On the variability of Species Abundance Distributions with trophic guild and community structure

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Abstract

Species Abundance Distributions (SADs) are one of the most studied properties of ecological communities, and their variability has been studied mostly in the context of horizontal communities, i.e. sets of species from a particular trophic guild. However, virtually all ecological communities encompass several trophic guilds, and the trophic interactions between them are key for explaining the persistence and abundance of individual species. Here I ask whether trophic interactions are also important in shaping Species Abundance Distributions of the different guilds of a community. I analyze the variation in SAD shape across trophic guilds in model and empirical communities. For that, I use a theoretical model that allows tracking the variations in abundances across trophic levels. The relationship between SAD shape and (1) trophic level, and (2) degree of predator specialization is analyzed using mixed-effect models. I combine this approach with an analysis of 4676 empirical datasets spanning terrestrial, marine and freshwater habitats, for which the variation in SAD shape is related to (1) trophic guild, and (2) habitat type. The evenness of model SADs is positively correlated to the trophic level of the guild considered, and also to the number of prey species per predator. These findings are confirmed by the empirical data: there is a significant relationship between SAD evenness and trophic guild, whereby primary producers display the most uneven SADs and pure carnivores the most even ones. Furthermore, regardless of trophic guild, SADs from marine habitats are the most even ones, with terrestrial SADs being the most uneven.

Keywords: Species Abundance Distribution, trophic level, trophic guild, community structure, species generalism, evenness, skewness.

Introduction

Most species, in any ecological community, are comparatively rare, and only a few of them are very abundant. This empirical observation is one of the few true universal laws in ecology, a pattern that is observed in all kinds of communities and guilds, from small arthropods (Basset and Kitching 1991) to tropical trees (He et al. 1997). The Species Abundance Distribution (SAD) describes precisely this variation in species abundances within a given assemblage. A wide variety of models have been proposed to characterize and explain the typical hollow curve of empirical SADs (see McGill et al. [2007] for a review). Importantly, the mechanisms that generate 1) the universal hollow SAD shape and 2) its variability across guilds or habitats, are still under debate, with proponents arguing over whether the hollow curve is a result of ecological mechanisms of selection (e.g. niche partitioning in its various incarnations, such as in Sugihara [1980]), the spatial distribution of individuals (McGill and Collins 2003), or a consequence of statistical or neutral constraints of the system (e.g. Locey and White [2013]).

In the debates on the mechanisms that shape SADs, virtually all theories and hypothesis that relate SAD shape to ecological processes at the local scale refer to horizontal communities, i.e. communities of a single trophic level. Thus, these theories emphasize the role of either neutral dispersal and drift (Hubbell 2001) or horizontal selection (Vellend 2016). But natural communities form a complex network of species linked by different types of biotic interactions both horizontally (within a given trophic guild) or vertically (across trophic guilds, Fig. 1). The influence of the interaction topology of communities on local SAD patterns has, to my knowledge, never been explored systematically.

Different lines of evidence point to the influence of vertical biotic interactions on community patterns such as SAD. First, several studies have demonstrated the variation on fundamental

properties, such as biomass or species richness, with trophic level. Richness pyramids have been shown to be widespread in empirical food webs, particularly in marine habitats (Turney and Buddle 2016). Another distribution, that of biomass across trophic guilds, also has a long history in ecology, starting with the seminal studies by Lindeman (1942) or Odum (1957). In a recent study, McCauley et al. (2018) analyzed the empirical prevalence of top-heavy distributions, and reviewed the mechanisms that can give rise to them. Focusing on the relationship between two adjacent trophic levels, Hatton et al. (2015) showed that the biomass of empirical guilds of herbivores and their associated predators scales generally with a power-law of exponent 3/4. They also showed that, in their data, the relationship between mean body mass and community biomass is non-significant for most of the functional groups they studied. As such, if body mass varies in a similar fashion in different trophic levels, the scaling in biomass should also be reflected in a scaling on number of individuals at each trophic level, as foretold by Ramón Margalef (1980).

Variability in species-level traits associated with population size may also drive variations in SAD shape across guilds. Niche breadth is one of such traits (Seagle and McCracken 1986). All else being equal, variability in niche breadth within a given assemblage can be expected to correlate with variability in species abundances, such that a high variability in niche breadth will drive a high heterogeneity in species abundances. It is unclear whether there is a general relationship between niche breadth and trophic position, or if, on the other hand, it varies more or less evenly for all trophic guilds across communities. Nevertheless, for any scale of variation, differences in niche breadth, i.e. on the degree of predator specialization, may indicate differences in SAD shape.

