New insights into the Weddell Sea ecosystem applying a network approach

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Abstract. The abstract goes here. It can also be on *multiple lines*.

1 Introduction

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The objective of this work was twofold: 1) estimate the strength for each interaction in the Weddell Sea food web, and 2) determine key trophic species considering weighted and unweighted properties and the influence on the stability of the network.

2 Methodology

2.1 Study area

The high Antarctic Weddell Sea shelf is situated between 74 and 78ºS with a length of approximately 450 km (Figure 1). Water depth varies from 200 to 500 m. Shallower areas are covered by continental ice, which forms the coastline along the eastern and southern part of the Weddell Sea. The shelf area contains a complex three-dimensional habitat with large biomass, intermediate to high diversity in comparison to benthic boreal communities and a spatially patchy distribution of organisms (Dayton, 1990; Teixidó et al., 2002).

2.2 Weddell Sea food web dataset

We obtained the dataset of the Weddell Sea food web from the GlobAL daTabasE of traits and food Web Architecture (GATEWAy, version 1.0) of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (Brose, 2018). This open access database is a list of predator-prey interactions that contains several highly-resolved food webs, including biological data about the consumer and resource species involved in each trophic interaction (i.e. mean mass). Furthermore, it incorporates information on the interaction itself, such as the dimensionality.

This marine food web compiles all the food web data available for the high Antarctic Weddell Sea collected since 1983, and is one of the most highly-resolved marine food webs documented to date. It's noteworthy that it is a summary network that ignores seasonal changes (Jacob et al., 2011).

2.3 Dataset analyses

We analysed the food web of the Weddell Sea by: a) estimating the strength of each interaction; b) studying the properties of the species in a network approach; and c) comparing the stability of the food web after performing species extinction simulations.

2.3.1 Interaction strength estimation and distribution

To estimate the strength of each interaction in the food web, we followed the methodology proposed by Pawar et al. (2012). The minimum data requirements are: body mass of the consumer (predator) and resource (prey), and the interaction dimensionality classified as 2 or 3 dimensions. GATEWAy v.1.0 does provide the mean mass for consumers and resources (except for 'detritus' and 'sediment') and the dimensionality for every interaction, though the latter is missing for 924 interactions. To solve this issue, we used information about movement type for consumer and resource included in GATEWAy. Then, we classified the interaction as 2D when both consumer and resource move in 2D (e.g., both are sessile or walking) or if a consumer moves in 3D and a resource in 2D (e.g., swimming consumer and sessile/walking resource). The interaction was classified as 3D when both consumer and resource move in 3D (e.g., both swimming) or if the consumer moves in 2D and resource in 3D (e.g., sessile/walking consumer, swimming resource) (Pawar et al., 2012).

The main equation we used for estimating the interaction strength IS was:

$$IS = \alpha x_R \frac{m_R}{m_C} \tag{1}$$

where α is the search rate, x_R is the resource density, and m_R and m_C are the body mass of the resource and the consumer, respectively (Pawar et al., 2012).

We obtained estimations for the resource density and the search rate from the scaling relationships with the resource and the consumer mass, respectively (Pawar et al., 2012). The coefficients of such relationships, determined by ordinary least squares regression, vary with the interaction dimensionality. On one hand, resource density scales with resource mass as a power-law with exponents $p = -0.79 \pm 0.09$ in 2D and $p = -0.86 \pm 0.06$ in 3D. Since mean mass for resources 'detritus' and 'sediment' were not available in GATEWAy, we estimated it considering the scaling relationship with consumer mass, also different in 2D and 3D (for details see equation S9 and figures 2c-d of Supplementary Information in Pawar et al. (2012)). On the other hand, search rate scales with consumer mass as a power-law with exponents $p = 0.68 \pm 0.12$ in 2D and $p = 1.05 \pm 0.08$ in 3D.

After this, we fit the distribution of the interaction strengths of the food web considering six candidate models (Uniform, Normal, Exponential, Power-law, log-Normal and Gamma) using maximum likelihood (**?**), and selected the model performance by computing the Akaike Information Criterion AIC (**?**).

2.3.2 Species properties

In order to individually characterize the species of the food web, we considered weighted and unweighted properties (Figure 2). The former is based on the estimation of the interaction strength described in the previous section. The latter is related to properties commonly used in qualitative (presence/absence of interaction) food web studies (Martinez, 1991; Dunne et al., 2002; Borrelli and Ginzburg, 2014).

