

# Hierarchical models to predict predation in complex trophic communities

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Trophic interactions make the backbone of ecological communities. From herbivory to predation, these interactions of varying strength shape ecosystem and their related functions. There is a pressing need to be able to predict interaction strength at the scale of whole communities. While functional responses focus at the pairwise interaction level, we question here if the same underlying mechanisms could be leveraged to make predictions at the scale of the community. In this study, we develop 4 hierarchical models of increasing complexity based on the type I and the type II functional responses to predict biomass fluxes between consumers and resources at the community level. The main objective is to determine if simple mechanism such as mass action (type I) and the saturation of fluxes (type II) are sufficient to predict biomass fluxes. To do so, we collected 19 Ecopath networks encompassing 1380 interactions across marine, aquatic and terrestrial ecosystems. While we can not reject the mechanism of saturating fluxes (type II), our results suggest that a mass action mechanism is sufficient and more robust, in the context of our data, to predict biomass fluxes between consumers and resources at the community level. We also recovered the expected allometric relationships between consumers body mass and their space clearance rate parameters within the mass action model, further solidifying our findings. Further modelisation is needed, specifically a trait-matching model with more data, to develop a model generalizable to more taxons and types of trophic interactions.

1 Trophic interactions make the backbone of ecological communities (Bellingeri & Bodini 2016; DeLong 2021;  
2 Wootton & Emmerson 2005), linking every component through nutrient and energy flows (Lindeman 1942).  
3 Consumer-resource interactions of varying strength play a crucial role in shaping important ecosystem functions  
4 and processes (Curtsdotter *et al.* 2019; Duffy 2002; Koltz *et al.* 2018; Montoya *et al.* 2003; Wilmers *et al.*  
5 2012) such as disease dynamics, invasive species and biogeochemical cycles (Estes *et al.* 2011). Identifying  
6 species interactions and quantifying their strength is necessary to understand community composition (Paine  
7 1992), stability (Bascompte *et al.* 2005; de Ruiter *et al.* 1995; Neutel 2002; Nilsson & McCann 2016) and the  
8 resulting associated ecosystem services (Montoya *et al.* 2003). Global changes have a diversity of impacts on  
9 species themselves, but also how they interact and the resulting assemblages and functioning (Koltz *et al.* 2018;  
10 Lurgi *et al.* 2012). Empirical observation of these interactions and the evaluation of their strength is however  
11 challenging, if not unfeasable due to their sheer amount, sampling biases and the emergence of novel  
12 interactions between species that never co-occurred (Aguiar *et al.* 2019; Jordano 2016; Wootton & Emmerson  
13 2005). The study of ecological networks has therefore recently moved to the development of predictive tools to  
14 overcome the limitations associated with empirical sampling of trophic interactions (Poisot *et al.* 2016).  
15 Different models are derived from food web theory, such as the niche model (Williams & Martinez 2000), the  
16 nested-hierarchy model (Cattin *et al.* 2004), trait-matching model (Bartomeus *et al.* 2016) or physical  
17 constraints (Portalier *et al.* 2019). More recently, Strydom *et al.* (2021) developed a general framework to  
18 predict interaction probabilities between species in a community context. These methods are however mostly  
19 qualitative, i.e. they are meant to predict if there is an interaction or not, and there is a pressing need to expand  
20 them to quantitative interactions, where the strength of interaction between any two organisms is described.  
21 There are many definitions of interaction strength (Berlow *et al.* 2004), and among them biomass flows can be  
22 particularly suited for the development of predictive models. Biomass flows between consumers and resources  
23 can be derived from functional traits, with the promise of a standardized measure independent of taxa involved  
24 (Berlow *et al.* 2004). Quantitative predictive models of biomass flows might also offer potential support to the  
25 study of biodiversity and ecosystem functioning relationship, as it seeks to depict all energy flows within  
26 communities (Barnes *et al.* 2018). Biomass flows are defined as a quantity of resource biomass that is  
27 consumed by a consumer per unit area and unit of time, reporting how energy circulates through the food web  
28 (Lindeman 1942). Interaction strengths between consumers and resources is closely related to predation rate in  
29 a food web model, namely the functional responses ](Rall *et al.* 2012). Functional response theory aims at  
30 describing the change in feeding rate of a consumer, or how many prey or resource a consumer can predate per

31 unit area over time, relative to prey or resource availability (Holling 1959a, b; Solomon 1949). Where the  
32 functional response describes the actual number of individual prey or resource predated by a consumer per unit  
33 area over time, biomass flows describes the amount of biomass flowing from a prey or resource to a consumer  
34 per unit area over time. Since both quantities report the rate of the same underlying process that is predation, we  
35 anchored the development of our modeling approach in functional response theory.

36 A fundamental principle underlying the majority of functional responses is the mass action, stating that predator  
37 and prey move randomly in an area and encounter at a rate proportional to the product of their abundance and  
38 their velocity. Here we will focus on the two most commonly used types of functional responses. The type I  
39 functional response describes mass action only, where the amount of resource consumed depends on the  
40 resource and consumer densities, and the rate (formerly referred to as attack rate and hereafter space clearance  
41 rate (DeLong 2021)) at which a consumer searches its home range for resources, leading to random encounters  
42 followed by detection, attack and consumption. The type II functional response describes the same process as  
43 the type I, but with the addition that consumption saturates with prey availability because of the time required to  
44 process prey. These processes are influenced by a multitude of functional traits and environmental conditions  
45 (Beardsell *et al.* 2021, 2022). The space clearance rate parameter varies with consumers and resources intrinsic  
46 characteristics such as absolute and relative velocities, perception of the environment and cognitive abilities  
47 (DeLong 2021). It is also influenced by externalities such as habitat complexity (Barrios-O'Neill *et al.* 2016;  
48 Hall *et al.* 2000; Manatunge *et al.* 2000) and the presence of refugia (Hoddle 2003) impeding detection  
49 probability. The dimensionality of an interaction, whether it takes place in a two or three dimensional plane,  
50 also impacts encounter rates and detection probability (Pawar *et al.* 2012, 2019). For instance, a predatory bird  
51 searching for preys from above or fishes grazing the benthic surface are examples of 2D planes while aerial  
52 insectivorous birds pursuing flying insects or fishes chasing preys in the water column would be in a 3D plane.  
53 Functional response theory therefore makes a good start to develop predictive models of quantitative  
54 interactions since widely measured functional traits can be combined with consumer and prey density to predict  
55 biomass flows.

56 The space clearance rate, in units of space per time, reports the amount of area search by the predator in a time  
57 interval. As with many biological processes, the space clearance rate was shown to vary with consumers body  
58 mass. Indeed, multiple studies, summarized in the FoRAGE database (Uiterwaal *et al.* 2022), showed an  
59 allometric scaling between the space clearance rate and the body mass of consumers. This observation is  
60 coherent with (Hirt *et al.* 2017, 2020) who documented that the maximum velocity of an organism scales with

61 its body mass. Handling time is also expected to follow the same scaling relationship (DeLong 2021), although  
62 recent studies are now suggesting that consumers handling time would not be as important at natural resources  
63 densities (Beardsell *et al.* 2021; Chan *et al.* 2017; Coblenz *et al.* 2023; Preston *et al.* 2018). Ultimately, an  
64 accurate evaluation of these parameters is necessary as they are widely used in theoretical models (Brose *et al.*  
65 2006; Brose *et al.* 2008; Pawar *et al.* 2012). Restraining the parameter space could greatly bonify studies of  
66 species coexistence, community stability and trophic regulation. It could also help the parameterization of  
67 global ecosystem models used for biodiversity scenarios (Harfoot *et al.* 2014}). Following (Yodzis & Innes  
68 1992), there are a few meta-analyses looking at the scaling of feeding rates with body-mass (Rall *et al.* 2012).  
69 These are however concentrated on a re-analysis of univariate functional responses, mostly from experimental  
70 studies, and there is currently no study aiming at reconstructing quantitative interaction networks.

71 Our main objective is to test if we could model quantitative interactions in complex food webs with easily  
72 accessible information such as abundance and body mass. We compared statistical models derived from  
73 functional response theory, including type I and type II forms. We also investigate if allometric relationships  
74 between space clearance rate, handling time and consumer body mass can contribute to the prediction of  
75 biomass flows in diverse food webs. To do so, we developed four hierarchical models of pairwise quantitative  
76 interactions of increasing complexity and evaluated them with empirical data of biomass flows between  
77 consumers and resources. We curated Ecopath networks (Christensen *et al.* 2005) describing marine, aquatic  
78 and terrestrial food webs and extracted 1380 pairwise trophic interactions between consumers and resources.  
79 Each model represents its own hypothesis and their comparison allow the evaluation of different mechanisms  
80 driving interactions.

