# Important, Unique, Central: Species' Relevance in Food Webs

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## Abstract

Estimating the species' relative importance in an ecosystem is integral to the biodiversity conservation efforts. Unfortunately, the species' diversity makes it hard to identify traits with a functional role across an entire ecosystem. Therefore, researchers have adopted a graph description of ecosystems in terms of trophic interactions (food webs) and graph-theoretical measures have been proposed to estimate species' importance. However, these measures are often derived from rigid models and their applicability to stochastic food webs is limited. Here, we compute, from topological data, species' position in a food web's abstract functional trait space and estimate the species' relative importance for the food web's stability, their contribution to the food web's functional diversity and their ecological uniqueness. We compare the species' relevance as determined by our novel measures and six classic measures. Finally, we explore the phylogenetic distribution of the species' relevance in the Serengeti National Park food web.

# 1 Introduction

The need for scientifically informed conservation policies boosted the attempts to estimate species' relative importance in food webs: the graphs describing the flows of energy between species in an ecosystem (May, 2009). A sound approach to assess a species' contribution to an ecosystem is based on the concept of functional diversity. As summarised by Petchey & Gaston (2006, pg. 742) "measuring functional diversity is about measuring functional traits diversity, where functional traits are components of an organism's phenotype that influence ecosystem level processes". In this context, the contribution of a species to the functional diversity of a food web is captured by the traits diversity loss that we would observe after the removal of that species (Villéger *et al.*, 2008; Fontana *et al.*, 2015). However, identifying suitable phenotypic traits and collecting all the necessary data across a full food web is often ambitious. The tangled intricacy of food webs, where there are often thousands of interactions between hundreds of plants and animals, motivates the use of complex-network tools for solving ecological problems (Proulx *et al.*, 2005). Centrality measures—graph theoretical measures developed in economic, social, technological and theoretical scenarios to identify crucial nodes in a network (Newman, 2010)—have been proposed to assess a species' centrality and to identify the species that play a crucial role within an ecosystem (Estrada, 2007; Lai *et al.*, 2012).

The evolutionary distinctiveness of species (i.e., the amount of *exclusive*

evolutionary information hinging on a species) is an intrinsinc component of biodiversity (Mace *et al.*, 2003) and the evolutionary diversity of species is used as a proxy for a species' functional diversity (Winter *et al.*, 2013). Evolutionary diversity has been shown to promote ecosystem stability (Cadotte *et al.*, 2012). Accordingly, it has been argued that the evolutionary distinctiveness of species should be one of the factors grounding conservation efforts (Faith, 1992; Redding & Mooers, 2006; Isaac *et al.*, 2007). However, the exact relationship between the evolutionary and food-web distinctiveness of a species is an open problem (Gerhold *et al.*, 2015; Miranda & Parrini, 2015).

The classic literature considers food webs to be discrete rigid objects (Coulson *et al.*, 2004), in which an interaction between two species (e.g., a predator and its prey) is either present (with a certain weight) or absent; once an interaction is observed between individuals of two species, at a particular point in time and space, that interaction is extended uniformly at the species level. However, there is sound empirical and theoretical evidence of stochastic variability in the structure of food webs, depending on biotic and abiotic factors (Mullon *et al.*, 2009; Poisot *et al.*, 2015). This motivates the distinction between a food web's backbone—its most statistically persistent structure—and its fine wiring, which is more sensitive to contingent ecological factors or stochastic noise (Grady *et al.*, 2012; Bellingeri & Bodini, 2015). A robust ordering of species based on their ecological relevance should not be too sensitive on the fine wiring of a food web (Livi *et al.*, 2011).

In another study (Dalla Riva & Stouffer, 2015), we introduced the random

4

dot-product graph model (RDPGs, see Tang *et al.* (2013)) for food webs and we showed that it offers an efficient approach to identifying food webs' backbones. The RDPG model receives a classic binary description of a food web (i.e., its adjacency matrix) and estimates the position of the species in a continuous, metric space of *abstract functional traits* determining the species' interaction probabilities. Each species in a food web is associated with a pair of functional trait vectors: the vulnerability functional trait vector, which describes a species as prey, and the foraging functional trait vector, which describes a species as a predator. The probability of observing an interaction from species $i$ to species $j$ (e.g., $j$ feeding on $i$) is given by the dot product of the vulnerability functional traits of $i$ and the foraging functional traits of $j$.