Combining these different lines of evidence and qualitative expectations, I propose the hypothesis that, despite SAD variability within a given trophic guild, a general relationship between SAD shape and trophic guild is likely to exist. In particular, and notwithstanding the inverted biomass pyramids explored by McCauley et al. (2018), if the abundance scaling proposed by Hatton et al.

(2015) holds generally, I hypothesize that SADs will display greater evenness as trophic level increases, due to 1) fewer number of total individuals, and 2) a higher probability of extinction of rare species from higher trophic levels (Duffy 2003). Furthermore, this relationship will be mediated by the structural patterns of the community network. For example, guilds or communities comprised of mostly generalist species will tend to display more even SAD shapes due to a higher similarity in resource use.

In this study I derive theoretical expectations for this hypothesis based on allometric relationships first proposed by Cohen et al. (2003). In their findings, the number of individuals of a given species is dependent on several factors, relating species-level traits, such as average body size, with network structural patterns such as the degree of prey and consumer specialization. Here I evaluate, using their framework, whether SAD shape varies consistently with trophic level and the degree of trophic specialization of species in the community. Finally, I compare the theoretical expectations with an analysis of empirical SAD datasets for different habitats and trophic guilds.

METHODS

The relationship between SAD properties and trophic level: what does theory predict?

Analyses of species abundance distributions are based, on their first stage, on the grouping of species that are supposed to share certain properties of interest, such as taxonomic relatedness, spatial location or resource use (Fauth et al. 1996). In this study, I focus on the role of the different groups in the local community, and the division in trophic levels is a straightforward and general way to divide species according to their network role. While trophic levels in nature are rarely discrete, division in discrete trophic levels or guilds is a standard procedure to study properties and feedbacks between groups of interacting species (e.g. Hatton et al. [2015], trophic level-size).

Intuitively, the variability in number of individuals between species of a given trophic level will depend on inter-specific variation in both species-level traits and resource use. Assuming, as a working hypothesis, that reproductive strategies, body size and other life-history traits are relatively homogeneous within the species of a given trophic level, it can hypothesized that the degree of resource overlap between the species will play an important role in determining their variation in abundance. In particular, I expect that the degree of specialization within a trophic level will be, all else being equal, positively related to the degree of heterogeneity in species abundances.

This intuitive, qualitative hypothesis can be more precisely formulated by combining network descriptors, body size and numerical abundance patterns, as first proposed by Cohen et al. (2003). These authors derive the resource productivity Π_j available to species *j* as a function of the abundance, body mass and vulnerability of its resource species:

$$\Pi_j = \sum_{i \in R_j} \frac{N_i \times M_i^{\alpha}}{V_i} \quad \text{eq. 1}$$

where R_j is the set of resource species for species *j*, N_i the abundance of resource species *i*, M_i^{α} its metabolic rate, and V_j its vulnerability, i.e. its number of predators. The vulnerability of species belonging to a certain trophic level (assuming that omnivory is negligible) is a measure of the specialization of species from the upper trophic level. Furthermore, the number of individuals of a species, *N*, is a function of its average body mass and the productivity available to it:

$$N_j = \frac{\Pi_j}{M_j} \quad \text{eq. 2}$$

Therefore, with the derivation from Cohen et al. (2003), one can estimate the numerical abundances of species from a given trophic level by knowing their trophic links, average body mass, and the abundances and body masses of their prey.

Throughout the study, I simplified eq. 1 by setting the scaling coefficient to one to avoid further sources of error, as productivity is thought to vary across guilds (Carbone et al. 2007).

I applied eq. 1 to two instances of a well-resolved food web (Tuesday Lake datasets of 1984 and 1986, see Cohen et al. [2003] and references therein), generating expected numerical abundances for every non-basal species. For evaluating the goodness of fit of the expected abundances, I used a linear mixed-effects model in which the predicted abundances were modelled as a function of the observed abundances as a fixed effect and the sampling year as a random effect. Log-transformation of the expected and observed abundances reduced the range of the data and the potential heteroscedasticity of the residuals. The R package 'lme4' (Bates et al. 2015) was used to implement the model.