As the weighted property we took into account the mean interaction strength, meaning the average strength of all interactions. After exploring the distribution of the species' log(mean interaction strength), we decided to apply the k-means clustering method, which aims to partition the species into k groups such that the sum of squares from points to the assigned cluster centres is minimized (**?**). Then we tested the goodness of this clustering measure with the Gap statistic, which is a kind of data mining algorithm to improve the clustering process by efficient estimation of the best number of clusters (**?**).

On the other hand, we considered the following unweighted properties: a) degree or the total number of trophic interactions, taking into account in- and out-coming interactions (role as predator and prey, respectively); b) trophic level or the position in the food web relative to primary producers/detritus; and c) trophic similarity or the trophic overlap between species based on shared and unique resources and consumers. The following are arguments to have selected the above properties. The degree has often been equated with importance to the structure and functioning of a community, i.e. perturbations to high-degree species may therefore have larger effects on the food web than perturbations to low-degree species (**?**; references in **?**). The trophic level offers information about how important a species is to its biotic community, i.e. top predators and primary producers are expected to have particularly large effects on the rest of their communities through top-down and bottom-up control, respectively (references in **?**). The trophic similarity measures the similarity of one of the most important aspect of species' niches, the trophic niche, and functional aspects of biodiversity (Martinez, 1991; **?**).

With the aim of studying the relationship between the interaction strength of the species and its unweighted properties, we performed linear regression analyses between the log(mean interaction strength) and each of the mentioned unweighted properties. The statistical significance of the fitted slopes was tested, as well as the difference between the groups' slopes applying least-squares means (**?**).

Formulas used to obtain the above species properties are described in Supplementary Material.

2.3.3 Stability and extinction simulations

Finally, we run extinction simulations and estimated its impact on the stability of the network. For this, we calculated a stability index called Quasi-Sign Stability (QSS), which is the proportion of stable networks using randomized Jacobians and keeping the predator-prey sign structure fixed (Allesina and Pascual, 2008). If this proportion is zero, then one should take into account the real part of the maximum eigenvalue of the Jacobian matrix, which is also a measure of stability (**?**).

With the aim of analysing the effect of each species on the food web's stability we deleted one species at a time, so the network size was reduced by one. After each species extinction, we calculated the stability for the food web minus one species (size = 489) and compared it with that of the whole network (size = 490). We performed 1000 simulations for each

species extinction and obtained a mean QSS and maximum eigenvalue. At last we statistically analysed such difference with an Anderson-Darling test considering a p-value < 0.01 (Scholz and Stephens, 1987). If the difference was positive, then the stability of the food web was impacted positively (higher stability) when that species become extinct, and viceversa. Details for the stability calculations are described in Supplementary Material.

Once we had the results for the impact on stability for each species extinction, we plotted them considering weighted (interaction strength) and unweighted properties, and species habitat.

All analyses were performed in R software, mainly using packages igraph (Csardi and Nepusz, 2005), cheddar (Hudson et al., 2013), and multiweb (Saravia, 2019). The source code and data are available at https://github.com/EcoComplex/WeddellSea.

3 Results

3.1 Interaction strength

In this work we have estimated the interaction strength for the most highly-resolved marine food web to date, which comprises 490 species and 16041 predator-prey interactions (Figure 3). The distribution of the interaction strength best fit to a log-Normal model, which indicates that there is a prevalent skew towards weaker interactions (Figure 4, Table 1).

3.2 Species properties

Regarding the distribution of the species mean interaction strength, the clustering method showed that species do form two distinct groups: 'High' and 'Low' interaction strength (Appendix Fig. A1). The so-called 'High IS' and 'Low IS' groups of species exhibited different and, in some cases, opposite relationships with unweighted properties. It's noteworthy that only the relationship with trophic level revealed a similar trend in the regression analysis for both groups: mean interaction strength increases with trophic level (Figure 5A). On the contrary, the linear regressions with degree and trophic similarity showed opposite relationships comparing groups. These mean that in species with relatively higher mean interaction strength, 'High IS', such strength decreases when the number of interactions (degree) increases; the opposite occurs in species with relatively lower interaction strength 'Low IS' (Figure 5B). Regarding trophic similarity, the interaction strength decreases in 'High IS' species while increases in 'Low IS' species (Figure 5C).