Here, we show how the abstract functional trait space, estimated by the RDPG model, offers a unified framework in which to assess species' importance, uniqueness and diversity. We propose three measures, relying only on topological food-web data, which can serve as proxies for measures based on phenotypic data.

In the paper, we assess the species' relative importance from their position in the estimated abstract functional trait space for the Serengeti National Park's food web (Baskerville *et al.*, 2011), a highly resolved data set for which a comprehensive dated phylogeny is available. Building on the existing measures of trophic similarity (Yodzis & Winemiller, 1999; Luczkovich *et al.*, 2003; Jordán *et al.*, 2009), we define the *uniqueness* of a species' role within

a food web as its isolation (i.e., the average distance to all the other species) in the abstract functional traits space estimated by the RDPG model. To measure the species' relative importance in a food web, we define a species' *strain* as the effect that removing that species has on the estimated abstract functional trait space: for each focal species in the food web we measure the total distance between the remaining species' positions in the abstract functional trait space before and after the removal of the focal species. The strain of a species captures a global effect at the whole food-web scale, rather than a local property of its interactions patterns. Borrowing from the functional diversity literature, we estimate the functional diversity of a food web as the volume of the convex hull enclosing all the species' abstract functional traits. Accordingly, we define the contribution of a species to the functional diversity of a food web as the loss in diversity caused by the removal of that species. Focussing on the vulnerability, on the foraging or both the vulnerability and foraging abstract functional traits, we can assess a species' relevance as prey, as a predator or as both predator and prey. We distinguish amog the species' strain, uniqueness, and contribution to the functional diversity as prey (*outward* strain, uniqueness, and contribution to the functional diversity), as a predator (*inward* strain, uniqueness, and contribution to the functional diversity) or as both a predator and prey (*total* strain, uniqueness, and contribution to the functional diversity).

We correlate these novel measures among each other as well as with six classic network centrality measures, and we explore their distribution among

6

the clades present in the food web. In particular, we test whether the distribution of ecological relevance among the tips of the Serengeti National Park food web's phylogeny is compatible with an evolutionary model of traits evolution. Finally, we examine the hypothesis that the species' ecological relevance and evolutionary distinctiveness are indeed correlated.

## 2    Data and methods

**Food webs and phylogenies**   We focus our analysis on the Serengeti National Park food web as published by Baskerville *et al.* (2011). It is a large food web with 129 plants, 23 herbivores and 9 carnivores. Most of the links (507 out of 590) are between herbivores and plants. The food web is less densely connected than other food webs, which is a consequence of the higher than the usual taxonomic resolution of plants. In the Supplementary Material, to support the general applicability of our framework, we summarise the results for other three large food webs: an independent compilation of the Serengeti National Park food web (de Visser *et al.*, 2011) and two marine food webs, one for the Caribbean Sea (Opitz, 1996) and one for the Antarctic Weddell Sea (Jennings *et al.*, 2002). The dated phylogenetic tree (available on-line) for the species in the two Serengeti food webs has been compiled from molecular data by De Zwaan *et al.* (Dalla Riva & Stouffer, 2015) (see the Supplementary Material for more information). We approximated the real phylogeny for the other webs via a cladogram obtained from

the species' taxonomy as given by the Integrated Taxonomic Information System (http://www.itis.gov; information retrieved on 11 November 2014).