Metrics for comparing Species Abundance Distributions

Methodologically, the comparison of SADs is still an unresolved problem in community ecology: there is no standard method for comparing SAD shape of guilds with arbitrary numbers of species or individuals, with most comparisons being qualitative (McGill et al. 2007) or being made between relatively similar communities that don’t differ much in richness or size (e.g. samples from polluted and unpolluted habitats, Matthews and Whittaker [2015]). In order to assess the variability between SADs in a general way, robust metrics need to be developed that are independent of number of species and individuals, i.e. that reflect solely the variability in the shape of the distribution. In this

study, I assess the variability in SAD shape through two complementary metrics, that quantify the evenness and the skewness of the distribution.

Evenness is defined after the “Hill number” of species diversity, also known as the effective number of species (Tuomisto 2012). This evenness metric has a series of desirable properties, summarized in Smith and Wilson (1996). It is also conceptually similar to the variance of a distribution, but the evenness metric has the advantage of a clear ecological meaning. The skewness metric is simply a robust version of the third moment of a statistical distribution (Brys et al. 2004). Throughout this study, I apply these metrics to the log-transformed abundances of both the simulated and compiled data.

Other recent methods to compare SAD shapes include evaluating the alpha parameter of the recently developed gambin distribution (Matthews et al. 2014), or the normalization of rank-abundance curves (Saeedghalati et al. 2017). These developments are conceptually similar to rarefaction methods, in which the metrics of interest are estimated repeatedly from samples of the data. When the difference between the sample size and the size of the dataset is high (e.g. differences in abundances in the order of 10^3 individuals or more, as assessed in preliminary analyses), these methods break down, so I did not consider them for this study.

Variability of SAD shape with degree of specialization and body size gradient

The framework by Cohen et al. (2003) can be applied to predict how variations in community structure will be reflected in the numerical abundances of consumers, and ultimately, in the shape of the SADs of the different trophic levels. I generated model communities with varying levels of average vulnerability, and estimated the evenness and skewness of the SAD of each trophic level. In particular, I simulated model communities of 100 species divided in four discrete trophic levels,

assigning 35 species to the basal trophic level, and 25, 25 and 15 to the upper ones, simulating a slight richness pyramid (Turney and Buddle 2016). Three levels of vulnerability were applied to generate trophic links: a minimum level, in which each prey had a single predator, and two more levels in which the number of predators is, respectively, 0.25 and 0.5 of the species in the upper trophic level. Trophic links were generated randomly for every pair of guilds, and for each level of vulnerability I generated 1000 model communities. Equation 1 requires, aside from the vulnerability and body size of each species, the abundances of the basal trophic level to be specified beforehand. I draw basal abundances from a Weibull distribution with scale = 5.6 and shape = 0.9, derived as the average best fit from 382 terrestrial plants datasets. Variation in these parameters did not alter the qualitative trends observed.

I modelled the response of the SAD metrics to the vulnerability levels and trophic level with regression models. In particular, evenness values are bounded within the interval [0,1]. A visual inspection showed that the distribution of evenness in the simulated data is highly right-skewed. While the beta distribution is an obvious choice for modelling continuous bounded variables, it cannot in principle accommodate values of exactly 0 and 1. Therefore, I modelled evenness through a one-inflated beta distribution as implemented in the R package 'gamlss' (Rigby and Stasinopoulos 2005). In that framework, distributions of the response variable are parameterized by up to four parameters, and need not be from the exponential family. I included replicate (e.g. the 1000 realizations simulated for each vulnerability level) as a random factor. Skewness was less complex, and was modelled through a linear mixed effects model (Bates et al. 2015), with the same predictors as the evenness model. The regression models chosen for both metrics in the simulated and empirical datasets are summarized in table 1.

Global SAD patterns across habitats and trophic guilds

In order to evaluate whether the signal of the trophic guild in SAD shape is observed in empirical datasets, I collected publicly available datasets of species abundance distributions, mainly from previous compilations by Ulrich and Gotelli (2010) and Baldridge et al. (2016). I grouped these datasets by the finest taxonomic group available and recorded the predominant diet of the species within each group (autotroph, herbivore, detritivore, omnivore, carnivore), assuming as a working hypothesis that trophic level generally increases with meat content in the diet, so that e.g. obligate carnivores are assumed to be top predators. Very broad groups or those with high variability in their diet were discarded (as well as parasites/parasitoids, due to their small representativity compared to other groups). Overall, I analyzed a total of 4676 SADs, with 1374 being from marine habitats, 1516 freshwater, and 1786 terrestrial. The most represented taxonomic groups were Actinopterygii (with 1488 SADs), followed by Reptilia (567 SADs), terrestrial plants (382 SADs), Coleoptera (332 SADs) and Amphibia (264 SADs).