3.3 Stability and extinction simulations

It's important to note that since the proportion of Jacobians that are locally stable or QSS was zero for the Weddell Sea food web, we considered the mean maximum eigenvalue as the stability index. Our results showed that the majority of the species had no significant impact on the stability of the food web when extinct (Anderson-Darling test p-value > 0.01). This is clearly observed in Figure 6 A-D, where most of the points lie around the zero value of the 'Stability difference' axis. This means that the stability for the food web minus a given species is similar to the stability for the whole network. However, there were few species that when become extinct generated positive significant differences in the stability of the food web, meaning that

they increased the network's stability when deleted. There is an exception, Pagetopsis macropterus (demersal fish), that when deleted decreased the stability. In total, 13 out of 490 species (2.65%) gave rise to significant changes in the network's stability.

When plotting the stability difference against species properties and the previous results regarding clustering, interesting insights arose (Figure 6). In the first place, all species with a significant impact on the stability belong to the 'High IS' group, denoting a high mean interaction strength (Figure 6A). Secondly, these species are positioned in high trophic levels (TL > 3.7) (Figure 6B). Thirdly, they have a relatively high number of interactions or degree (Degree > 25) (Figure 6C). Regarding trophic similarity, species have mid to low values (TS < 0.13) (Figure 6D). Habitat wise, species live in all the habitats, except for are benthic (Figure 6E). Table 2 shows these results per species.
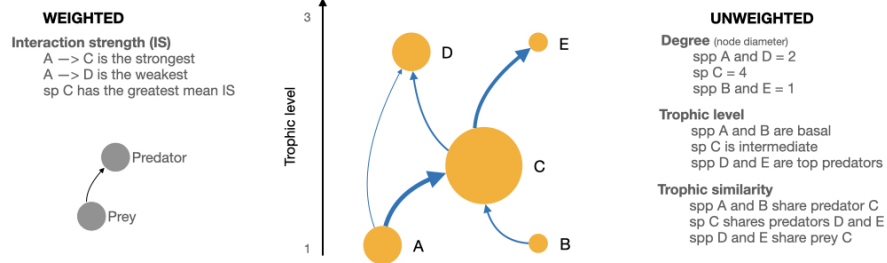
4   Discussion

"Low functional redundancy at key trophic levels makes these ecosystems (polar pelagic) particularly sensitive to change". (**?**)

5 Conclusions

The conclusion goes here.
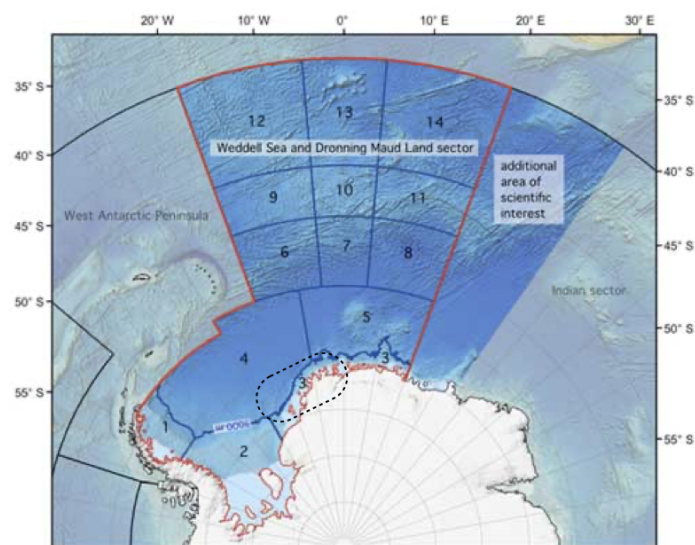
Figure 1. Map of the Weddell Sea and Dronning Maud Land sector highlighting the high Antarctic shelf as a dashed-line contour. Modified from www.soos.aq.