## 2.1 Ecological and Evolutionary relevance

**Random dot product graphs** Let $A$ be a food web including $S$ species. Given a dimension $d$, under the RDPG model, each species $i$ in $A$ is associated to a pair of abstract functional trait vectors of dimension $d$. The two vectors are the *rank-d vulnerability* traits (or outward traits), which describes the species as a prey or a resource, and the *rank-d foraging* traits (or inward traits), which describes the species as a predator or a consumer. The probability of observing an interaction from species $i$ to species $j$ is given by the dot product of the out traits of $i$ and the in traits of $j$. For an observed food web $A$, the species'traits are estimated through a scaled, truncated, singular value decomposition of the adjacency matrix of $A$ (Dalla Riva & Stouffer, 2015) (see the Supplementary Material for more details). The task of identifying a suitable range for the model's dimension is akin to a dimensionality reduction problem, discussed for the Principal Component Analysis scenario in Jolliffe (2002). This can be solved through the examination of the sequence of singular values of the adjacency matrix of $A$. Here, we rely on the results of Dalla Riva & Stouffer (2015).

**Strain** The strain of species $i$ measures the effect that the removal of $i$ from the food web has on the remaining species' abstract functional traits,

as estimated from the RDPG model. The effect is measured for species either as predators, as prey or as both. Let $X(A)$ be the matrix of either the inward, outward or total rank-$d$ abstract functional traits (the last one being the matrixin which the first $d$ columns are given by the inward traits and the next $d$ columns are given by the outward traits). We use $X(A)^{r(i)}$ to denote the matrix of the (inward, outward or total) functional traits for all the species in the food web $A$ excpet $i$ (i.e., the matrix obtained by $X(A)$ removing the $i$th row). The matrix $X\left(A^{d(i)}\right)$ is the matrix of traits for the species in the food web $A$ that has been computed after having dropped the species $i$ from the food web with all its interactions (i.e., the matrix of traits computed after removing the $i$th row and column from $A$). Both $X(A)^{r(i)}$ and $X\left(A^{d(i)}\right)$ are matrices with $S-1$ species (each species in $A$ but $i$) and $d$ columns (the model's dimension). In $X(A)^{r(i)}$, the functional traits are computed before removing $i$, in $X\left(A^{d(i)}\right)$ they are computed after the removal event. The (inward, outward or total) rank-$d$ strain of the species $i$ is the Procrustes distance between $X(A)^{r(i)}$ and $X\left(A^{d(i)}\right)$.

We are interested in the use of RDPG-based measures to value species in a way that is robust to model parameters. Therefore, we tested whether the species' ordering by strain was sensitive to the choice of model dimensionality and performed a pairwise correlation test for each pair of dimensions in the range $[1,\ldots,15]$. Notice that the latter upper range limit is much greater than the suitable upper bound for model dimensionality found in Dalla Riva & Stouffer (2015).

**Uniqueness**  We define the rank-$d$ *uniqueness* of a species in a food web, either as a predator, prey or both, as the average of its Euclidean distance to every other species in the $d$-dimensional (inward, outward or total) abstract functional trait space.

**Diversity**  The volume of the convex hull of a community of species in the traits space is a proxy for its functional diversity (Villéger *et al.*, 2008). Here, we define the contribution of species $i$ to a food web's abstract functional diversity as the difference in volume between the convex hull of the species traits, in the (inward, outward or total) abstract functional space, before and after species $i$ is removed (i.e, the difference between the volume of the convex hull of $X(A)$ and $X(A)^{r(i)}$).

**Keystone centralities**  We assessed the keystone centrality of a species $i$ in a food web $A$ by using six different (topological) network measures following Estrada (2007): degree centrality, betweenness centrality (Brandes, 2001), closeness centrality (Freeman, 1979), eigenvector centrality (Bonacich & Lloyd, 2001), information centrality (Stephenson & Zelen, 1989), subgraph centrality (Estrada & Rodriguez-Velazquez, 2005). All the measures we introduce and the six examined by Estrada (2007) are computable for unweighted food webs (weighted extensions are definable, but we do not address them here). More details about the above theoretical measures can be found in (Jordán *et al.*, 2009). We chose these measures as their evaluation does not rely on morphological trait data nor on interaction weights.