The variability of the evenness metric in the empirical datasets, as a function of trophic guild and habitat type, was modelled in the same fashion as that of the simulated data, using a one-inflated beta distribution. The taxonomic group of the guilds was included as a random covariate. The skewness metric of these datasets presented a complex, multimodal distribution with peaks at 0 and 1. I opted for simplifying the response by categorizing it into three response levels: “low skewness”, with values in the interval [-0.5,0.5], “high positive skewness” and “high negative skewness”, with positive and negative values higher than 0.5, respectively. I modelled this categorical response by fitting a multi-logistic regression with the same predictors as the evenness metric, using the 'ordinal' R package (Christensen 2015).

RESULTS

Numerical log-transformed abundances of the Tuesday Lake datasets obtained with Eq. 1 are significantly correlated with the observed log-transformed abundances (Fig. 2, r-squared = 0.77). The regression parameters are given in table 2. Applying eq. 1 to communities with varying levels of vulnerability shows that the evenness of the different SADs clearly increases with trophic level, while skewness remains approximately constant (Fig. 3, supplementary Figure 1). These visual results are confirmed by examining the coefficients from the regression models: evenness increases significantly with increasing average vulnerability in the modelled communities and with increasing trophic level (supplementary Table A1). Skewness is significantly related to vulnerability level, albeit with small coefficients and opposing trends, as it decreases with medium vulnerability and increases with high vulnerability (supplementary Table A2).

The broad analyses of the compiled empirical datasets support these theoretical expectations (Fig. 4 and supplementary Tables A3 and A4). Evenness in SADs increases with trophic level, although statistically significant estimates are observed only for carnivore datasets. The signal of habitat type is clearer, with significant decreases in evenness from marine to freshwater and, particularly, terrestrial habitats. Concerning the skewness of empirical guilds, most datasets presented low values of this metric, across all habitat types and trophic guilds (supplementary Figure 2). As reported by the multi-logistic regression, omnivores and carnivores are more likely to display lower skewness than other trophic guilds, while the effect of habitat is small and not significant.

DISCUSSION

The abundance of species within a guild is contingent on a wide variety of factors. Traditionally, analyses of Species Abundance Distributions have focused on either interactions with species of the same guild, as in, for example, the variety of niche partitioning models, or the effect of extrinsic factors such as pollution (Matthews and Whittaker 2015), habitat fragmentation (Gilbert et al. 2006) or management modes (Simons et al. 2017) . The role of interactions between trophic guilds on driving abundance variations has been much less studied, despite some acknowledgement of its potential importance (McGill et al. 2007).

In this study, I derived baseline predictions about the variability in SAD shape across trophic levels and degree of predator specialization in model communities. In accordance with the initial hypothesis, model SADs become significantly more even with increasing trophic level, and with increasing predator generalism (Fig. 3). Analysis of a compilation of abundance distributions from freshwater, marine and terrestrial habitats showed similar qualitative trends, with the added insight that marine habitats consistently show more even SAD shapes, for every trophic level (Fig. 4). The other metric used to quantify SAD shape, skewness, did not show clear trends either in the theoretical or in the empirical data, being close to zero in most cases. In the following, thus, I will focus the discussion on the variations in the evenness metric.

The framework by Cohen et al. (2003), from which eq. 1 is taken, is an elegant way of relating the trophic interactions between any two adjacent trophic levels with their net abundances. In it, species consume a certain fraction of the productivity available from the immediately lower trophic level. As no linkage rules were imposed in this first exploration, different realizations of the food web result in a form of random sampling of the prey species pool and, on average, variability in abundances decreases with trophic level as sample space decreases as well. This is apparent even

when vulnerability is set to one, i.e. all consumers are complete specialists (upper panels of Fig. 3). Increases in vulnerability (i.e. the sample space of consumers) quickly homogenize the abundances of consumer species. In this first approach, I did not consider correlations between trophic level and the other important element of eq. 1, average body size. However, I expect that linkage rules given by food web assembly models such as the niche model (Williams and Martinez 2000) would not vary the qualitative trends observed, as they generate trophic guilds by grouping species with preys of similar sizes.

It is important to note that abundances derived with eq. 1 reflect only bottom-up energy flows, and a fixed interaction topology. First, basal abundances are taken as given. In community dynamics, top-down processes may play an important role in determining abundances of lower trophic levels all the way down to primary producers, thus exerting complex feedbacks on the overall SAD variation. I also assumed that vulnerability in a given community did not vary with trophic level or show any kind of heterogeneity (e.g. nestedness). Furthermore, the modelled communities are closed systems, while the influence of transient species in SAD shapes is well known (Magurran and Henderson 2003). In that regard, movement capacity generally increases with trophic level, which implies that species in upper trophic levels are likely less restricted, obtaining resources from different source communities. Overall, these assumptions imply that the patterns obtained with this approach should be viewed as static and simplified representations of an otherwise dynamic complex structure.

