
OPTIMAL AMOUNT OF GUT CONTENT DATA REQUIRED TO PREDICT TROPHIC INTERACTIONS

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Abstract

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- 2) 2
- 3) 3
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Keywords gut content data · ADBM · food web accuracy · food web prediction

1 Alternate titles

- Predicting trophic interactions using incomplete gut content data
- Effect of the amount of gut content data on the accuracy and precision of food web prediction

2 Introduction

2.1 Why knowing trophic interactions is important?

Knowledge about the trophic interactions in a food web can be used to answer crucial ecological questions: Which species is a keystone species in a food web (Jordán 2009)? How would a food web respond if the top predators are removed (Knight et al. 2005)? Which species should be given priority when conservation efforts are implemented (McDonald-Madden et al. 2016)? How robust is a food web to extinctions (Dunne, Williams, and Martinez 2002)?

2.2 What are the methods for knowing interactions?

Species interactions can be directly or indirectly inferred from different types of methods such as gut content analysis (Peralta-Maraver, Lopez-Rodriguez, and de Figueroa 2017), stable isotope ratio analysis of tissues (Layman et al. 2007), experimentation (Warren 1989), DNA metabarcoding (Roslin and Majaneva 2016) and food web model (Gravel et al. 2013; Petchey et al. 2008; Williams and Martinez 2000).

2.3 What are the shortcomings of the methods mentioned above?

These food web methods have many shortcomings. Stable isotope ratio analysis of the organism’s tissue does not give a direct information of the diet of that organism but rather approximate trophic position of that species in the food web. Although mixing models can be used to determine what prey items are most likely fed upon by a predator but this results in uncertainty in the estimates (Kadoya, Osada, and Takimoto 2012; Crawford, McDonald, and Bearhop 2008). Experimentation (e.g. feeding trials) may create unrealistic conditions where a predator is confined in a small space with a potential “prey” and is effectively “forced” into eating it (citreqd). DNA metabarcoding could have many issues such as failure to relate OTUs to species,

or inability to distinguish secondary predation, i.e. the DNA signature of the prey consumed by the prey consumed by the primary item found in the predator’s gut.

2.4 Gut content analysis

One of the common method of knowing the trophic links is by gut content analysis of predator guts. Gut content data have been used to predict the diet of a predator in a food web (Eitzinger et al. 2018; O’NAMalley et al. 2017; Dixon et al. 2017; McClain-Counts, Demopoulos, and Ross 2017; Peralta-Maraver, Lopez-Rodriguez, and de Figueroa 2017). A single gut content data of a predator gives the information what the predator has consumed recently. The diet of that individual can be inferred from the items in the stomach.

2.5 Why inferring interactions is not easy?

As a food web can be quite complex with many species and trophic interactions (Williams and Martinez 2000; Berlow et al. 2009), inferring these trophic interactions with high accuracy and low uncertainty would require a large amount of food web data (citreqd). E.g. One would need to sample many individuals for gut content data, and processing these guts require a large amount of effort and time as well.

A single gut content of a predator provides information of the prey individuals that have been consumed by the predator in a small temporal and spatial scale. Therefore, sampling of gut content data needs to be taken place is a broad temporal and spatial scale. There is also a possibility that some of the information provided by these types of food web data are redundant i.e. taking into account any further food web data does not necessarily increase the food web prediction significantly. E.g. This can happen if the guts of two predator individuals give the same information about the prey the predator has consumed. This issue can be resolved by using a yield-effort curve which suggests when sampling of new predator guts can be stopped (Hernandez and Sukhdeo 2008).

2.6 Undersampled food web

When interactions are difficult to observe in a food web, this results in an undersampled food web i.e there are missing links in the food web. Limitations of resources and time can also lead to an undersampled food web because collecting and analysing gut content data is tedious and expensive task (citreqd). It is crucial to have well sampled food web because food web properties are highly sensitive to varying levels of sampling effort (Goldwasser and Roughgarden 1997). It is important to predict food web properties with high accuracy and high precision.