## 81 Material and methods

82 A litterature search was performed to gather empirically sampled trophic networks with measurements of  
83 biomass flows from resources to consumers, along with population densities. Food web data are notoriously  
84 heterogeneous (Mestre *et al.* 2022) and we therefore relied on Ecopath models (Christensen *et al.* 2005) to  
85 normalize data collection. Ecopath is a modelling software that relies on a mass-balance premiss and a  
86 multitude of parameters (production/biomass ratio, consumption/biomass ratio, diet compositions etc.) to  
87 provide a realistic static image of the flows of biomass between resources and consumers in an ecosystem  
88 (Christensen *et al.* 2005). It was shown the Ecopath methodology reduces biases in comparative analyses

89 among food webs (Brimacombe, in review). We therefore collected openly available models from Ecobase  
90 (Colléter *et al.* 2013) and worked with a subset of the models present in (Jacquet *et al.* 2016). Taxonomic  
91 resolution of Ecopath models is highly variable and it is not uncommon that species are lumped into functional  
92 groups. The models were therefore selected based on the taxonomic resolution with the criteria that most nodes  
93 must be resolved at the species level, or that species within functional groups were taxonomically resolved. We  
94 thus curated 19 Ecopath models (detailed list in supplementary material) from aquatic, marine and terrestrial  
95 environments (fig. 1), and trophic guilds spanning from mammal carnivores and herbivores, birds, pelagic  
96 carnivorous and herbivorous fish, demersal carnivorous and herbivorous fish and invertebrates.

97 [Figure 1 about here.]

98 Species identity in the Ecopath models were validated with the original publication and estimates of adult mean  
99 body mass was retrieved from literature. Body mass for terrestrial species came from different sources such as  
100 the GATEWAv database (Brose 2018), the original publication for which the Ecopath model was developed or  
101 grey literature. Body mass for marine and freshwater species came from Fishbase (Froese *et al.* 2023) and  
102 Sealifebase (Palomares *et al.* 2023). When only body length was available, Fishbase and Sealifebase calculated  
103 weight from body length using a bayesian length-weight model. The midpoint between the minimum and  
104 maximum measurements was taken when a mean was not available. Density (number of individuals per unit  
105 surface,  $N/\text{km}^2$ ) was computed by dividing total biomass per unit surface  $B$  (metric tons/ $\text{km}^2$ ) by mean body  
106 mass  $M$  (metric tons). The 19 Ecopath models were aggregated in an edge list with quantitative biomass flows  
107 (metric tons/ $\text{km}^2/\text{year}$ ), for a total of 1380 interactions between 154 consumer species and 153 resource  
108 species.

## 109 Model description

110 We developed four different hierarchical models of increasing complexity based on the type I and type II  
111 functional responses, and a null model. Models were then parametrized with Hamiltonian Monte Carlo  
112 (Monnahan *et al.* 2017), compared and ranked from better to worst based on their prediction accuracy. The  
113 functional form of these relationships are presented below.

114 **Model 0 - Null model**

115 The null model acts as a basis of comparison with the other models and does not portray any ecological realism  
116 of a trophic interaction. Model 0 hypothesizes that the flow of biomass  $F_{ij}$  from a prey  $i$  to its predator  $j$  is  
117 constant with average  $K$ , irrespective of predator identity:

$$F_{ij} = K$$

118 **Model 1 - General mass action**

119 Model 1 implements a general version of the type I functional response and thereby focuses on the law of mass  
120 action. The flow of biomass  $F_{ij}$  depends on the available prey biomass  $B_i$  and the abundance of the predator  $N_j$   
121 where they encounter each other at a given the  $\alpha$  space clearance rate of the consumer  $N_j$ . Explicitely, only the  
122 consumer's mobility is considered as it searches for resources. For the purpose of comparison, model 1  
123 hypothesizes that all consumers have the same space clearance rate  $\alpha$ :

$$F_{ij} = \alpha B_i N_j$$

124 **Model 2 - Consumer-specific mass action**

125 Model 2 follows the previous one with the hypothesis that space clearance parameter  $\alpha_j$  is a specific parameter  
126 for each consumer species  $j$ :

$$F_{ij} = \alpha_j B_i N_j$$

127 **Model 3 - Single-species saturating model**

128 Model 3 keeps the assumptions of model 2 with the addition of handling time, thereby representing a single  
129 species Type II functional response. The space clearance rate parameter  $\alpha_j$  and the handling time  $h_j$  are both  
130 consumer-specific:

$$F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j B_i N_j}$$

131 **Model 4 - Multi-species saturating model**

132 Building on model 3, model 4 implements a multi-species version of Type II functional response (Smout *et al.*  
 133 2010). Parameters are the same as the ones used in model 3, the difference is found at the denominator where  
 134 handling is aggregated over all species in the food web:

$$F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j \sum_{i=1}^{n_{prey}} B_i N_j}$$

| Model name                      | Model equation   | Number of parameters |
|---------------------------------|--|----------------------|
| Null model                      | $F_{ij} = K$   | 2                    |
| General mass action             | $F_{ij} = \alpha B_i N_j$  | 2                    |
| Predator specific mass action   | $F_{ij} = \alpha_j B_i N_j$  | 157                  |
| Single species saturating model | $F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j B_i N_j}$                       | 313                  |
| Multi species saturating model  | $F_{ij} = \frac{\alpha_j B_i N_j}{1 + h_j \alpha_j \sum_{i=1}^{n_{prey}} B_i N_j}$ | 313                  |

135  $F_{ij}$  represents the flux of biomass (metric tons/km<sup>2</sup>/year),  $K$  is a parameter representing mean biomass flow  
 136 (metric tons/km<sup>2</sup>/year),  $\alpha$  is the general space clearance rate (km<sup>2</sup>/consumer/year),  $\alpha_j$  is the  
 137 consumer-specific space clearance rate (km<sup>2</sup>/consumer/year),  $B_i$  is the prey biomass (metric tons/km<sup>2</sup>),  $N_j$  is  
 138 the consumer abundance (individual/km<sup>2</sup>) and  $h_j$  is the consumer handling time  
 139 (metric tons of resource biomass/km<sup>2</sup>/year). {#tbl:table\_model}

140 **Model evaluation**

141 All biomass fluxes and body-mass were log-transformed. Biomass fluxes were modelled with a hierarchical  
142 bayesian approach where  $F_{ij}$  follows, after being log-transformed, a normal distribution with mean  $\mu$  and  
143 standard deviation  $\sigma$ , where the mean corresponds to the five different models described above respectively.  
144 Species-specific parameters  $\alpha_j$  and  $h_j$  were considered as random effects following normal distributions. As we  
145 lacked prior knowledge on potentiel distribution for the parameters, we opted for generic weakly informative  
146 priors. The mean and standard deviation for  $\alpha$  and  $h_j$  were 0 and 1 respectively and were the same for all  
147 models. The analysis was performed with Stan version 2.32.2 (Stan Development Team 2024) via the package  
148 rstan in R version 4.3.3 (R Core Team 2024).

149 After fitting the data to each model respectively, we used the LOO package (Vehtari *et al.* 2024) to compute the  
150 expected log pointwise predictive density (ELPD) to perform a leave-one-out (LOO) cross validation based on  
151 (Vehtari *et al.* 2017) to estimate prediction accuracy. We computed Pareto diagnostic values per model to  
152 evaluate reliability. Models were ranked by predictive accuracy based on their respective ELPD score. We also  
153 compared the ELPD score between models to evaluate prediction accuracy and their bayesian  $R^2$  (Gelman *et al.*  
154 2019). Finally, we tested with linear regression allometric relationships of the space clearance rate parameter  $\alpha$   
155 and handling time  $h_j$  with consumer body mass.

156 **Code and data availability**

157 All the R scripts for model evaluation and figures are available on Github at  
158 <https://github.com/BenMerSci/master>.

159 **Results**

160 All models (with the exception of the null hypothesis) had good fit to the data, with  $R^2$  ranging from 0.697  
161 (model 1 - details at tbl. ?? and  $R^2$  posterior distributions in fig. ??) to 0.835 (model 3). The model ranking  
162 based on the predictive accuracy with LOO, where higher values are better, revealed that the best performing  
163 model is the single species saturating model (model 3) with an ELPD score of -2452.8, almost equal to the  
164 multi species saturating model (model 4) and the consumer specific mass action model (model 2) with ELPD  
165 scores of -2713.5 and -2749.4 respectively. The the null model (model 0) and the general mass action model

166 (model 1) followed with ELPD score of -3529.1 and -4056.1, respectively. Model ranking reveals that, with the  
167 exception of model 4, every hypothesis that is added to the model contribute significantly to ELPD and R<sup>2</sup>. The  
168 most significant increases is observed between model 1 and model 2, indicating that, once we account for mass  
169 action (model 1), the most important element is predator specific consumption rate (model 2). Adding  
170 saturation only marginaly improves the fit (model 3), while accounting for multi-species saturation has no  
171 significant impact (model 4).