Despite the simplicity of the theoretical model, the derived expectations are consistent with patterns obtained from empirical datasets. In the collected SADs, guilds higher in the trophic chain tended to have a more even SAD, regardless their habitat. Considering the biomass scaling across trophic levels proposed by Hatton et al. (2015), a reduction in net biomass in higher trophic levels coupled with a smaller set of resources to feed upon may drive higher evenness in species at the top of the food chain. This interpretation may be refined with further knowledge about general relationships

between trophic level and at least a) degree of omnivory, and b) generalism/specialization. Such relationships, if they exist, would be exceedingly difficult to evaluate, given the sheer variability in community structure and functioning across the globe.

Interestingly, for all trophic guilds analyzed, SADs of marine habitats are consistently more even than freshwater or terrestrial ones. If this pattern is driven by the degree of vulnerability in different habitats, it would suggest that, overall, marine habitats have, on average, more generalist species than freshwater and terrestrial ones. Other factors that have been hypothesized to drive SAD evenness are habitat complexity (Cotgreave and Harvey 1994) and productivity (Hurlbert 2004). SAD patterns may be driven indirectly by these factors through their influence on trophic interactions. The relationship between habitat complexity and trophic interactions, for example, is itself complex and context-dependent (e.g. Grabowski et al. [2008]). The data collected for this study, however, does not allow the testing of such relationships, as datasets come from vastly different communities with no information about their structure or productivity; targeted studies are needed for gathering data on SAD of different trophic levels across gradients of community productivity and complexity.

Body-size increments with trophic level are well established for water habitats (Layman et al. 2005; Arim et al. 2010; Romanuk et al. 2011), but terrestrial habitats present much more variability in body size within a given trophic level (think for instance about wolves and wolf spiders, which are both top predators); these variations in body size may represent different energetic pathways in the food web, and are likely to introduce further variability in species abundances (but see Cotgreave and Harvey [1994]). Furthermore, the terrestrial datasets compiled are biased towards species with small body size, particularly in carnivore datasets, most of which are from arachnids and reptiles. This bias reflects the overall absence of large carnivores in terrestrial habitats: whether the increase in evenness observed would hold in terrestrial communities with large carnivores remains an open

question. In order to test the robustness of the trophic level relationship with evenness, and its variability across habitat types, dedicated experimental observations of different community types are needed.

All the results presented here assume that trophic interactions are the main driver of variation in species abundances across guilds. In the theoretical results, energy flows from trophic interactions are the only ones considered, whereas the empirical datasets were grouped considering only the trophic guild of the species. This approximation is clearly a simplification of the complex networks of interactions observed in nature. The persistence and abundance of all species in a community is influenced by the whole set of interactions in which they engage, among other factors (Pocock et al. 2012; García-Callejas et al. 2018). However, the distribution and frequency of most non-trophic interactions in empirical communities is not known, so no hypothesis can be formulated at this point regarding their influence on local SADs. In communities in which non-trophic interactions are known, functional guilds can be differentiated by accounting for the set of all interactions in which they engage rather than just trophic ones (Sander et al. 2015; Kéfi et al. 2016); this functional grouping may further reduce intraguild functional variability and thus increase across-guild differences, better reflecting differences in SAD shape across guilds. On the other hand, there is virtually an unlimited number of functional guilds in nature, and establishing a general, cohesive, and manageable set of functional guilds that can be applied to group every potential community seems unfeasible for the time being. Therefore, grouping by trophic guild represents a compromise between generality (as every community can be divided in such manner) and intraguild versus across-guild variability.