2.7 What is a food web model and how can it be used to compensate for undersampling?

When we have an undersampled food web, food web models can be used to predict which trophic interactions are feasible and which are not (Allesina, Alonso, and Pascual 2008; Cohen, Newman, and Steele 1985; Gravel et al. 2013; Petchey et al. 2008; Tamaddoni-Nezhad et al. 2013). Food web model are set of rules governed by ecological theory which defines trophic interactions in a food web. For example, Petchey et al. (2008) based on foraging traits allometrically scaled using body size data of species predicted trophic interactions where the model was parameterised using known presence and absence of trophic interactions. Another approach to infer missing links is literature research which involves assuming that a link will occur because another author described it in some other system, or for related predator/prey species, e.g. from the same genus or family (Gray et al. 2015; Cohen and Mulder 2014; Goldwasser and Roughgarden 1993) (citreqd). This typically results in a food web that will be very oversampled (citreqd).

2.8 Research question

How much gut content data is required when a food web model is used to predict trophic interactions? We are interested in maximizing the accuracy and precision of the predicted food web and simultaneously minimizing the amount of gut content data used, because we do not want to spend a lot of resources in sampling gut content data.

2.9 What we do in our study and how?

In this paper, we answer what is the optimum number of gut content data to predict a food web structure with high accuracy and high precision. Using allometric diet breadth model (ADBM), we predict trophic interactions from incomplete gut content data.

3 Materials and Methods

In the upcoming sections, we present the allometric diet breadth model (ADBM) and the gut content data used to infer trophic interactions. We also give a detailed account of using partial gut content data to parameterise the ADBM using approximate Bayesian computation (ABC). We assessed model predictions using true skill statistic and various structural food web properties for comparison across food webs.

3.1 Allometric Diet Breadth Model (ADBM)

The allometric diet breadth model (ADBM) is based on optimal foraging theory, specifically the contingency foraging model (MacArthur and Pianka 1966). The ADBM predicts the set of prey species a consumer should feed upon to maximise its rate of energy intake (Petchey et al. 2008). The foraging variables in the model: energy content of the resources, handling times of the prey, space clearance rate and prey densities are allometrically scaled to the body sizes of the species.

3.2 Broadstone Stream food web

Broadstone Stream (51° 05' N 0° 03' E; 120 m above sea-level) is a second-order tributary of the River Medway in south-east England. It is dominated by invertebrates as the acidity of the stream (pH 4.7-6.6) excludes fish. The stream consists of 25 common invertebrate species (Woodward, Speirs, and Hildrew 2005a). Among the predators, the three large species are *Cordulegaster boltonii* Donovan, *Sialis fuliginosa* Pict. and *Plectrocnemia conspersa* [Curtis] and the three small species are the larvae of the tanypod midges *Macropelopia nebulosa* [Meigen], *Trissopelopia longimana* [Staeger], and *Zavrelimyia barbatipes* [Kieffer]. Broadstone Stream food web is one of the most completely described food webs available for any system (Schmid-Araya et al. 2002; Hildrew 2009; Layer et al. 2010; and Woodward, Speirs, and Hildrew 2005b).

3.3 Celtic Sea food web

Description of Celtic Sea food web here

3.4 Food web construction

Presence and absence interactions of food web data can be aggregated in different ways (Gilljam et al. 2011). A common way of aggregating food web data is the taxonomic approach, where a species is defined as predating on another if at least one prey species individual was found in the gut of a predator species individual. Whereas in size-class food web, a feeding link was assigned if at least one prey item within a size class was found in the gut of a predator of another size class, irrespective of their taxonomy. In our study, we aggregate the food web on the basis of size class.

3.5 Inferring food web using partial gut content data

From a pool of gut content data, we draw a set of gut content data randomly. Then we used the rejection ABC to accept a parameter value which would have resulted in the minimum distance, where distance = 1 - True skill statistic and the true skill statistic was computed between the predators' diet predicted from the ADBM and the sampled gut content data. We repeated this process for n ($= 100$) number of times for every i number of guts, where i lies between 1 and total number of gut content data in the pool.

Input:

- Predators $P : P = \{p_1, p_2, \dots, p_k\}$
- A pool of gut content data $G : G = \{g_1, g_2, \dots, g_n\}$, where g_n is a one-dimensional matrix containing ones and zeros.