**Phylogenetic diversity**    Phylogenetic diversity (Hartmann & Steel, 2007) offers an alternative way to evaluate the diversity of a community of species. The phylogenetic diversity of an evolutionary tree is the total sum of branch lengths in that phylogeny. This concept has been applied in the prioritisation of species for conservation purposes (Faith, 1992; Mace *et al.*, 2003). We each estimated species' evolutionary distinctiveness by measuring its fair proportion value (Isaac *et al.*, 2007), equal splits value (Redding & Mooers, 2006) and the length of the terminal phylogenetic branch leading to that species, following Faye *et al.* (2015). The fair proportion and equal split scores attempt to apportion the total evolutionary history of a phylogeny among the extant species. These three measure are known to be positively correlated.

More details on the implementation of these diversity measures can be found in the Supplementary Material.

## 2.2   Comparative analysis

Because of their shared evolutionary histories, we would expect to observe more similar traits for more closely related species, a concept recognised at least since the work of Felsenstein (1985). The evolutionary dependency of species arises the statical issue of controlling and correcting for the phylogenetic covariation structure of the observed species' traits. To select the appropriate evolutionary model, we compute the relative Akaike information criterion corrected for finite sample size (AICc, see Hurvich & Tsai (1989)) of four distinct models (Garamszegi & Mundry, 2014). We consider an uncor-

related null model, a Brownian motion model (Felsenstein, 1985), a Brownian motion with attraction toward an optimum (Ornstein–Uhlenbeck) model (Hansen, 1997) and a model with early eurst of differentiation (Harmon *et al.*, 2010). We test for linear correlations among the (inward, outward and total) novel measures (of strain, uniqueness, and contribution to functional diversity) and among (inward, outward and total) strain and uniqueness and the six keystone centralities. To do so, we use generalised least square regression techniques, either controlling for the appropriate phylogenetic covariance structure associated with the evolution model with the highest AICc weight, or under the null evolutionary model.

# 3   Results

We computed the species strain for $d \in [1, \ldots, 15]$ (Fig. 1 a). In (Dalla Riva & Stouffer, 2015) we estimated a suitable model dimension $d = 3$ for the Serengeti National Park food web. The species' strain (model dimension $d = 3$) has an average value of 0.032 and a variance of 0.017; a small number of species have a high strain (Fig. 1b). The three species with the highest strain are all in the Afrotheria clade (and represent the totality of that clade in the food web). These are *Procavia capensis* (rock hyrax, strain = 1.316), *Heterohyrax brucei* (yellow-spotted rock hyrax, strain = 0.884) and *Loxodonta africana* (the African bush elephant, strain = 0.317). The ordering of species based on their strain is robust to the choice of model dimension,

in the range $d \in [1, \ldots, 15]$ (Fig. 1 c). Every pairwise ordering correlation in the analysed interval is significant at $p < 0.01$ (this result is also confirmed by the analysis of the independent assembly of the Serengeti National Park food XXX web by de Visser *et al.* (2011); see the Supplementary Material).

The Afrotheria are also characterized by high uniqueness in terms of their mean distance to the other species in the abstract functional trait space. The observation can be extended the species' phylogeny, noticing that the two measures are non-uniformly distributed among the tips of the phylogenetic tree (Fig. 2 a). There is also support for an Ornstein–Uhlenbeck (Brownian motion with attraction toward an optimum) model of evolution for both strain and uniqueness (Fig. 2 b). The correlation between species' (outward and total) strain and uniqueness is significant at $p < 0.01$, while the species' inward strain and uniqueness are not consistently correlated for $d > 4$ (Fig. 3 a). The computation of the species' contribution to the abstract functional diversity for $d > 4$ (species as both predators and prey) and $d > 7$ (species as either predators or prey) was not possible because of software limitations. However, in the feasible range of $d$, the species' total strain is significantly positively correlated with both the species' total uniqueness and their contribution to the total functional diversity (Fig. 3 b). The correlations for the partial (either inward or outward) measures are not consistently significant and depend on the measure considered.