The existence of an intrinsic variability in SAD shape across functional guilds has important consequences for both fundamental and applied community ecology. In theoretical models, the contributions of intraguild and interguild interactions need to be integrated in a general mechanistic

framework, in order for their relative importance to be estimated. This shift from intraguild, competitive interactions to multi-trophic, community scale thinking is mirrored by recent developments in other areas of community ecology. For example, modern coexistence theory, deeply rooted in the study of competitive outcomes (Chesson 2000), has been expanded to incorporate effects of predator-prey interactions (Chesson and Kuang 2008), and its connections to network theory have been recently put forward (Godoy et al. 2018). Empirical analyses of SADs would also benefit from incorporating information about the communities that harbor the guilds under study. In studies analyzing intraguild drivers of SAD shape, the community context of the study should be used to establish null expectations of interguild influence, for example, based on the trophic relationships with other guilds, as in eq. 1. If the guilds under study are not functionally homogeneous (e.g. taxonomic assemblages sensu Fauth et al. [1996]) deriving mechanistic explanations about SAD shape is usually not possible, due to interspecific differences in resource use, trophic position, etc. In such descriptive studies, therefore, the community context is unnecessary. Meta-analyses of Species Abundance Distributions have shown great disparity regarding the most appropriate statistical models for fitting SADs (Ulrich et al. 2010; Baldridge et al. 2016). If the results presented here hold, accounting for this null expectation may help clarify which statistical models are best suited to fit each set of data.

Conclusions

I have presented the first evidence of a novel pattern in the distribution of abundances across trophic guilds and habitat types. Analyses of both theoretical derivations and 4676 empirical SADs indicate that evenness in SAD shape consistently increases with increasing trophic level. In model communities, increasing vulnerability (number of predators for a given prey) also has a positive, and stronger, effect on SAD evenness. The habitat type (freshwater, marine or terrestrial) of the empirical datasets also has a significant influence on SAD shape, with marine habitats having the

most even SADs across all trophic guilds, and terrestrial habitats being the most uneven. The confirmation of this pattern would shed new light on both theoretical and applied analyses of Species Abundance Distributions, and would help in the integration of classic horizontal community ecology patterns in the context of multiple trophic levels and interaction types.

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Table 1: regression models for the SAD metrics in the simulated and empirical datasets. Syntax of the regression formulae follow the convention of the 'lme4' R package (Bates et al. 2015).

dataset type	response	response distribution	regression formula	type of regression model
empirical	evenness	one-inflated beta	trophic guild + habitat + (1| taxonomic group)	mixed effects
empirical	skewness	categorical (3 response levels)	trophic guild + habitat + (1| taxonomic group)	multi-logistic mixed effects over a bayesian framework (gaussian priors)
simulations	evenness	one-inflated beta	vulnerability + trophic level + (1| replicate)	mixed effects
simulations	skewness	gaussian	vulnerability + trophic level + (1| replicate)	linear mixed effects

table 2: estimated regression parameters for the abundances predicted with eq. 1. The estimated standard deviation for *dataset* is 0.417.

	estimate	std. error	t value	p-value
Intercept	1.584	0.746	2.124	< 0.05
log(N_observed)	0.935	0.074	12.656	< 0.05

Figure 1: A schematic ecological community with three disjoint trophic guilds. The areas within the ellipses represent the domain of horizontal community ecology that is the subject of most SAD studies, focusing on intra-guild interactions (dashed grey lines) and assuming that interactions with other guilds (full grey lines) are negligible. In this study, I focus on how interactions across guilds drive variations in SAD shape.

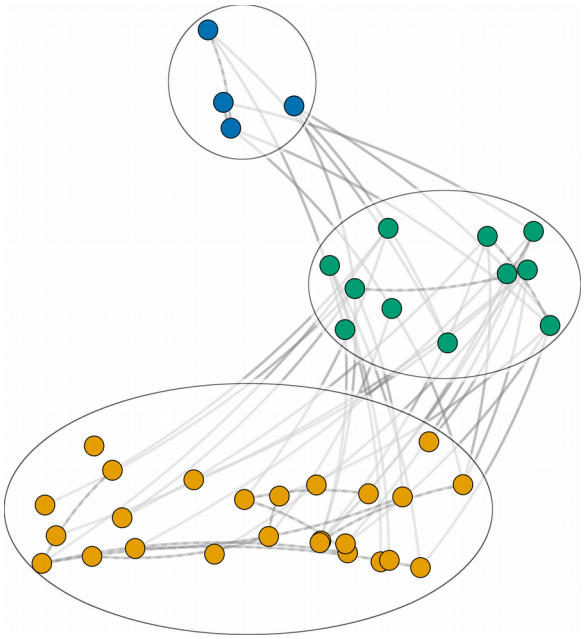

Figure 2: log-transformed abundances of the species present in the Tuesday Lake in 1984 and 1986, and values predicted by applying eq. 1.