- A model prediction $model(\theta) : ADBM(\theta) = \{d_{p_1}, d_{p_1}, \dots, d_{p_k}\}$, where d_{p_k} is a one-dimensional diet matrix of predator k containing ones and zeros.
- A summary statistic $s(x) : s(x) \subseteq model(\theta)$
- A distance function $d(x_i, y) : d(x_i, y) = 1 - TSS(x_i, y)$
- An observed food web $Y : Y = \{d'_{p_1}, d'_{p_1}, \dots, d'_{p_k}\}$

Sampling:

for $i = 1, \dots, t_{gut}$ where t_{gut} is the total number of gut content data in the pool G

- for $j = 1, \dots, n_{sample}$ where n_{sample} is the number of independent samples to be drawn
 - Draw a set of gut content data $y = \{g_1, g_2, \dots, g_i\}$ from the pool of gut content data G
 - for $k = 1, \dots, n_{par}$ where n_{par} is the number of parameter values to be sampled
 - * Draw a set of parameter values θ_k from the prior distribution $\pi(\theta)$
 - * Compute the model result $x_i = model(\theta_k)$
 - * Compute $s(x_i)$ and $d(s(x_i), y)$
 - Accept θ_j , which results in the $\min_i \{d(s(x_i), y)\}$
- Compute $TSS_i(x, y) = \{TSS(x_i, y) : x_i = ADBM(\theta_j), \theta_j \text{ computed from previous step}\}$ using the accepted $\theta_1, \dots, \theta_{n_{sample}}$

Output:

A prediction interval containing TSS between observed and predicted food webs for every i number of gut content data drawn from the pool of gut content data.

3.6 Assessment of prediction

The accuracy of the predicted diet of the predators was defined using true skill statistic (TSS) which takes into account the true and false predictions of both the presence and absence of links defined as:

$$TSS = \frac{ad - bc}{(a + c)(b + d)}$$

where a is the number of observed links that are predicted by the model (true positives), d is the number of observed absences of links that are correctly predicted (true negatives), b is the number of false positives, and c is the number of false negatives.

The TSS ranges from -1 to 1 , where $+1$ indicates a perfect prediction. A TSS value of zero or less indicates a performance no better than random (Allouche, Tsoar, and Kadmon 2006).

4 Results

We first present how the accuracy of the food web model vary in predicting trophic interactions when we increase the amount the gut content data provided to the food web model. Then, we calculate the number of gut content data for each food webs corresponding to which the accuracy results in 90% of the maximum true skill statistics predicted by the food web model. We also compute the goodness of the food web model in predicting structural properties from incomplete gut content data. We did that by computing mean standardised error in food web properties.

4.1 Inferring trophic interactions using ADBM and incomplete gut content data

There food webs generated using incomplete gut content data and the ADBM, improved quickly for lower number of predator guts (Fig. 1). The uncertainty in the TSS reduced with the increasing number of predator guts. With only 232 number of gut content data which is 23% of the total gut content data, the ADBM predicted the food web with TSS of 0.69 which was 91% of the mean TSS (0.75) achieved using complete gut content data by the ADBM for Broadstone Stream food web (Fig. 1(a)). In the case of the Celtic Sea food web, only 113 gut content data was required by the ADBM to predict food web with TSS equal to 92% of the mean TSS (0.68) achieved using complete gut content data by the ADBM (Fig. 1(b)).

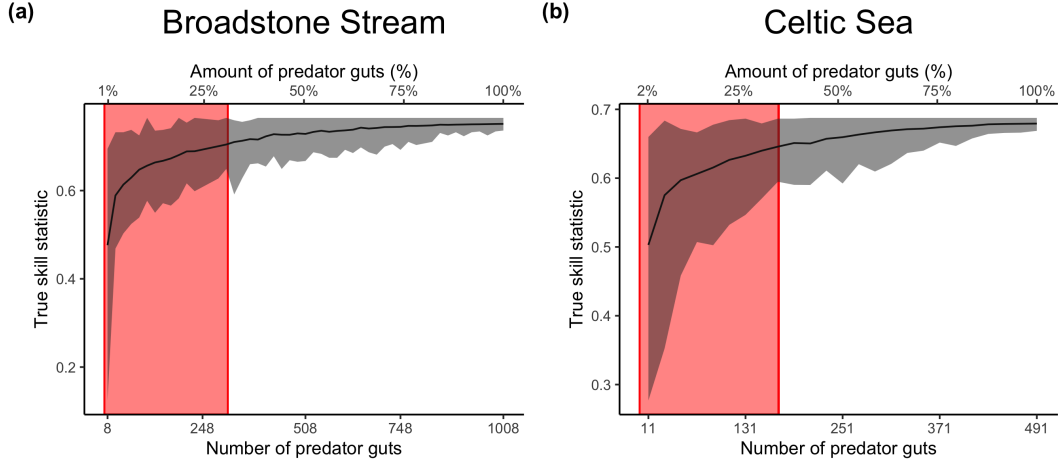


Figure 1: Accuracy of the predicted food web represented by the true skill statistics, predicted using incomplected gut content data by the ADBM for Broadstone Stream and Celtic Sea. Line and shaded grey region represents the mean and the prediction interval of 100 independent samples respectively. Shaded red region represents the region where using the model compensate for missing links in the undersampled food web constructed using partial gut content data (See SI Fig. 4 for details).