WEIGHTED

Interaction strength (IS)
A —> C is the strongest
A —> D is the weakest
sp C has the greatest mean IS

Predator

Prey

Trophic level

UNWEIGHTED

Degree (node diameter)
spp A and D = 2
sp C = 4
spp B and E = 1

Trophic level
spp A and B are basal
sp C is intermediate
spp D and E are top predators

Trophic similarity
spp A and B share predator C
sp C shares predators D and E
spp D and E share prey C

Figure 2. Scheme of a network showing the weighted and unweighted properties we used to characterize the species of the Weddell Sea food web.
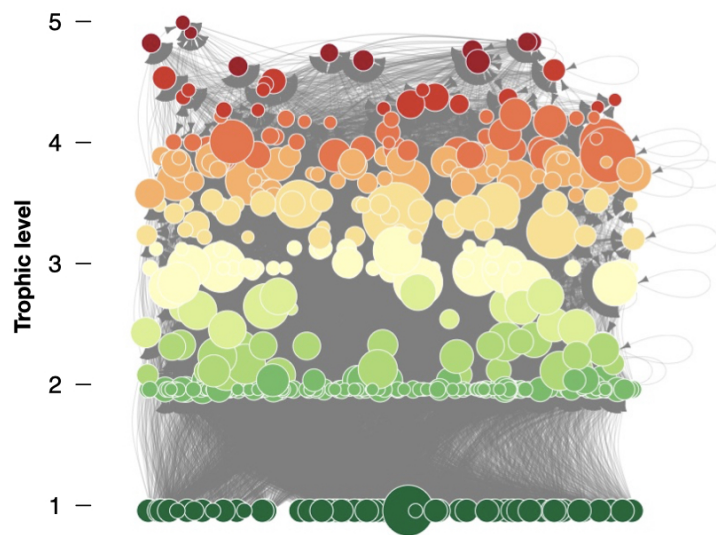
Figure 3. Graphic representation of the Weddell Sea food web. Species (nodes) are arranged verticaly and colored by trophic level. The diameter of the node indicates the total number of interactions. Predator-prey interactions are represented by the arrows, from the prey to the predator.
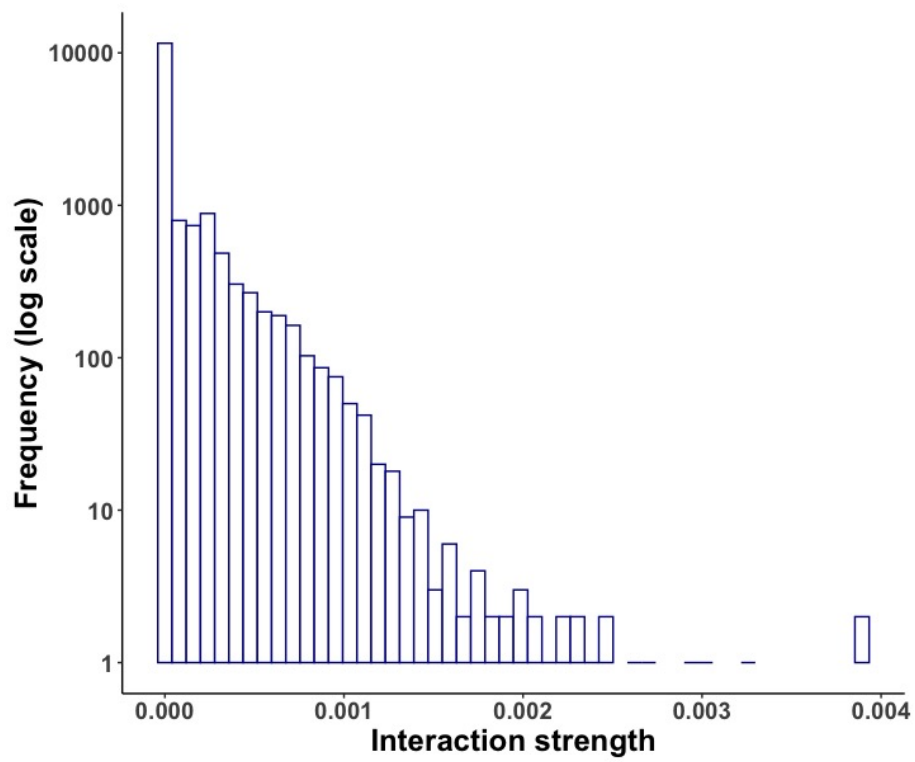