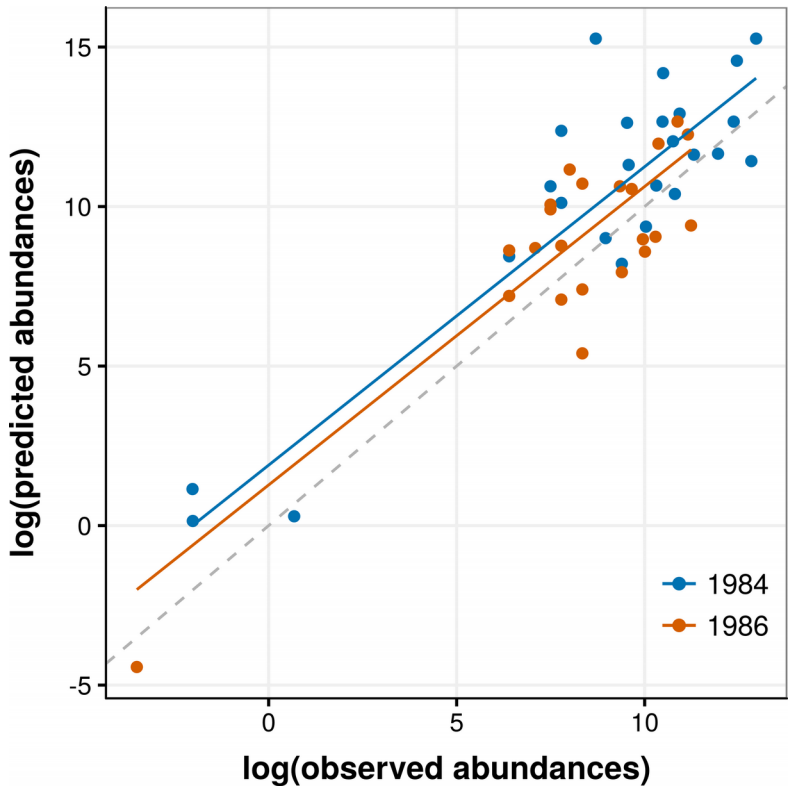

Figure 3: Evenness and skewness values for each combination of trophic level (horizontal axis) and vulnerability (vertical axis) in datasets simulated with eq. 1. In the panels, each point represent one of 1000 replicates. The colored point represents the centroid of the two-dimensional distribution, and the colored encircling represents the area containing 95% of the points.