For low number of gut content data represented by red shaded region in Fig. 1, ADBM can compensate for missing links in the undersampled food web constructed using partial gut content data. Outside the red shaded region, using the ADBM for predicting food web does not result in further increase in the TSS that was already achieved from the food web structure constructed using gut content data alone.

5 Discussion

5.1 Why incomplete gut content data can be used to infer trophic interactions?

- Model fills up the missing interactions
- Partial data helps to constrain the parameter space

5.2 How is the uncertainty in the gut content data propagated to model prediction?

5.3 Comparing our study with other studies of predicting food webs using incomplete data

Some studies have presented how the accuracy of food web prediction change when we vary the amount of food web data (Gray et al. 2015).

5.4 What is the generalisability of our results?

- Dependent on how size structured a food web is, how the food web is aggregated, the type of interactions

5.5 Assumption that the food web constructed with the total gut content data is the true food web

5.6 How can we include other food web data type?

- experimentation (feeding trials)
- DNA Metabarcoding

5.7 Extending the approach to other food web models

- Current approach could be implemented with other food web models

6 Conclusion

7 Supplementary Information

7.1 Gut content data simulation

We simulated a food web using the ADBM for a given set of parameters. For a given set of predators, we subset the diet from the simulated food web. Then using a probability mass function (distribution), we sampled the gut content data from predators' diet thereby incorporating the uncertainty in the gut content data. We repeated this process multiple number of times for every predator in the food web.

Input:

- Predators whose diet are to be simulated $P = \{p_1, \dots, p_n\}$
- A simulated food web $ADBM(\theta_i) = \{d_{p_1}, d_{p_1}, \dots, d_{p_k}\}$, where d_{p_k} is a one-dimensional diet matrix of predator k containing ones and zeros.
- A function which describes uncertainty in the diet $U(d)$
- Number of independent guts to be simulated for a predator $p_i : ngut$

Sampling:

- for $p_i \in P$
 - for $j = 1, \dots, ngut$, where $ngut$ is the number of guts to be simulated
 - * Simulate a single gut of a predator $p_i : g(p_i) = d_{p_i} * U(d_{p_i})$
 - Set of gut of a predator $p_i : G(p_i) = \{g(p_i) : g(p_i) = d_{p_i} * U(d_{p_i})\}$

Output:

- We simulated a pool of gut content data which contains simulated gut content data $G(p_i)$ for every predator p_i

7.2 Prediction using simulated gut content data from a simulated food web

The true skill statistics (TSS) between the predicted food web and observed food web saturated with an increasing number of distinct predator guts in a sample (Fig. 2). The TSS of the predicted food webs estimated using the complete individual gut data had shorter prediction intervals resulting in less uncertainty, and higher mean TSS than that using the partial individual gut data. The maximum limit of the prediction interval of TSS estimated using the complete gut data and the partial gut data were almost equal, with the minimum limit of the prediction interval of TSS using partial gut data being lower than that from the complete gut data. Eventually, the gap between the mean TSS using the partial gut data and the complete gut data reduced with an increasing number of distinct predator guts suggesting when we have enough predator species' gut data, the achieved TSS was almost constant and hence independent of the amount of gut data.

The maximum TSS estimated using the complete gut data was very close to one and almost remained constant with an increasing number of different predator species sampled. With the gut data sample of only five distinct predator species, 95% of the maximum mean TSS was achieved when complete individual gut data was used, while the same was achieved with 15 predator species for partial gut data. This shows that one does not need to know the gut data of all the species to predict the food web and the accuracy is dependent on the completeness of an individual gut data.