172 It is to be noted that both model 3 and model 4 had higher Pareto K diagnostic values (> 0.7), which might  
173 indicate non-robust model or highly influential observations (Vehtari *et al.* 2017).

| Model predictive density (ELPD) | Expected log pointwise difference | Standard error | Effective number of parameters (p-LOO) | Number of parameters | mean R <sup>2</sup> |
|---------------------------------|-----------------------------------|----------------|--|----------------------|---------------------|
| model 3 -2455.4                 | 0.0                               | 0.0            | 202.5                                  | 313                  | 0.833               |
| model 4 -2717.7                 | -                                 | 28.8           | 149.5                                  | 313                  | 0.795               |
| model 2 -2751.3                 | -                                 | 30.2           | 142.2                                  | 157                  | 0.803               |
| model 0 -3529.1                 | -                                 | 35.7           | 2.4                                    | 2                    | 0.000               |
| model 1 -4056.5                 | -                                 | 37.3           | 2.1                                    | 2                    | 0.696               |
|                                 |                                   | 1601.1         |  |                      |                     |

174 Model ranking based on ELPD with LOO. Models are ranked from best to worst based on their predictive  
175 accuracy with the LOO package. {#tbl:table\_ranking}

176 Model comparison suggests that mass action only catches most of the variability in biomass fluxes, but the  
177 graphical representation of predicted biomass flows against observed biomass flows reveals a very significant  
178 bias that is solved with species-specific space clearance rates (figure fig. 2). Since the bias in predictions  
179 disappears in all three species-specific models and that model 1 ranked below our null model, it was dismissed.  
180 Model ranking and the R<sup>2</sup> suggest the single species saturating model (model 3) is better than model 2 and 4,  
181 but the difference is hardly significant both from statistics (Table tbl. ??) and graphical representation (figure  
182 fig. 2). The consumer specific mass action model (model 2) and the multi-species saturating model (model 4)

183 are the closest together regarding their ELPD score. Furthermore, the added multi-species aspect of model 4,  
184 relative to the single-species model 3, does not improve the fit, neither from statistics nor from graphical  
185 representation, therefore dismissing model 4. The *extreme* Pareto K values of model 3 and 4 would also suggest  
186 that both models might not be suited to make prediction as is (Vehtari *et al.* 2017).

187 [Figure 2 about here.]

188 At first glance based on the model ranking and the  $R^2$ , the single species saturating model (model 3) seems to  
189 have better prediction accuracy than model 2 and 4. The prediction against observations plots is hinting at the  
190 same conclusion, where all three models look pretty similar but the points in model 3 are more grouped around  
191 the diagonal line. The consumer specific mass action model (model 2) and the multi-species saturating model  
192 (model 4) are the closest together regarding their ELPD score. Since model 3 and model 4 are both based on the  
193 type II functional response, showing barely no difference in fit and model 3 ranking better, we dismissed model  
194 4. This decision is also based on parsimony, the extreme Pareto K values and model 2 having a higher  $R^2$  than  
195 model 4. Posterior distributions of the space clearance rate (figure fig. 3) are very similar across the three  
196 models, with the distinction that the distribution of model 3 and 4 were wider while model 2 were narrower.  
197 Handling time also varies significantly between species (figure fig. 4), with some species having very wide  
198 distributions and without clear differences between trophic guilds.

199 [Figure 3 about here.]

200 [Figure 4 about here.]

201 We lastly investigated the relationships between space clearance rate, handling time and body mass. We found a  
202 significant relationship between body masses and the space clearance rate for the specific mass action model  
203 (model 2, figure {fig. 5}.A). Relationship with the space clearance rate and consumers body mass was  
204 significant with a slope of 0.98 (p-value < 0.05, adjusted  $R^2$  of 0.56). This relationship was not significant  
205 however for space clearance rates extracted from model 3 (model 3, figure fig. 5 .B and fig. 5 .C), neither was  
206 the relationship between body mass and handling time.

207 [Figure 5 about here.]

208 **Discussion**

209 The motivation of this study was to develop predictive models of quantitative interactions for entire food webs.  
210 There are already several techniques to predict the occurrence of interactions and to reconstruct binary  
211 interaction networks such as the niche model (Williams & Martinez 2000), trait-matching model (Bartomeus *et*  
212 *al.* 2016) and machine learning models (Pichler *et al.* 2020). There are also quite a few meta-analyses of  
213 functional responses, none of them can be applied to entire food webs as they were mostly based on single  
214 species analyses. Here we developed these one step further with the prediction of biomass flows as a function of  
215 mass action, allometric scaling and the full web composition. To do so, we investigated an ensemble of models  
216 to predict biomass flows between populations of consumers and resources inspired from functional response  
217 theory. Four mechanistic model of increasing complexity based on the type I and the type II functional response  
218 were compared to test different hypotheses. In contrast with functional response studies, where the variation of  
219 consumption rates of consumers with resource density is evaluated, here we attempted to predict biomass fluxes  
220 between all pair of species within a community context. Upon initial inspection of the fits of each model, it  
221 appears that models based upon functional response type I (mass action model) and type II (saturating model)  
222 are well suited to predict biomass fluxes. We discuss hereafter the inherent properties of each model and  
223 compare them regarding their predictive capabilities of biomass fluxes. Specifically, we compared the different  
224 underlying mechanisms and discuss whether mass action is enough or if the incorporation of saturation with  
225 consumers handling time is an important addition to predict biomass flows. We follow by exploring whether the  
226 expected allometric relationships with both parameters of interest (space clearance rate and handling time) are  
227 observed. We conclude by addressing the limitations of the study and potential next avenues for improving the  
228 model.

229 Overall, based on the Bayesian R<sup>2</sup>, the model ranking (table *tbl. ??*) and their graphical representation, we found  
230 that all the models (except the null model) had a good fit. While model 1 looks like a good one by looking at the  
231 performance metrics, it had a discernable and clear bias in terms of data fitting which undoubtedly arose from  
232 the non-specific space clearance rate. Model 1 portrayed a mass action process where consumption rates simply  
233 follows encounters between consumers searching their environment for resources based on a rate at which they  
234 clear space (DeLong 2021; O'Dwyer 2019). Space clearance rate is expected to vary with species body mass  
235 and other traits (DeLong 2021; Rall *et al.* 2012) and our data comprised a variety of organisms ranging from  
236 small fish to terrestrial mammals. The improvement in fit of model 2 in contrast to model 1 further consolidate

237 this hypothesis, where the implementation of a consumer-specific space clearance rate greatly improved model  
238 fitting and resulting  $R^2$ , thus dismissing model 1. With this said, model 2, 3 and 4 all had similar outcomes  
239 regarding  $R^2$  and predictive accuracy (table [tbl. ??](#)), while portraying different ecological mechanisms. While  
240 model 2 implemented a mass action process with consumer-specific space clearance rates, model 3 and 4  
241 incorporated a second mechanism of saturating biomass fluxes with consumers handling time. Both models 3  
242 and 4 were based upon a type II functional response, where the main difference was that model 3 was saturating  
243 biomass fluxes over the biomass of one prey (single-species) while model 4 was accounting for the biomass of  
244 all prey species available in the community (multi-species). While we expect consumers consumption rates over  
245 a resource to vary depending on the availability of all its resources of interest (Smout *et al.* 2010), the  
246 multi-species saturating model underperformed compared to the single-species saturating model. Accounting  
247 for all resource biomass did not seem to improve the fit, thus dismissing model 4. Given the great diffrence in  
248 number of parameters between model 2 and 3 (table ([table:table\\_model?](#))), their similar fit, and the high  
249 Pareto K values of model 3, model 2 seems to be the most parcimonious choice. Additionally, there seems to be  
250 a tradeoff between the space clearance rate and handling time parameter which introduces variability in the  
251 estimation of space clearance rate (figure [fig. 3](#)). This tradeoff also seems to impact the expected allometric  
252 relationships of space clearance rate and handling time with consumers body mass in model 3 (figure [fig. 5](#)  
253 -B-C). Even though model 3 had the highest  $R^2$  and ELPD score, it may also suffer from misspecification as  
254 indicated by the high Pareto K values (Vehtari *et al.* 2017). While the saturating model might still be relevent  
255 and can not totally be dismissed from our analysis, it seems that a simple model such as our consumer-specific  
256 mass action model gives a satisfying approximation of biomass fluxes.

## 257 Allometric relationships

258 The form of the functional response has been the subject of a longstanding debate (Barbier *et al.* 2021) since  
259 first formalized by Holling (1959a). The statistical models we developed operate on a different scale than single  
260 species functional response studies, taking advantage of the wide variability of feeding rates among species of  
261 different population sizes in a full community, instead of focusing on pairwise interactions with experimental  
262 manipulation of a single resource density. We nonetheless expected to observe similar functional responses and  
263 associated parameters since both approach describe the same underlying processes. Larger organisms are  
264 expected to have larger space clearance rate, whereas handling time might vary with consumers and resource  
265 body mass [Rall *et al.* (2012); Uiterwaal & DeLong (2020); Coblenz *et al.* (2023); DeLong (2021)].