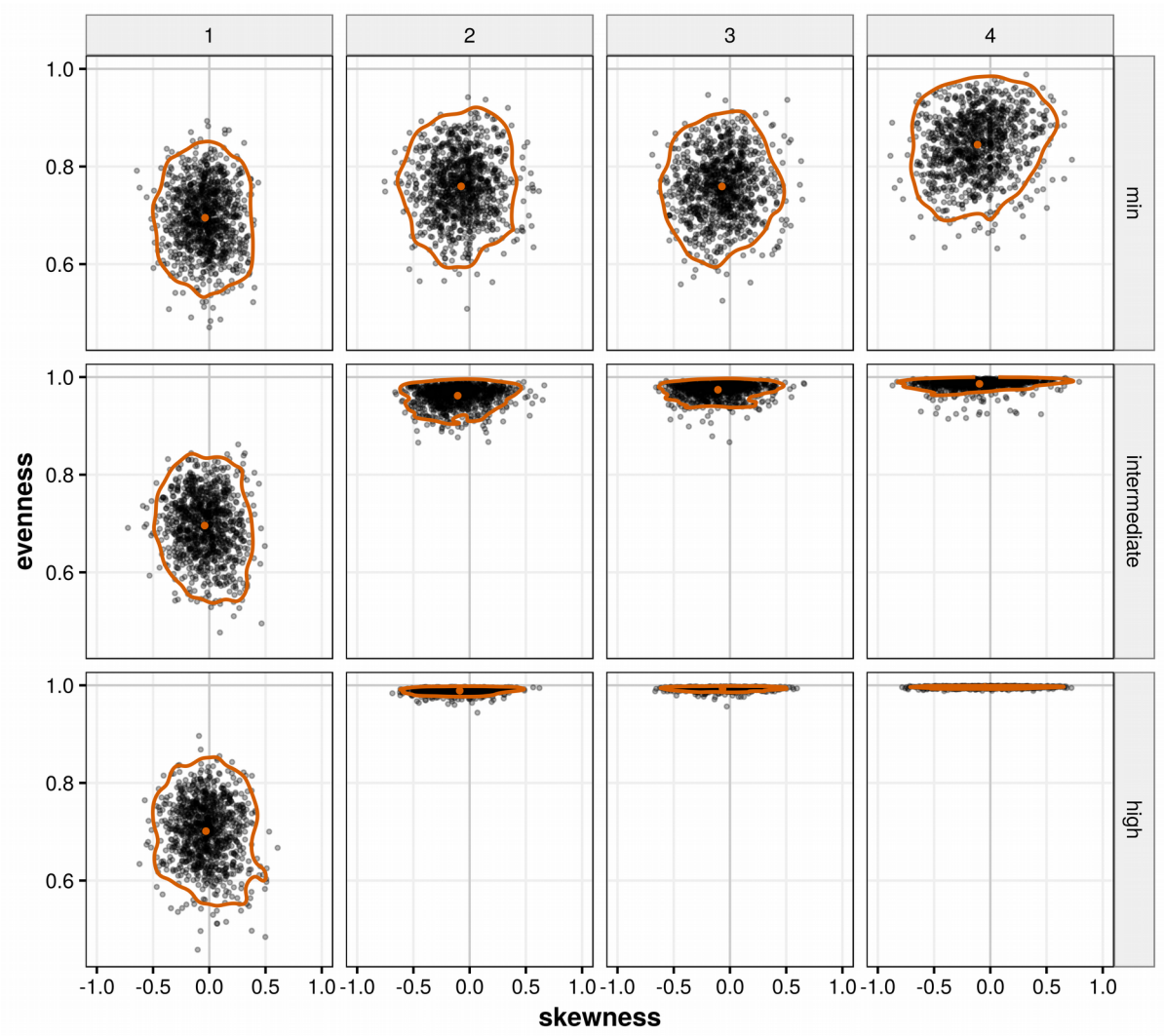
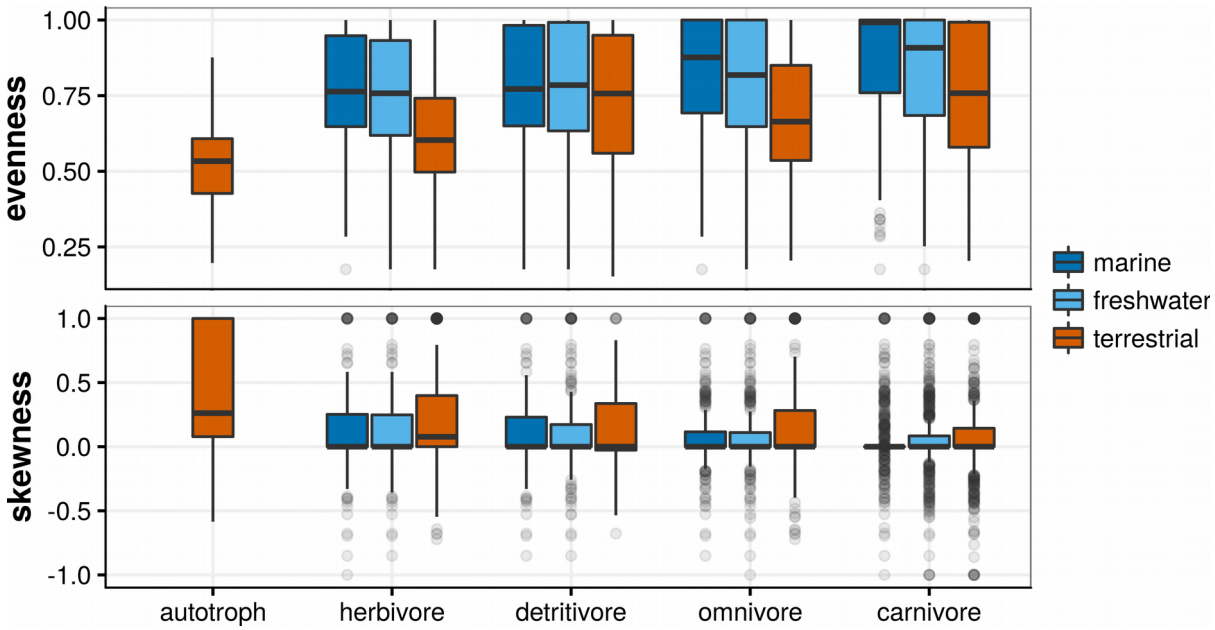
Figure 4: Evenness and skewness distribution for each habitat type and trophic guild in empirical datasets. The line inside the boxes represents the median values, lower and upper hinges correspond to the first and third quantiles and whiskers extend to the smallest/largest value no further than 1.5 times the inter-quartile range.