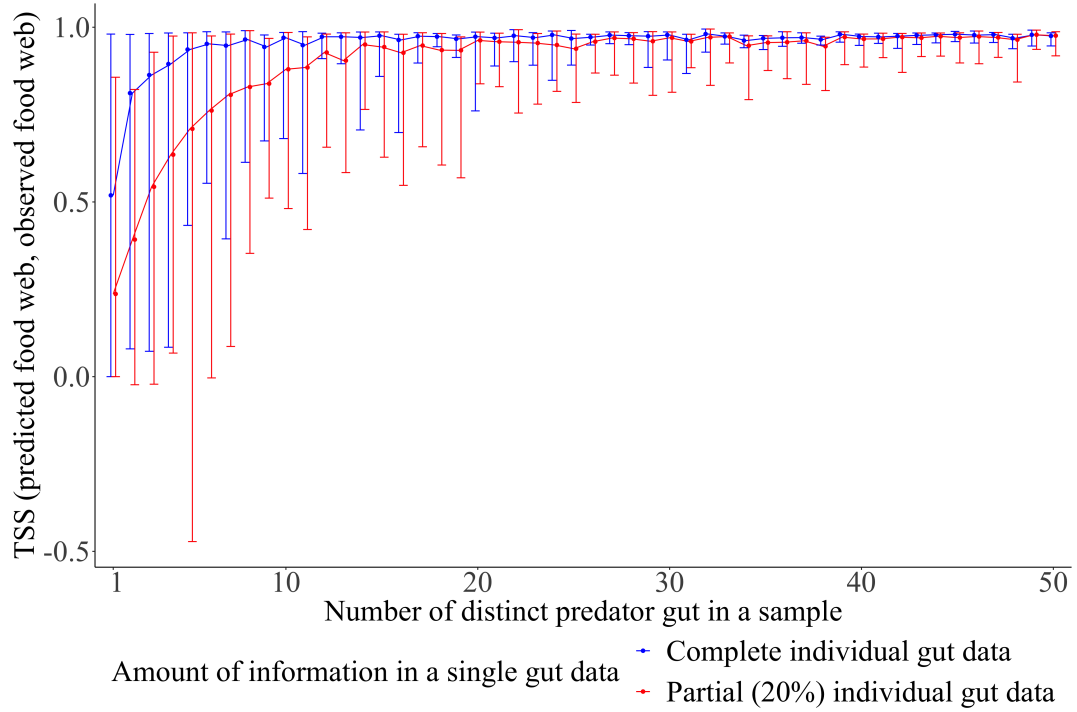


Figure 2: True skill statistics between predicted food web and observed food web for a simulated small reef food web estimated for distinct predator guts in a sample. The observed simulated food web consists of 50 species and ...links. The vertical bars correspond to the prediction intervals of the true skill statistics with filled circles representing the corresponding mean. A prediction interval of the TSS is formed using a set of 100 accepted TSS values using the ABC method.

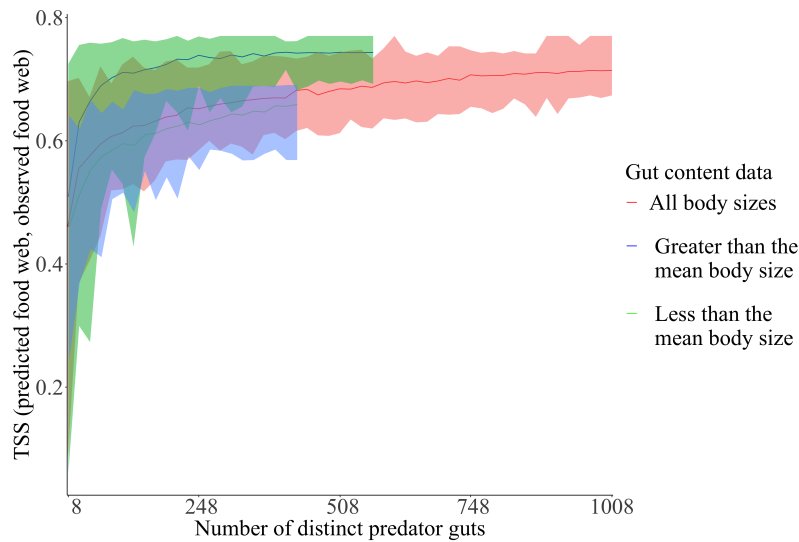


Figure 3: True skill statistics between predicted food web and observed food web estimated for different number of distinct predator guts. The estimation is done for three sets of gut data: gut content data of predators whose body sizes are smaller than the mean body size, larger than the mean body size, and all the gut content data.