Figure 4. Frequency distribution of interaction strengths for the Weddell Sea food web (n = 490).
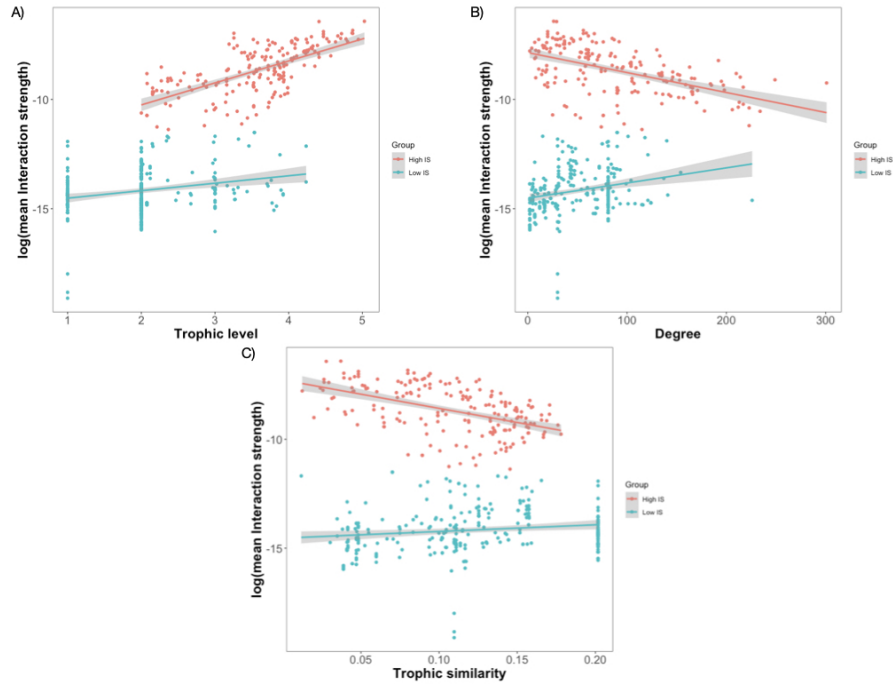
Figure 5. Relationships between weighted (interaction strength) and unweighted species properties. Linear regressions are shown between log(mean interaction strength) and trophic level (A), degree (B) and trophic similarity (C) for each group: 'High IS' and 'Low IS'. All regression slopes are significant and statistically different among groups ($p < 0.01$).
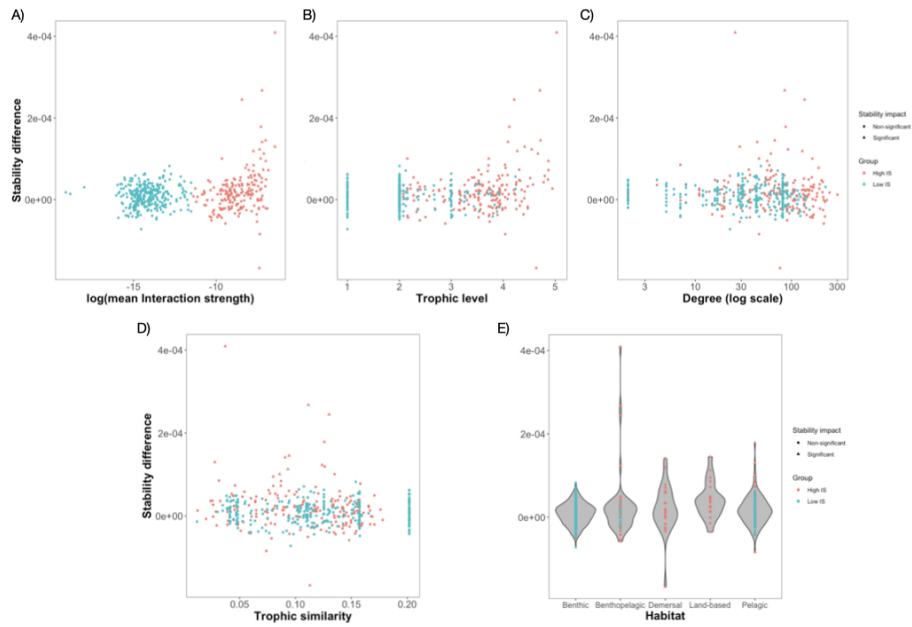
Figure 6. Quasi-Sign Stability (QSS) difference between the whole Weddell Sea food web (n = 490) and the food web minus one species (n = 489), considering weighted (interaction strength) and unweighted species properties, and species habitat. Each point represents a species, where color represents 'High IS' and 'Low IS' groups. Shape indicates the impact on the QSS; if significant the extinction of that species altered the stability of the food web.

