NetworkExtinction: an R package to explore the propagation of extinctions through complex ecological networks

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Running headline: NetworkExtinction in trophic networks

Abstract

1. Biodiversity loss is one of the current drivers of global change with an acute impact on community structure. Different measures and tools (e.g., simulations of extinction events) have been developed to analyze the structure of ecological systems and their stability under biodiversity loss, especially in complex settings with multiple interacting species, such as food webs. However, there remains the need for tools that enable a quick assessment of the ensuing impacts on food webs structure due to species extinction. Here, we develop an R package to explore the propagation of species extinctions through food webs, measured as secondary extinctions, according to user-defined node removal sequences.

2. In the NetworkExtinction package, we seek the integration between theory and computational simulations by developing six functions to analyze and visualize the structure and robustness of food webs represented as binary adjacency matrices. Three functions simulate the sequential extinction of species; a fourth function compares food web metrics between random and non-random extinction sequences; a fifth function visualizes the change in a given network metric along with the steps of sequential species extinction; a sixth function allows the user to fit and visualize the degree distribution of the network, fitting linear and non-linear regressions. We illustrate the package's use and its outputs by analysing a Chilean coastal marine food web.

3. By using the NetworkExtinction package, the user can estimate the food web robustness after performing species' extinction routines based on several algorithms. Moreover, the user can compare the number of simulated secondary extinctions against a null model of

random extinctions. The visualizations allow graphing topological indexes that the deletion sequences functions calculate after each removal step. Finally, the user can fit the degree distribution of the food web.

4. The NetworkExtinction R package is a compact and easy-to-use package to visualize and assess the food web structure (degree distribution) and robustness to different sequences of species loss. Therefore, this package is particularly useful to evaluate the ecosystem response to anthropogenic and environmental perturbations that produce non-random species extinctions. In that way, it also allows us to assess the contribution of central nodes to food webs stability.

Keywords: network science, food webs, extinction analysis, R packages

Introduction

Biological systems can be represented as complex networks of interactions through which information, matter and energy flow in a structured way (Benedek et al., 2007; Pascual and Dunne, 2006; Proulx et al., 2005). A myriad of perturbations can substantially alter these fluxes at different temporal and spatial scales (Donohue et al., 2016; Radchuk et al., 2019; Venter et al., 2016), modifying the network components, by adding or removing species, or interactions from the network, re-wiring pathways of connection and changing interaction strengths. Therefore, the relationship between topology and the propagation of such disturbances through the main system offers useful avenues in the understanding of complex biological phenomena represented as networks (Gao et al., 2016).

Ecological networks are under strong perturbations produced by climate change and/or direct human activities, which in many cases might lead to a local or global extinction of species, or to a severe reduction in their abundance (e.g. total biomass) (Barnosky et al., 2011; Costello et al., 2016; May et al., 1995; Pimm et al., 2019; Scheffer et al., 2001; Vitousek et al., 1997). As a consequence of this, beyond the directly affected species, significant impacts may induce the extinction of other species in the network, or alter the stability and resilience of the ecosystem (Dunne et al., 2002*b*). Whether cascading effects are observed or not following removal or addition of a node depends, to some extent, on the complex structural attributes that define the network. Since the extinction of species and/or the modification of their interactions may directly induce degradation of ecosystem services, thus impacting human well-being, anticipating the potential propagation of these effects is of paramount importance (Barnosky et al., 2011; Dirzo and Raven, 2003). Therefore, the understanding of ecosystem stability and resilience to different

perturbations inducing species extinctions, has received considerable attention in the literature (Allesina and Pascual, 2009; Curtsdotter et al., 2011; Dunne et al., 2002*a*; Hastings et al., 2016; Jordan, 2009; Pimm et al., 2019; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2009).

On topological properties shaping the stability of complex networks

The complexity of biological networks imposes some challenges to develop an integrated framework and tools to study these systems. However, some general attributes that characterize most empirically constructed ecological networks do exist. For instance, the number of connections that each node in the network has, i.e., the degree distribution, usually follows a fat tail degree distribution (Bascompte, 2009; Dunne et al., 2008). Theoretical models show that the degree distribution of the network is strongly associated with its robustness to species loss (Sole and Montoya, 2001) and, therefore, linking degree distribution to resilience and robustness of different types of ecological networks seems to be a promissory research venue (de Santana et al., 2013). For example, power-law degree distributions, where superconnected nodes are more common, are more vulnerable to the removal of the most connected nodes (de Santana et al., 2013; Dunne et al., 2002*a*; Estrada, 2007; Sole and Montoya, 2001). More generally, a directed attack to the nodes with higher degree, can have larger whole-sale consequences in the network (Albert and Barabási, 2002; Albert et al., 2000). Similarly, the role of diversity and connectance has been emphasized as providing robustness to food webs, to the extent that increasing number of species and connectance among them seem to delay the onset of a cascade of secondary extinctions Dunne et al. (2002*b*).

Assessing what is the model that best describes an empirical degree distribution has been an active research area and is a common task in the analysis of ecological networks. Different statis-

tical approaches have been proposed to fit the degree distribution, such as maximum likelihood (Clauset et al., 2009), ordinary least squares, or linear versus non-linear regression (Xiao et al., 2011). As in other fields, the use of linear and non-linear regressions has been controversial (Xiao et al., 2011). Some have suggested that the linearization using a logarithmic scale is flawed and that instead, the analysis should be conducted on the original scale using non-linear regression methods (Xiao et al., 2011). In part, this is because when using linear regressions (LR) on log-transformed data the error distribution may not confirm the assumptions needed to statistically compare across different models; hence, a second group of approaches considers the use of non-linear regression using general least squares, in combination with Akaike's information criteria to select the best model that fits the degree distribution.