The strain and mean distance of species in the Serengeti National Park are, in general, positively correlated with the common keystone centralities

13

(Fig. 4). The significance and strength of the correlations depend on the particular combination of the centrality measure, the model dimension and the functional space considered (either inward, outward or total). We observed the most consistent correlations with the Betweenness, Subgraph and Degree centralities. The correlation results are qualitatively confirmed by performing the regression analysis either accounting for or ignoring the species' phylogenetic covariance structure. Hence the correlations hold whether or not we consider the phylogenetic structure of the food web. This general agreement between our novel measures and the common graph-theoretical indices used to identify keystone species supports the applicability of the RDPG model for food webs.

Although there are species with both high phylogenetic distinctiveness and high strain or uniqueness (Tab. 1), we did not detect any significant linear correlation between the species' evolutionary and ecological relevance measures.

## 4 Discussion

For each species in the food web, we researched its position in the (inwad, outward and total) abstract functional trait space for $d \in [1, \ldots, 15]$ and computed three measures of ecological relevance (strain, uniqueness and contribution to functional diversity). We verified that species' ordering based on the measures we introduced is robust to the choice of the model's dimension

*d.* The RDPG model for food webs allows us to distinguish between the low-dimensional, stochastic backbone of a food web and its fine wiring. The stochastic backbone is robust to food web variability and to misspecifications of the food web structure, such as a missed observation of an interaction or an erroneous recording. Being based on the estimated (low-dimensional) structural food-web backbone, the measures we introduced are themselves robust to the variability of complex food webs. Other classic measures of trophic uniqueness (Yodzis & Winemiller, 1999; Luczkovich *et al.*, 2003; Jordán *et al.*, 2009) do not make this distinction.

The RDPG model allows us to estimate the abstract functional diversity of a food web by relying solely on topological data. It remains to be ascertained whether there is a correspondence between the classic morphological functional diversity and our novel concept of abstract functional diversity. If verified, the abstract functional diversity may serve to estimate the (classic) functional diversity without the burden of identifying suitable phenotypic traits with a functional role across all the species in a food web—an ambitious task, given species' heterogeneity. Our results appear to point toward a positive answer. The range of suitable abstract space dimensions estimated under the RDPG model (not higher than five, see (Dalla Riva & Stouffer, 2015)), is in good accordance with the number of (classic) functional traits that Maire *et al.* (2015) estimated for an optimal (classic) functional diversity analysis.

We showed that a species' abstract functional trait uniqueness is posi-

15

tively correlated with its classic centrality in the Serengeti National Park food web. The result was also confirmed for the Weddell Sea food web (Jennings *et al.*, 2002), the Caribbean Sea food web (Opitz, 1996) and the independent compilation of the Serengeti National Park food web by de Visser *et al.* (2011) (see the Supplementary Material for details). A positive correlation between classic functional uniqueness, *sensu* Yodzis & Winemiller (1999), and the degree centrality—the number of trophic interactions—has already been established by Petchey *et al.* (2008). The result is even more interesting if read in comparison with the negative correlation found by Lai *et al.* (2012) between the classic centralities and the trophic uniqueness of a species *sensu* Luczkovich *et al.* (2003) and Jordán *et al.* (2009). Further comparative analyses are therefore needed to explain this difference and explore the relationship between the abstract functional uniqueness of a species and its trophic uniqueness as otherwise defined. Similarly, a species' strain is positively correlated with its classic centrality and that a species' uniqueness predicts its strain. In addition, both strain and uniqueness are are positively correlated with a species' contribution to the abstract functional diversity of the food web. Petchey *et al.* (2008) have shown that trophically unique species are exposed to a higher risk of secondary extinction, highlighting their fragility. Conversely, the correlation between uniqueness and strain supports the notion that food webs are particularly fragile to the extinction of functionally unique species, as already suggested by O'Gorman *et al.* (2010).