266 Consistent with the anticipated relationship, largest space clearance rate in model 2 are related to larger  
267 organisms such as large and medium mammal predators, predatory birds and sharks, while lower space  
268 clearance rate are related to smaller organisms such as invertebrates, shrimps and small pelagic fish omnivores  
269 (figure fig. 3). The space clearance rate in model 3 mostly displays the same relationship with consumers body  
270 mass while having larger flat distributions (figure fig. 3). The allometric relationship with handling time is  
271 however less precise, where higher or lower handling time are not specifically related to larger or smaller  
272 organisms (figure fig. 3) Based on field observations and modeling, handling time would not be as important in  
273 consumptions as resource individuals needed to saturate a consumer's consumption rates could rarely be  
274 observed in natural context [Preston *et al.* (2018); Beardsell *et al.* (2021); Coblenz *et al.* (2023)}. While not  
275 necessarily relevant in explaining the poor unobserved body mass relationship of our handling time parameter,  
276 it might lend additional support for model 2. Overall, the inter-consumer distribution of the space clearance rate  
277 parameter for model 2 and 3 fall well within the range values reported in other studies [Rall *et al.* (2012);  
278 Portalier *et al.* (2022); Coblenz *et al.* (2023)}.

279 As with many other biological processes, feeding rates are tightly linked with consumers and resources body  
280 mass (Brose 2010; DeLong 2021; DeLong & Vasseur 2012; Preston *et al.* 2018; Schneider *et al.* 2012;  
281 Schröder *et al.* 2016). More specifically, the underlying space clearance rate and handling time parameters of  
282 the feeding process are expected to scale with consumer body mass (DeLong 2021; Kalinkat *et al.* 2013;  
283 Vucic-Pestic *et al.* 2010; Yodzis & Innes 1992). A review of several functional response studies summarized in  
284 the foRAGE database (Uiterwaal *et al.* 2022) showed a clear allometric scaling relationship between consumers  
285 body mass and space clearance rate among multiple taxonomic groups (DeLong 2021). The allometric scaling  
286 of movement speed is hypothesized to be the mechanisms underlying variability in the relationship between  
287 consumers body mass and their space clearance rate as it is a function of consumers velocity (DeLong 2021).  
288 Maximum velocities were shown to be allometrically linked with their body mass, displaying a linear increase  
289 on the log-scale up to certain extreme values of body mass (Bejan & Marden 2006; Hirt *et al.* 2017). The  
290 estimates of the slope of this relationship however varies significantly between studies, with values that are  
291 usually much smaller than 1 (Rall *et al.* 2012; **Delong2012DynExpa?**). We found an estimated slope of 0.98 on  
292 the log-scale (figure fig. 5 -A), with a relatively narrow confidence interval, suggesting a linear relationship  
293 between consumer body mass and the space clearance rate, which is coherent with a certain portion of the  
294 relationship developed by Hirt *et al.* (2017). Although most of the consumers in model 2 seem to display the  
295 expected relationship between space clearance rate and consumers body mass (figure fig. 5 -A), we can clearly

discern some species having an upward offset. The consumers of concern here are all terrestrial carnivores or omnivores belonging to the Arctic networks originating from the same set of study. As Ecopath compute estimates over a year step (Christensen *et al.* 2005; Christensen & Walters 2004) and the data from the Arctic networks were seasonally assessed for summer observations, we can not overlook that this offset might arise from a methodological bias. Alternatively, the higher space clearance rate of these terrestrial species might also arise from other impacting factors such as interaction dimensionality and habitat heterogeneity (Pawar *et al.* 2012). We also note that the allometric relationship disappears with the single-species saturating model (figure 5 -B-C). We believe this may happen because of a ridge in the likelihood space consequent to a tradeoff between space clearance rate and handling time, making the model non-identifiable. Perhaps this problem could be solved with stronger priors, for instance using parameters found in traditional functional studies such as Rall *et al.* (2012). Overall, the allometric relationship displayed in the consumer-specific mass action model represents another supporting element in favor of a simple mass-action model, which would significantly facilitates the parameterization of quantitative food web models.

### Quantitative predictions: general extent, scope and limitations

Many techniques were proposed recently to infer ecological interactions from proxies (Morales-Castilla *et al.* 2015), some informed by theory (Portalier *et al.* 2019), others more flexible and using all of the information contained in the data (Strydom *et al.* 2021). These methods are motivated by on-going changes in biodiversity (Jordano 2016), urging for a more integrated description of community structure. There is however an inherent challenge in documenting interactions because their number scales with the square of species richness (MacDonald *et al.* 2020), some interactions are difficult to document (Poisot *et al.* 2021; Wootton & Emmerson 2005), and also because novel assemblages are made of species that were never seen co-occurring before (Lurgi *et al.* 2012; Montoya & Raffaelli 2010). The variety of available methods allow some flexibility, depending on the objective of the study and data availability. They are however all limited to binary interactions, i.e. if a pair of species are interacting or not. Quantitative information on the strength of interaction is required to move to a next stage of interpretation, just like abundance is a more accurate description of community structure than presence-absence. We successfully predicted biomass fluxes with a very limited amount of information which suggests that, paired with a method to predict binary interactions, the reconstruction of quantitative interaction networks is accessible. Our model analysis was inspired by theory, and despite a different methodological approach, our results are in agreement with previous meta-analyses of functional responses (Rall *et al.* 2012;

325 Uiterwaal & DeLong 2020), further strengthening the confidence in our models. We found also coherence in  
326 parameter estimates across ecosystems and feeding guilds, suggesting that a general approach is within reach.  
327 Nonetheless, although our models were built upon the best available data at the time, it should not be overlooked  
328 that our results strongly depend on Ecopath model outputs, and thus their limitations. As such, the interpretation  
329 of our results should reflect this reality. The obvious next step will be to catch some of the residual variance,  
330 likely with the addition of other traits. Inspired by the methods used for binary interactions, the next model  
331 generation will have to account for trait-matching between consumer and resource. Interactions could also be  
332 made conditional on the environment, for instance on temperature affecting movement rates (Dell *et al.* 2014),  
333 or the presence of refuges (Barrios-O'Neill *et al.* 2016; Chan *et al.* 2017). The parameterization we offered here  
334 should eventually contribute to inform theoretical studies (Schneider *et al.* 2016) as well as global ecosystem  
335 models that are developed to investigate the consequences of biodiversity changes (Harfoot *et al.* 2014).

## 336 References

- 337 Aguiar, M.A.M. de, Newman, E.A., Pires, M.M., Yeakel, J.D., Boettiger, C., Burkle, L.A., *et al.* (2019).  
338 [Revealing biases in the sampling of ecological interaction networks](#). *PeerJ*, 7, e7566.
- 339 Barbier, M., Wojcik, L. & Loreau, M. (2021). [A macro-ecological approach to predation density-dependence](#).  
340 *Oikos*, 130, 553–570.
- 341 Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., *et al.* (2018). [Energy](#)  
342 [Flux: The Link between Multitrophic Biodiversity and Ecosystem Functioning](#). *Trends in Ecology &*  
343 *Evolution*, 33, 186–197.
- 344 Barrios-O'Neill, D., Kelly, R., Dick, J.T.A., Ricciardi, A., MacIsaac, H.J. & Emmerson, M.C. (2016). [On the](#)  
345 [context-dependent scaling of consumer feeding rates](#). *Ecology Letters*, 19, 668–678.
- 346 Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). [A](#)  
347 [common framework for identifying linkage rules across different types of interactions](#). *Functional Ecology*,  
348 30, 1894–1903.
- 349 Bascompte, J., Melian, C.J. & Sala, E. (2005). [Interaction strength combinations and the overfishing of a](#)  
350 [marine food web](#). *Proceedings of the National Academy of Sciences*, 102, 5443–5447.

