp_i \tag{3}$$

would not behave as a suitable index of diversity, as it does not reflect the functional variability of all species in the assemblage.

Nonetheless, if standard abundance-based diversity (Eq. 2) is additively decomposable into distinct species-level contributions, *FD* can still be expressed in terms of specificity as:

$$FD = \sum_{i=1}^{N} \left(p_i \times \rho(p_i) \right) Sp_i = \sum_{i=1}^{N} \delta_i \times Sp_i \tag{4}$$

where

$$\delta_i = p_i \times \rho(p_i) \tag{5}$$

is the contribution of species *i* to overall abundance-based diversity *D*.

As mentioned in the main text, the primary difference between expected functional rarity *FD* and expected specificity *Sp* is that functional rarity refers to the total number of individuals in a community that exhibit the properties of a focal species, including the individuals of the focal species itself. Conversely, specificity pertains to the degree of functional differentiation of a particular species from the other species in the community (Scheiner 2019). Therefore, for the calculation of specificity the abundance of the focal species is not considered. It follows that community-level functional diversity can be expressed as the summation of the specificity of individual species *i* multiplied by the contribution of *i* to overall abundance-based diversity *D*. Likewise, let

$$R = D - FD = \sum_{i=1}^{N} p_i \left(\rho(p_i) - \rho(\omega_i) \right) \tag{6}$$

be a generalized measure of functional redundancy. In terms of nonspecificity, it is easily shown that functional redundancy can expressed as:

$$R = \sum_{i=1}^{N} \left(p_i \times \rho(p_i) \right) NSp_i = \sum_{i=1}^{N} \delta_i \times NSp_i \qquad (7)$$

Note that for the special case of Rao's quadratic diversity, Eq. 4 and 7 reduce respectively to:

$$Q = \sum_{i=1}^{N} p_i(1 - p_i) \times Sp_i \qquad (8a)$$

and

$$R = S - Q = \sum_{i=1}^{N} p_i(1 - p_i) \times NSp_i \qquad (8b)$$

That is, we can express functional diversity (redundancy) as the specificity (nonspecificity) of species i multiplied by the species-level contribution of i to the classical (abundance-only) Simpson diversity $\delta_i = p_i(1 - p_i)$. As such, Q and $S - Q$ can be viewed as special cases of the weighted Simpson index proposed by Guiasu and Guiasu (2012).
Ricotta et al. (2016) further defined a normalized version of functional diversity and redundancy as:

$$FD_n = \frac{FD}{D} \qquad (9a)$$

and

$$R_n = \frac{D - FD}{D} \qquad (9b)$$

respectively, such that $0 \leq FD_n \leq 1$, $0 \leq R_n \leq 1$, and $FD_n + R_n = 1$.
The primary distinction between the normalized measures of functional diversity and redundancy FD_n and R_n and their non-normalized counterparts FD and R, lies in how the measures are scaled. FD_n and R_n are scaled by their local maximum D. That is, by the maximum value that FD_n and R_n can reach while maintaining the relative abundance vector of species unchanged and imposing $d_{ij} = 1$ for all $i \neq j$. On the other hand, FD and R are bounded between their theoretical (i.e., global) minimum and maximum values, which are zero and one, respectively (Ricotta et al. 2023).
Accordingly, normalized diversity and redundancy can be both expressed in terms of specificity/nonspecificity as:

$$FD_n = \sum_{i=1}^{N} \frac{p_i(1 - p_i)}{S} \times Sp_i = \sum_{i=1}^{N} \frac{\delta_i}{S} \times Sp_i = \sum_{i=1}^{N} \pi_i \times Sp_i \qquad (10a)$$

and

2

$$R_n = 1 - FD_n = \sum_{i=1}^{N} \frac{p_i(1-p_i)}{S} \times NSp_i = \sum_{i=1}^{N} \frac{\delta_i}{S} \times NSp_i = \sum_{i=1}^{N} \pi_i \times NSp_i \qquad (10b)$$

Hence, similar to Eq 3, FD_n and R_n can both be expressed as mean community-level measures of specificity/non-specificity with $0 < \pi_i \leq 1$ and $\sum_{i=1}^{N} \pi_i = 1$. However, in this case, the weights of individual species $\pi_i = \delta(p_i)/S$ represent their relative contributions to overall abundance-based diversity D instead of species relative abundances.

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