The ecological relevance—strain and uniqueness—of the species in the

Serengeti food web is not uniformly distributed across the phylogeny (in fact, it is compatible with the distribution we would expect under a Ornstein-Uhlenbeck model of evolution). We did not detect a significant correlation between the species' ecological relevance and their evolutionary distinctiveness. However, a small number of species have both high ecological relevance and high evolutionary distinctiveness. This is the case in the Afrotheria clade (i.e., the African elephants and two hyrax species). The peculiarity of the Afrotheria clade has already been suggested by Baskerville *et al.* (2011) on the basis of the particularity of the hyrax's trophic role. Our results confirms the importance of considering both ecological and evolutionary factors in the evaluation of species for conservation purposes.

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# Figure 1

The distribution of species' strain in the Serengeti National Park food web (Baskerville *et al.*, 2011). (a) The line trace strain of each species ($\texttt{Log}_{10}$ transformed) along an increasing model dimension ($d \in [1, \ldots, 15]$). The strain has been computed for species as both predators and prey. (b) A cross-section of (a) for $d = 3$ (corresponding to the suitable model dimension we identified in (Dalla Riva & Stouffer, 2015)). (c) Pearson product-moment correlation coefficients for the species ordering induced by the species' total strain across the model dimensions $d \in [1, \ldots, 15]$. The ordering is robust to the choice of the model dimension $d$: the Pearson's $r$ is consistently above 0.5 (and all the pairwise correlations are significant at $p < 0.01$).
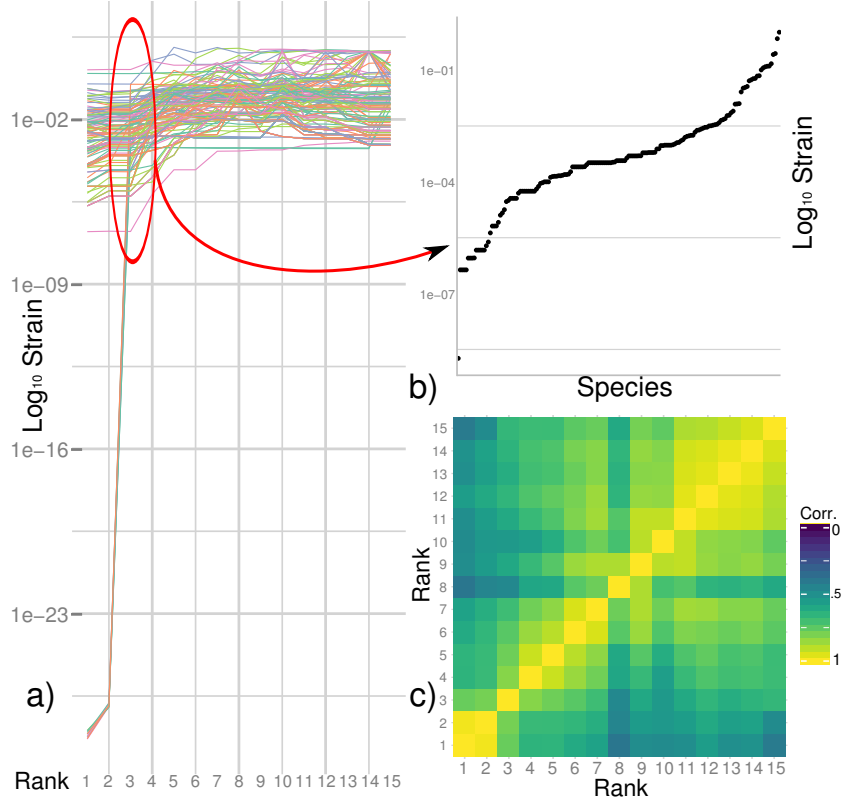