- 351 Beardsell, A., Gravel, D., Berteaux, D., Gauthier, G., Clermont, J., Careau, V., *et al.* (2021). Derivation of  
352 Predator Functional Responses Using a Mechanistic Approach in a Natural System. *Frontiers in Ecology*  
353 and Evolution, 9.
- 354 Beardsell, A., Gravel, D., Clermont, J., Berteaux, D., Gauthier, G. & Bêty, J. (2022). A mechanistic model of  
355 functional response provides new insights into indirect interactions among arctic tundra prey. *Ecology*, 103.
- 356 Bejan, A. & Marden, J.H. (2006). Unifying constructal theory for scale effects in running, swimming and  
357 flying. *Journal of Experimental Biology*, 209, 238–248.
- 358 Bellingeri, M. & Bodini, A. (2016). Food web's backbones and energy delivery in ecosystems. *Oikos*, 125,  
359 586–594.
- 360 Berlow, E.L., Neutel, A.-M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004).  
361 Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73, 585–598.
- 362 Brose, U. (2010). Body-mass constraints on foraging behaviour determine population and food-web dynamics.  
363 *Functional Ecology*, 24, 28–34.
- 364 Brose, U. (2018). GlobAL daTabasE of traits and food Web Architecture (GATEWAy) version 1.0.
- 365 Brose, U., Ehnes, R.B., Rall, B.C., Vucic-Pestic, O., Berlow, E.L. & Scheu, S. (2008). Foraging theory predicts  
366 predator–prey energy fluxes. *Journal of Animal Ecology*, 77, 1072–1078.
- 367 Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex food  
368 webs. *Ecology Letters*, 9, 1228–1236.
- 369 Cattin, M.-F., Bersier, L.-F., Banašek-Richter, C., Baltensperger, R. & Gabriel, J.-P. (2004). Phylogenetic  
370 constraints and adaptation explain food-web structure. *Nature*, 427, 835–839.
- 371 Chan, K., Boutin, S., Hossie, T.J., Krebs, C.J., O'Donoghue, M. & Murray, D.L. (2017). Improving the  
372 assessment of predator functional responses by considering alternate prey and predator interactions.  
373 *Ecology*, 98, 1787–1796.
- 374 Christensen, V. & Walters, C.J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological*  
375 *Modelling*, 172, 109–139.
- 376 Christensen, V., Walters, C. & Pauly, D. (2005). Ecopath with Ecosim: A User's Guide. *Fisheries Centre*,  
377 *University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia*, 12.

- 378 Coblenz, K.E., Novak, M. & DeLong, J.P. (2023). Predator feeding rates may often be unsaturated under  
379 typical prey densities. *Ecology Letters*, 26, 302–312.
- 380 Colléter, M., Valls, A., Guitton, J., Lyne, M., Sánchez, F.A.-., Christensen, V., *et al.* (2013). *EcoBase: A*  
381 *repository solution to gather and communicate information from EwE models* (Research Report No. 21).  
382 Fisheries Centre, University of British Columbia, Canada.
- 383 Curtsdotter, A., Banks, H.T., Banks, J.E., Jonsson, M., Jonsson, T., Laubmeier, A.N., *et al.* (2019). *Ecosystem*  
384 *function in predator-prey food webs—confronting dynamic models with empirical data*. *Journal of Animal*  
385 *Ecology*, 88, 196–210.
- 386 de Ruiter, P.C., Neutel, A.-M. & Moore, J.C. (1995). *Energetics, Patterns of Interaction Strengths, and Stability*  
387 *in Real Ecosystems*. *Science*, 269, 1257–1260.
- 388 Dell, A.I., Pawar, S. & Savage, V.M. (2014). Temperature dependence of trophic interactions are driven by  
389 asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, 83, 70–84.
- 390 DeLong, J.P. (2021). *Predator Ecology: Evolutionary Ecology of the Functional Response*. Oxford University  
391 Press.
- 392 DeLong, J.P. & Vasseur, D.A. (2012). *Size-density scaling in protists and the links between consumer-resource*  
393 *interaction parameters*. *Journal of Animal Ecology*, 81, 1193–1201.
- 394 Duffy, J.E. (2002). *Biodiversity and ecosystem function: The consumer connection*. *Oikos*, 99, 201–219.
- 395 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., *et al.* (2011). *Trophic*  
396 *Downgrading of Planet Earth*. *Science*, 333, 301–306.
- 397 Froese, R., Pauly, D. & Editors. (2023). FishBase.
- 398 Gelman, A., Goodrich, B., Gabry, J. & Vehtari, A. (2019). *R-squared for Bayesian Regression Models*. *The*  
399 *American Statistician*, 73, 307–309.
- 400 Hall, R.O., Wallace, J.B. & Eggert, S.L. (2000). *Organic matter flow in stream food webs with reduced detrital*  
401 *resource base*. *Ecology*, 81, 3445–3463.
- 402 Harfoot, M.B.J., Newbold, T., Tittensor, D.P., Emmott, S., Hutton, J., Lyutsarev, V., *et al.* (2014). *Emergent*  
403 *Global Patterns of Ecosystem Structure and Function from a Mechanistic General Ecosystem Model*. *PLOS*  
404 *Biology*, 12, e1001841.

- 405 Hirt, M.R., Jetz, W., Rall, B.C. & Brose, U. (2017). [A general scaling law reveals why the largest animals are](#)  
406 [not the fastest](#). *Nature Ecology & Evolution*, 1, 1116–1122.
- 407 Hirt, M.R., Tucker, M., Müller, T., Rosenbaum, B. & Brose, U. (2020). [Rethinking trophic niches: Speed and](#)  
408 [body mass colimit prey space of mammalian predators](#). *Ecology and Evolution*, 10, 7094–7105.
- 409 Hoddle, M.S. (2003). [The effect of prey species and environmental complexity on the functional response of](#)  
410 [Franklinothrips orizabensis: A test of the fractal foraging model](#). *Ecological Entomology*, 28, 309–318.
- 411 Holling, C.S. (1959a). [Some Characteristics of Simple Types of Predation and Parasitism](#). *The Canadian*  
412 *Entomologist*, 91, 385–398.
- 413 Holling, C.S. (1959b). [The Components of Predation as Revealed by a Study of Small-Mammal Predation of](#)  
414 [the European Pine Sawfly](#). *The Canadian Entomologist*, 91, 293–320.
- 415 Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P., et al. (2016). [No](#)  
416 [complexity–stability relationship in empirical ecosystems](#). *Nature Communications*, 7, 12573.
- 417 Jordano, P. (2016). [Chasing Ecological Interactions](#). *PLOS Biology*, 14, e1002559.
- 418 Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. & Brose, U. (2013). [Body masses, functional](#)  
419 [responses and predator–prey stability](#). *Ecology Letters*, 16, 1126–1134.
- 420 Koltz, A.M., Classen, A.T. & Wright, J.P. (2018). [Warming reverses top-down effects of predators on](#)  
421 [belowground ecosystem function in Arctic tundra](#). *Proceedings of the National Academy of Sciences*, 115,  
422 E7541–E7549.
- 423 Lindeman, R.L. (1942). [The Trophic-Dynamic Aspect of Ecology](#). *Ecology*, 23, 399–417.
- 424 Lurgi, M., López, B.C. & Montoya, J.M. (2012). [Novel communities from climate change](#). *Philosophical*  
425 *Transactions of the Royal Society B: Biological Sciences*, 367, 2913–2922.
- 426 MacDonald, A.A.M., Banville, F. & Poisot, T. (2020). [Revisiting the Links-Species Scaling Relationship in](#)  
427 [Food Webs](#). *Patterns*, 1, 100079.
- 428 Manatunge, J., Asaeda, T. & Priyadarshana, T. (2000). [The Influence of Structural Complexity on](#)  
429 [Fish–zooplankton Interactions: A Study Using Artificial Submerged Macrophytes](#). *Environmental Biology*  
430 *of Fishes*, 58, 425–438.

- 431 Mestre, F., Rozenfeld, A. & Araújo, M.B. (2022). Human disturbances affect the topology of food webs.
- 432 *Ecology Letters*, 25, 2476–2488.
- 433 Monnahan, C.C., Thorson, J.T. & Branch, T.A. (2017). Faster estimation of Bayesian models in ecology using
- 434 **Hamiltonian Monte Carlo**. *Methods in Ecology and Evolution*, 8, 339–348.
- 435 Montoya, J.M. & Raffaelli, D. (2010). Climate change, biotic interactions and ecosystem services.
- 436 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 2013–2018.
- 437 Montoya, J.M., Rodríguez, M.A. & Hawkins, B.A. (2003). Food web complexity and higher-level ecosystem
- 438 services. *Ecology Letters*, 6, 587–593.
- 439 Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from
- 440 proxies. *Trends in Ecology & Evolution*, 30, 347–356.
- 441 Neutel, A.-M. (2002). Stability in Real Food Webs: Weak Links in Long Loops. *Science*, 296, 1120–1123.
- 442 Nilsson, K.A. & McCann, K.S. (2016). Interaction strength revisited—clarifying the role of energy flux for
- 443 food web stability. *Theoretical Ecology*, 9, 59–71.
- 444 O'Dwyer, J.P. (2019). Beyond an ecological ideal gas law. *Nature Ecology & Evolution*, 4, 14–15.
- 445 Paine, R.T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*,
- 446 355, 73–75.
- 447 Palomares, M.L.D., Pauly, D. & Editors. (2023). SeaLifeBase.
- 448 Pawar, S., Dell, A.I., Lin, T., Wieczynski, D.J. & Savage, V.M. (2019). Interaction Dimensionality Scales Up to
- 449 Generate Bimodal Consumer-Resource Size-Ratio Distributions in Ecological Communities. *Frontiers in*
- 450 *Ecology and Evolution*, 7, 202.
- 451 Pawar, S., Dell, A.I. & Van M. Savage. (2012). Dimensionality of consumer search space drives trophic
- 452 interaction strengths. *Nature*, 486, 485–489.
- 453 Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M. & Hartig, F. (2020). Machine learning algorithms to infer
- 454 trait-matching and predict species interactions in ecological networks. *Methods in Ecology and Evolution*,
- 455 11, 281–293.
- 456 Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., et al. (2021). Global knowledge
- 457 gaps in species interaction networks data. *Journal of Biogeography*, 48, 1552–1563.