Table 1. Model comparison for the distribution of interaction strengths of the Weddell Sea food web. Order by best fit. References: df = degrees of freedom, AIC = Akaike Information Criterion, deltaAIC = difference with best fit. Log-Normal is the best model.

Model	df	AIC	deltaAIC
log-Normal	2	-356579	0
Gamma	2	-352575	4004
Power-law	2	-347646	8933
Exponential	1	-262852	93726
Normal	2	-222785	133793
Uniform	2	-178001	178578

Table 2. Properties of the species that when become extinct generated a significant impact on the stability of the Weddell Sea food web, ordered by significance (Anderson-Darling p value). All species belong to the 'High IS' group. References: meanIS = mean interaction strength, TL = trophic level, Deg = degree, TS = trophic similarity, StabDif = stability difference, ADvalue = Anderson-Darling p value.

Species	meanIS	TL	Deg	TS	Habitat	StabDif	ADvalue
Orcinus orca	0.00163	5.03	26	0.037	Benthopelagic	0.00040	1.38e-51
Macrourus holotrachys	0.00074	4.70	85	0.112	Benthopelagic	0.00027	2.75e-18
Abyssorchomene nodimanus	0.00022	4.21	137	0.130	Benthopelagic	0.00024	1.02e-15
Dissostichus mawsoni	0.00069	4.12	87	0.126	Pelagic	0.00018	1.06e-10
Pagetopsis macropterus	0.00063	4.64	76	0.113	Demersal	-0.00017	1.66e- 9
Macrourus whitsoni	0.00064	4.55	92	0.124	Benthopelagic	0.00012	4.97e- 8
Hydrurga leptonyx	0.00092	4.72	67	0.094	Land-based	0.00014	5.59e- 6
Mesonychoteuthis hamiltoni	0.00161	4.41	29	0.028	Pelagic	0.00013	6.53e- 6
Notothenia marmorata	0.00073	4.09	44	0.091	Demersal	0.00014	2.10e- 5
Champsocephalus gunnari	0.00068	3.72	46	0.086	Pelagic	0.00010	7.97e- 5
Arctocephalus gazella	0.00083	4.67	61	0.093	Land-based	0.00011	9.52e- 5
Ommatophoca rossii	0.00093	4.87	56	0.080	Land-based	0.00009	1.20e- 3
Notothenia coriiceps	0.00044	4.27	130	0.126	Demersal	0.00012	1.33e- 3
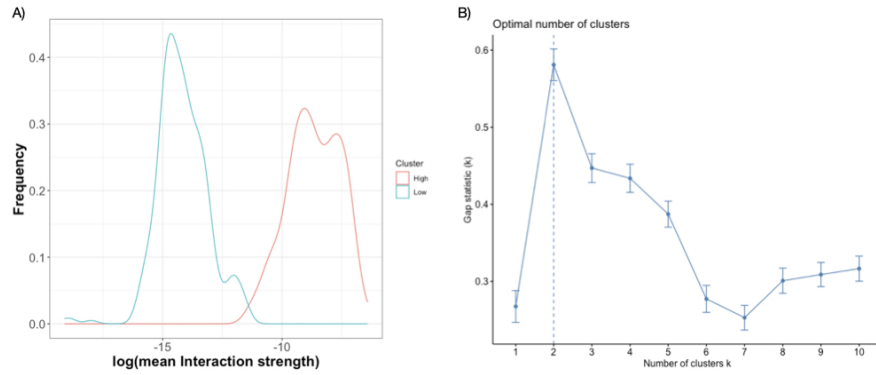
Figure A1. A) Frequency distribution for the mean interaction strength of the species of Weddell Sea food web. B) Visualization of the optimal number of clusters applying the Gap statistic.

. TIM and LAS: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Coding (lead); Writing – original draft (lead); Writing – review and editing (lead). SK: Conceptualization (lead); Formal analysis (supporting); Methodology (supporting); Coding (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

. The authors declare no competing interests.

. Thanks to the rticles contributors!

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