24

# Figure 2

(a) Distribution of rank-3 species' strain and uniqueness in the phylogeny (lighter yellow for lower values; darker blue for higher values) for species as both predators and prey (all). The silhouettes (from phylopic.org) mark the corresponding clades: Afrotheria (hyraxes and elephants) are the species with the highest strain and uniqueness. (b) Akaike Information Criterion (corrected for sample size) weights for four models of species' (inward, outward and total) strain and uniqueness evolution: uncorrelated, Z; Brownian motion, B (Felsenstein, 1985); Ornstein-Uhlenbeck, OU (Hansen, 1997); Early Burst, E (Harmon *et al.*, 2010). The data consistently supports an OU model, except for the low-dimension strain evolution, in which there is also good support for the B model.
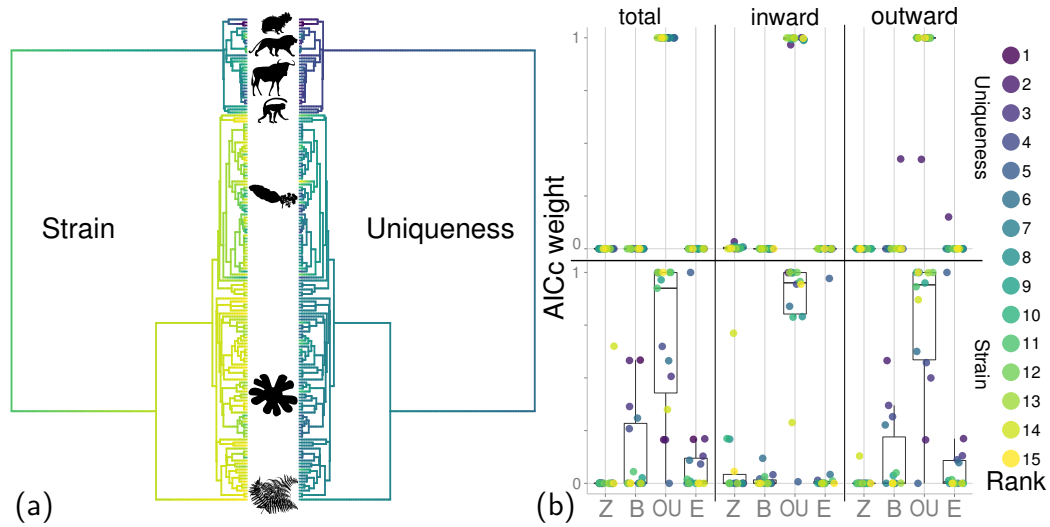
# Figure 3

(a) There is a significant correlation between a species' uniqueness and strain for the species as prey (outward) and as predators and prey (total). For model dimensions $d > 3$, the correlation is not consistently significant for the species as a predator (inward). (b) There is a significant correlation between the species' (inward and total) strain and uniqueness and the species' contribution to the functional diversity (the loss of abstract functional diversity after the removal of a species). The correlation between a species' outward strain and contribution to functional diversity is not significant for low dimensions. The dashed red lines correspond to $p = 0.05$.
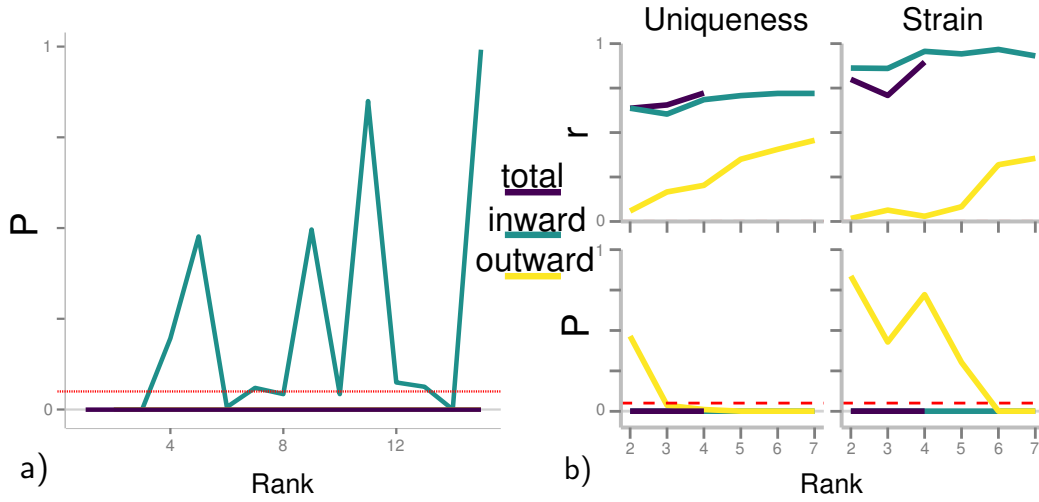
# Figure 4