- 458 Poisot, T., Stouffer, D.B. & Kéfi, S. (2016). [Describe, understand and predict: Why do we need networks in](#)  
459 [ecology?](#) *Functional Ecology*, 30, 1878–1882.
- 460 Portalier, S.M.J., Fussmann, G.F., Loreau, M. & Cherif, M. (2019). [The mechanics of predator–prey](#)  
461 [interactions: First principles of physics predict predator–prey size ratios.](#) *Functional Ecology*, 33, 323–334.
- 462 Portalier, S.M.J., Fussmann, G.F., Loreau, M. & Cherif, M. (2022). [Inferring Size-Based Functional Responses](#)  
463 [From the Physical Properties of the Medium.](#) *Frontiers in Ecology and Evolution*, 9.
- 464 Preston, D.L., Henderson, J.S., Falke, L.P., Segui, L.M., Layden, T.J. & Novak, M. (2018). [What drives](#)  
465 [interaction strengths in complex food webs? A test with feeding rates of a generalist stream predator.](#)  
466 *Ecology*, 99, 1591–1601.
- 467 R Core Team. (2024). R: A Language and Environment for Statistical Computing.
- 468 Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., *et al.* (2012). [Universal](#)  
469 [temperature and body-mass scaling of feeding rates.](#) *Philosophical Transactions of the Royal Society B:*  
470 *Biological Sciences*, 367, 2923–2934.
- 471 Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. (2016). [Animal diversity and ecosystem functioning in](#)  
472 [dynamic food webs.](#) *Nature Communications*, 7, 12718.
- 473 Schneider, F.D., Scheu, S. & Brose, U. (2012). [Body mass constraints on feeding rates determine the](#)  
474 [consequences of predator loss.](#) *Ecology Letters*, 15, 436–443.
- 475 Schröder, A., Kalinkat, G. & Arlinghaus, R. (2016). [Individual variation in functional response parameters is](#)  
476 [explained by body size but not by behavioural types in a poeciliid fish.](#) *Oecologia*, 182, 1129–1140.
- 477 Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., Thirgood, S., *et al.* (2010). [The](#)  
478 [Functional Response of a Generalist Predator.](#) *PLOS ONE*, 5, e10761.
- 479 Solomon, M.E. (1949). [The Natural Control of Animal Populations.](#) *Journal of Animal Ecology*, 18, 1–35.
- 480 Stan Development Team. (2024). Stan Modeling Language Users Guide and Reference Manual.
- 481 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021). [A](#)  
482 [roadmap towards predicting species interaction networks \(across space and time\).](#) *Philosophical*  
483 *Transactions of the Royal Society B: Biological Sciences*, 376, 20210063.

- 484 Uiterwaal, S.F. & DeLong, J.P. (2020). Functional responses are maximized at intermediate temperatures.
- 485     *Ecology*, 101, e02975.
- 486 Uiterwaal, S.F., Lagerstrom, I.T., Lyon, S.R. & DeLong, J.P. (2022). FoRAGE database: A compilation of
- 487     functional responses for consumers and parasitoids. *Ecology*, 103, e3706.
- 488 Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., *et al.* (2024). Loo: Efficient
- 489     leave-one-out cross-validation and WAIC for Bayesian models.
- 490 Vehtari, A., Gelman, A. & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out
- 491     cross-validation and WAIC. *Statistics and Computing*, 27, 1413–1432.
- 492 Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010). Allometric functional response model: Body
- 493     masses constrain interaction strengths. *Journal of Animal Ecology*, 79, 249–256.
- 494 Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.
- 495 Wilmers, C.C., Estes, J.A., Edwards, M., Laidre, K.L. & Konar, B. (2012). Do trophic cascades affect the
- 496     storage and flux of atmospheric carbon? An analysis of sea otters and kelp forests. *Frontiers in Ecology and*
- 497     *the Environment*, 10, 409–415.
- 498 Wootton, J.T. & Emmerson, M. (2005). Measurement of Interaction Strength in Nature. *Annual Review of*
- 499     *Ecology, Evolution, and Systematics*, 36, 419–444.
- 500 Yodzis, P. & Innes, S. (1992). Body Size and Consumer-Resource Dynamics. *The American Naturalist*, 139,
- 501     1151–1175.

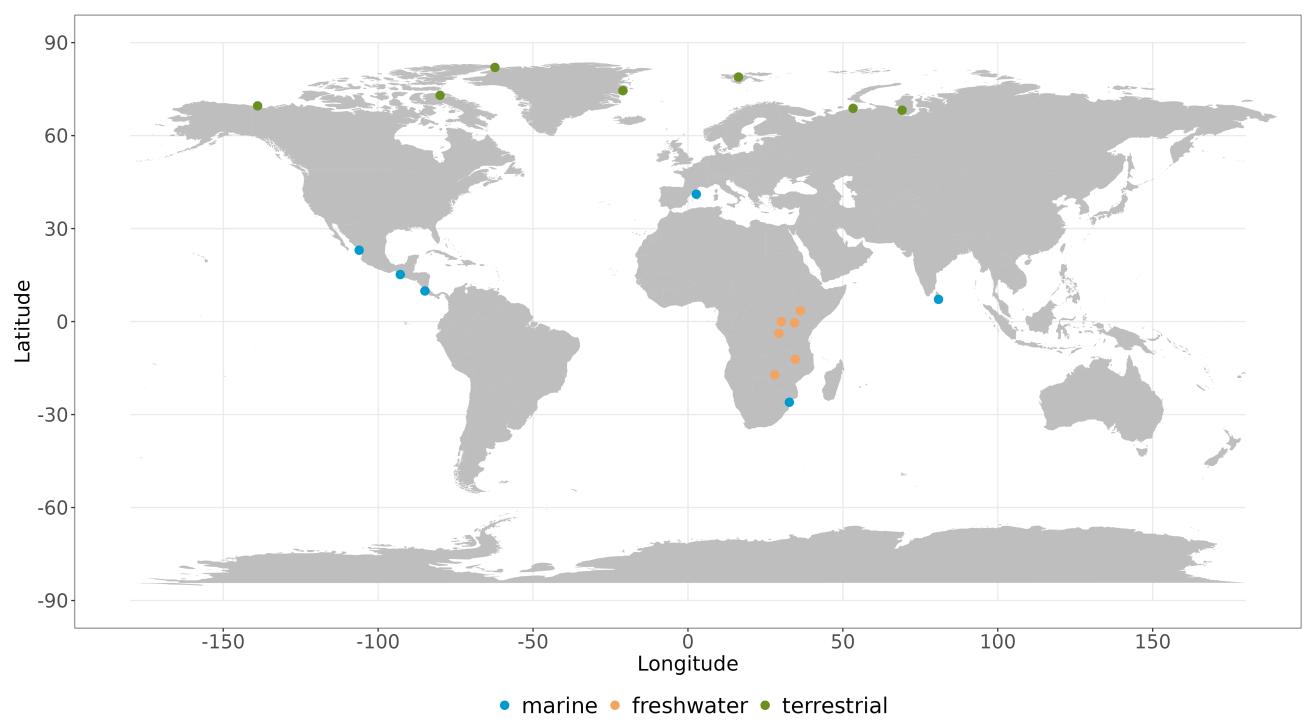


Figure 1: Map of Ecopath models locations used in the present study.