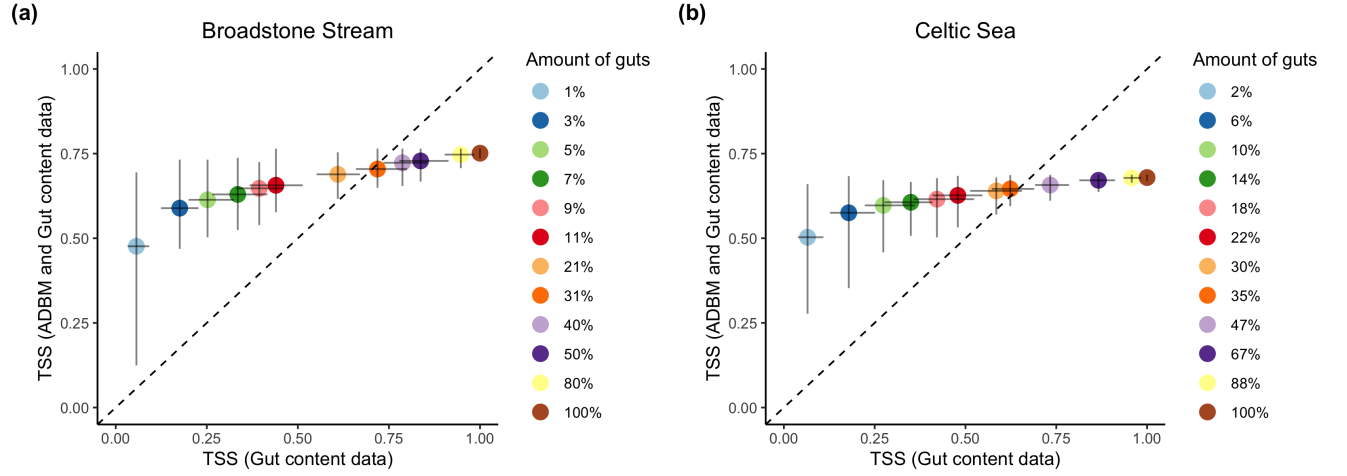


Figure 4: True skill statistic between predicted food web using ADBM and incomplete gut content data, and observed food web against the true skill statistic between food web constructed using incomplete gut content data, and observed food web. Error bars represent prediction intervals of 100 independent samples. Dashed line is 1:1 line for reference.

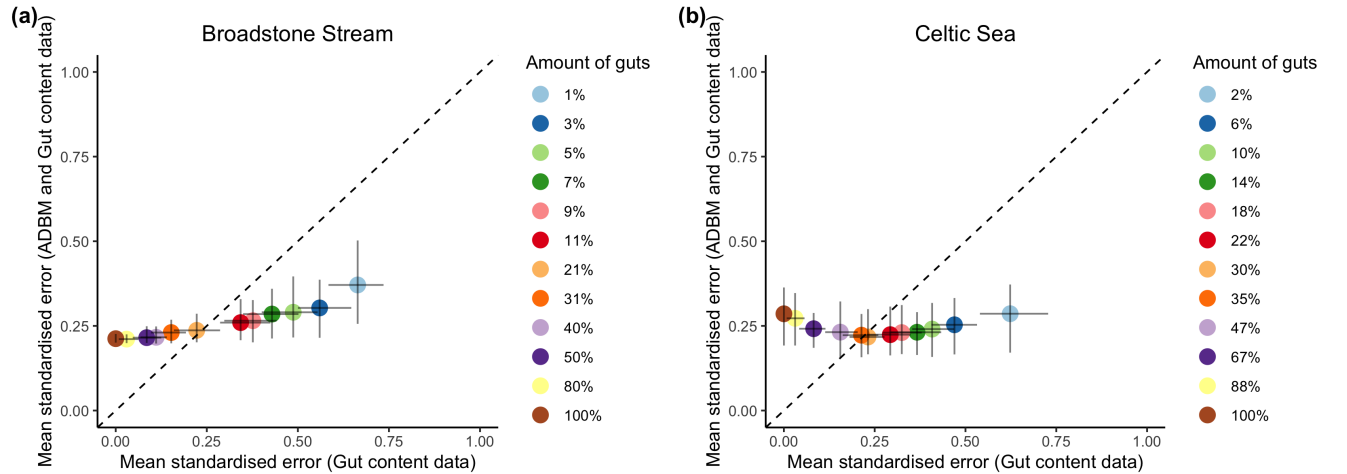


Figure 5: Mean standardised error in structural properties in the food web predicted using ADBM and incomplete gut content data against structural properties in the predicted food web constructed using incomplete gut content data. Error bars represent prediction intervals of 100 independent samples. Dashed line is 1:1 line for reference.

8 Acknowledgements

9 Author contributions

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