Correlation between a species' strain and uniqueness (as a predator, inward; prey, outward; predator and prey, total) and the species' betweenness (BC), closeness (CC), degree (DC), eigenvector (EC), information (IC), and subgraph (SC) centralities. Strengths and significances depend on the combination of the centrality index (the correlation is significant for most centralities except EC and IC), functional space (the correlation with the outward strain and uniqueness is weak) and model dimension (the correlation is stronger for low $d$). The dashed red lines correspond to $r = 0$ and $p = 0.05$.
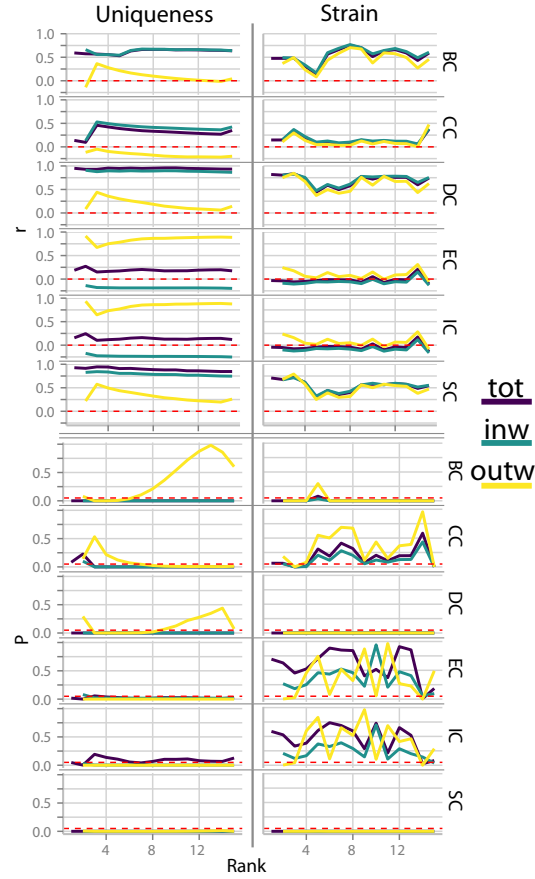
## Table 1

The 10 species in the Serengeti National Park food web (Baskerville *et al.*, 2011) with the highest strain (as both predators and prey) and their ordering based on ecological uniqueness (as both predators and prey), contribution to functional diversity (diversity, as both predators and prey) and equal splits (a measure of evolutionary distinctiveness). Strain, uniqueness and contribution to functional diversity are positively correlated. However, although there are species (e.g., the Afrotheria clade) with a high score in all four measures, in general, there is no significant linear correlation between ecological relevance and evolutionary distinctiveness.

| Species | Strain | Uniqueness | Diversity | Equal Splits |
|---|---|---|---|---|
| *Procavia capensis* | 1.32 | 1 | 3 | 6.5 |
| *Heterohyrax brucei* | 0.88 | 2 | 1 | 6.5 |
| *Loxodonta africana* | 0.32 | 7 | 6 | 2 |
| *Panthera pardus* | 0.31 | 3 | 10 | 148.5 |
| *Panthera leo* | 0.18 | 6 | 4 | 148.5 |
| *Eudorcas thomsonii* | 0.17 | 8 | 19 | 150.5 |
| *Nanger granti* | 0.16 | 5 | 13 | 150.5 |
| *Connochaetes taurinus* | 0.15 | 4 | 14 | 138 |
| *Madoqua kirkii* | 0.15 | 11 | 2 | 100 |
| *Aepyceros melampus* | 0.12 | 13 | 0 | 100 |