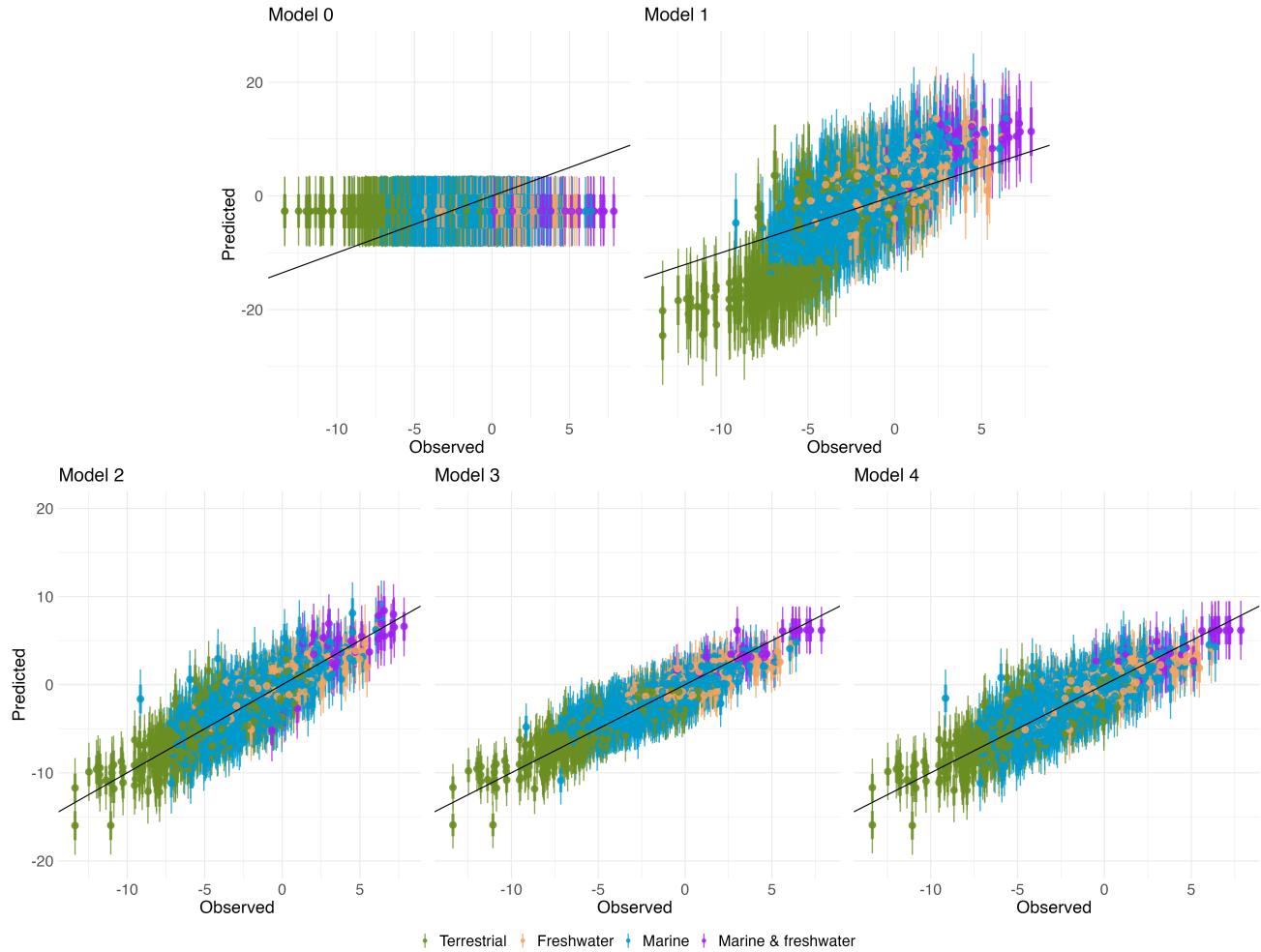


Figure 2: Models prediction of biomass fluxes compared to the observed biomass fluxes (log-scale) (metric tons/km<sup>2</sup>/year). The black line represents a one for one line. Points represent the mean predicted value and thick and fine error bars represent the 0.66 and 0.95 quantile distribution respectively. ‘Marine and freshwater’ points represent biomass fluxes from consumers that are present both in marine and freshwater ecosystems such as Zooplankton and Zoobenthos.

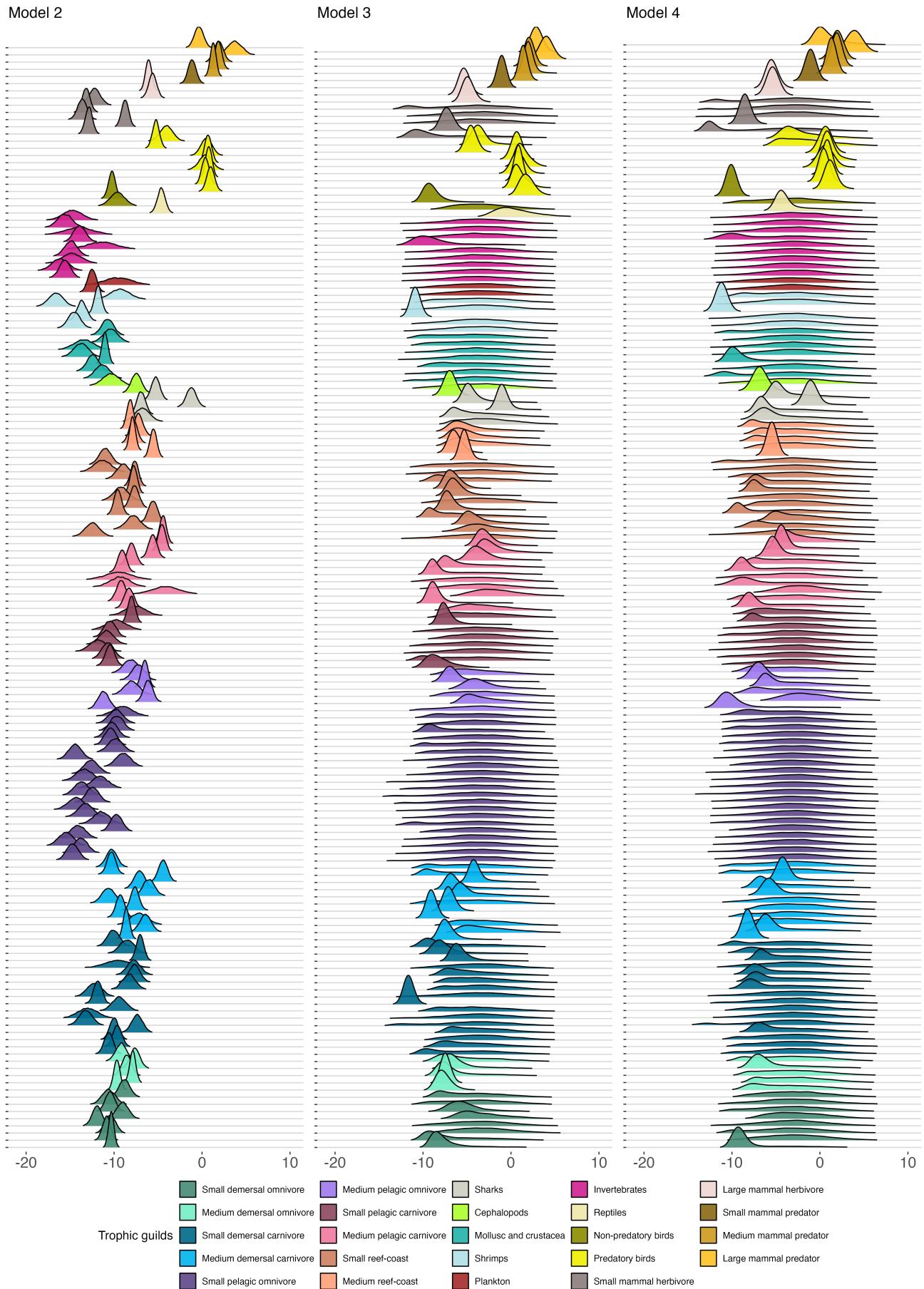
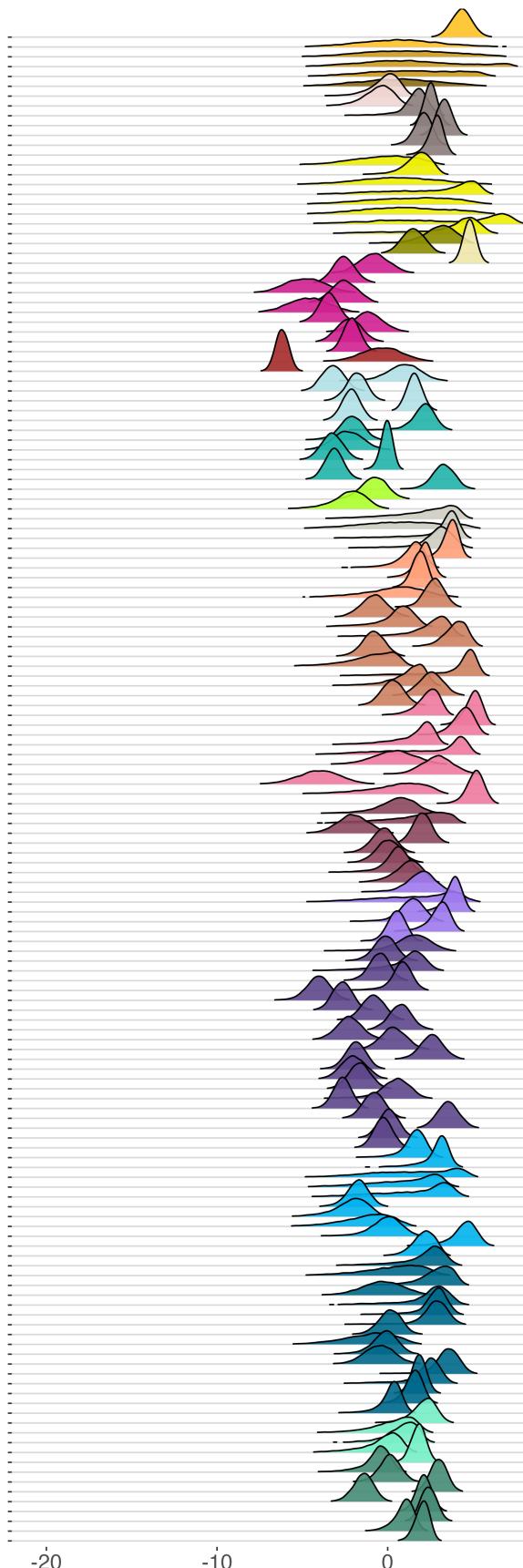
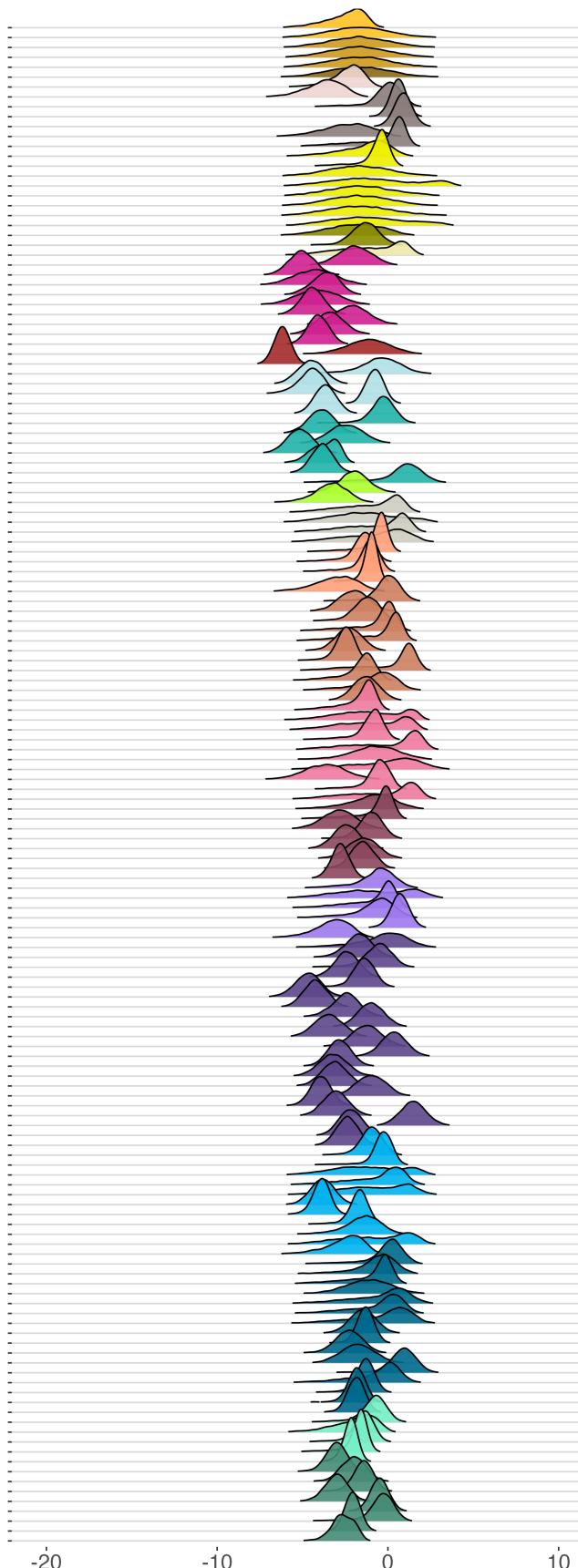


Figure 3: Posterior distribution of the space clearance rate parameter (log-scale) for model 2, 3 and 4 of 21

Model 3



Model 4



|                           |                          |                       |                     |                        |
|---------------------------|--------------------------|-----------------------|---------------------|------------------------|
| Small demersal omnivore   | Medium pelagic omnivore  | Sharks                | Invertebrates       | Large mammal herbivore |
| Medium demersal omnivore  | Small pelagic carnivore  | Cephalopods           | Reptiles            | Small mammal predator  |
| Small demersal carnivore  | Medium pelagic carnivore | Mollusc and crustacea | Non-predatory birds | Medium mammal predator |
| Medium demersal carnivore | Small reef-coast         | Shrimps               | Predatory birds     | Large mammal predator  |
| Small pelagic omnivore    | Medium reef-coast        | Plankton              |                     | Small mammal herbivore |

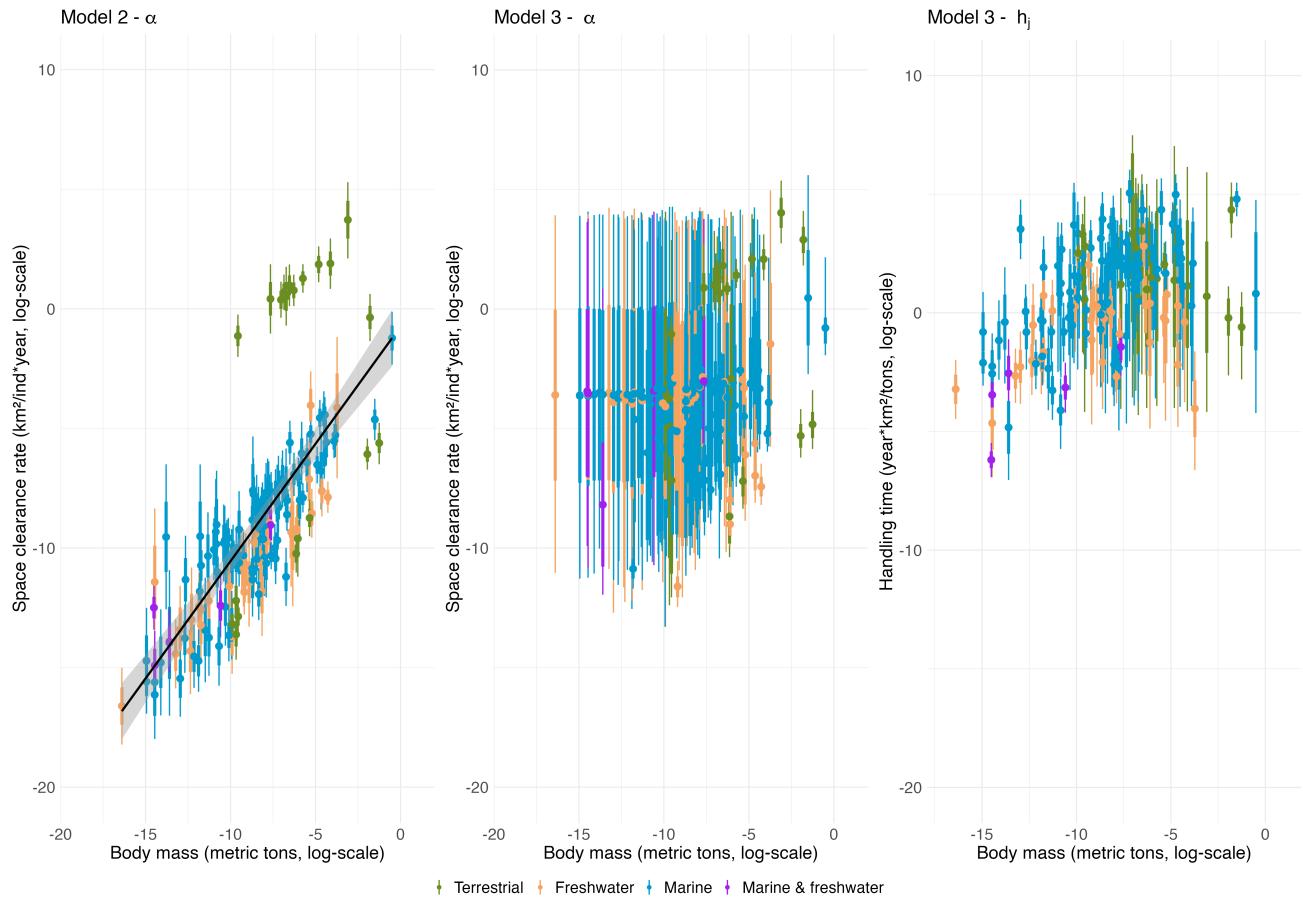


Figure 5: Relationships of the space clearance rate and handling time parameters with consumers body mass (log-scale). A clear and discernable relationship is present for model 2 space clearance rate and absent for model 3 space clearance rate and handling time parameters. The allometric relationship for model 2 space clearance rate is also accompanied by a linear regression with a slope of 0.98 (black line) and its 0.95% confidence interval (grey area). Points represent the mean space clearance rate and thick and fine error bars represent the 0.66 and 0.95 quantile distribution respectively.