Other topological measures are relevant to the persistence of ecological networks. For example, several studies have evaluated the importance of species traits (Binzer et al., 2011; Curtsdotter et al., 2011), species centrality (Albert and Barabási, 2002; Allesina and Pascual, 2009; Dunne et al., 2002*a*,*b*; Jordan, 2009) or species vulnerability to environmental conditions (Berg et al., 2015). In particular, *in silico* experiments suggest that species' degree and species centrality are key to food web persistence. The assessment of the importance of species on food web persistence is typically carried out by performing a sequence of species removals, followed by the evaluation food web robustness measured as the number of secondary extinctions.

Several indices and open source R packages have been created to visualize and analyze the topology and the dynamics occurring within networks (Table S1). However, despite the recent diversification of analytical tools, we still lack a way to efficiently asses food web robustness to a 'user-defined' sequence of species loss implemented in an open source platform, such as R. Simulating food web responses to an extinction sequence involve a number of computation-

ally demanding steps following the removal of the target nodes, which can be challenging and time consuming for researchers. Some node metrics (e.g node degree) are dynamically changing through the process and they must be calculated after each step. Assigning the next species to the extinction sequence depends on the calculations made after the previous one was removed. Similarly, to calculate other metrics, such as node richness or network connectance, it is necessary to remove all secondarily-extinct and totally isolated nodes (which are assumed extinct by definition). Our goal here is to develop an open-source free-access package aiming to facilitate the exploration of network resilience and changes in attributes following the removal or extinction of nodes in complex food webs. Here, we present the R package *NetworkExtinction*, which carries out the statistical analysis and visualization of the degree distribution of networks and summarize their topological changes to the simulated extinction of focal species.

Description and use of the package

The NetworkExtinction R package

The *NetworkExtinction* package analyzes unweighted food webs represented by nodes (e.g. all the same biomass) and the occurrence of trophic interactions. Species biomass and variation in interaction strengths between nodes are not considered. Thus, the input data corresponds to an adjacency matrix with 1s indicating a trophic interaction or 0s, the absence of that interaction for a pair of species.

Network representation in R and empirical example

The *NetworkExtinction* package interacts with other R packages, especially with the *network* package (Butts et al., 2008). From *network*, *NetworkExtinction* inherits the network class of the starting object, which allows the use of some functions to perform network analysis. To show how our package works and its outputs, we will use an empirical marine intertidal rocky shore food web (hereafter, `"chilean_intertidal"`), which has 107 species, 1381 trophic interactions, connectance of 0.12 and a mean trophic level of 1.64 (Kéfi et al., 2015).

The package, functions, and outputs

Let us begin by installing and loading the package into the R environment:

```
R> install.packages(NetworkExtinction)

R> library("NetworkExtinction")
```

The package contains six functions. We developed three functions to measure the food web topology and robustness after performing a given species deletion sequence. These sequences are: 1) deletion based on species' degree (*Mostconnected*), 2) a user-defined order (*ExtinctionOrder*) and 3) a random sequence (*RandomExtinctions*). A fourth function, *Comparison*, compares the number of secondary extinctions produced by any of the first two options, against the random deletion sequence. A fifth function, *ExtinctionPlot*, allows to visualize the changes in any of the network statistics that the deletion sequence generates after each removal step. Finally, a sixth function fits the degree distribution of the food web using two approaches, the linear (on log-transformed data) and the non-linear regression (*degree_distribution*).

Extinction functions

- *Mostconnected*

This function begins by sorting the species from the most to the least connected node, considering their total degree (in-degrees plus out-degrees), and storing the information in a vector. Then, the function calculates the species richness, number of links and network connectance, as topological indices of the network. Then, it removes the most connected node in the network, recalculating the topological indexes of the network and counting the secondary extinctions, i.e., how many species, except primary producers, results with an in-degree=0 after the primary extinction. All the extinct species are removed from the network. After that removal, the algorithm recalculates the degree ranking, iterating the process until the number of links in the network is zero (Dunne and Williams, 2009; Dunne et al., 2002*a*; Sole and Montoya, 2001). The function has the following argument:

  - *Network*: Network class. The name of the network object to analyze,

```
R> data("chilean_intertidal")

R> Mostconnected(Network = chilean_intertidal)
```

This function returns a data frame with the metrics of the network after every step of species removal (Table 1). The first column (Spp) shows the vertex position of the removed species in the vector. From the the second to the fifth column, we represent the following topological indexes: richness (S), number of links (L), food web connectance (C = L/S^2) and link density (Link_density = L/S). The sixth column (SecExt) indicates the number of secondary extinctions produced after each removal step, which was quantified as the number of nodes (except for the

basal nodes) that results with an indegree = 0 after producing a primary extinction. The seventh column (Pred_release) represents the number of species that were released from predation after each removal step, which was quantified as the number of nodes resulting with zero predators (outdegree) after a primary extinction. The predation release index does not consider the initial top predators in their calculation. Finally, from the 8th to the 11th columns we represent the number of nodes that result with a total degree = 0 (Iso_nodes), the cumulative number of secondary extinctions (AccSecExt), the cumulative number of primary removals (NumExt) and the total number of extinctions (TotalExt = NumExt + AccSecExt).

- `ExtinctionOrder`

The `ExtinctionOrder` function removes nodes using an user-defined order. Then, it calculates the secondary extinctions and the same topological network indexes are calculated by the `Mostconnected` function. This function requires the following arguments:

  - *Network*: Network class. The name of the network to analyze.
  - *Order*: Numeric vector. The removal sequence of interest with the node position of the species sorted in order of interest.

In our example, the customized order is a vector with the species ordered by vulnerability, from the most to the least vulnerable according the number of predators.

```
R> data("chilean_intertidal")

R> ExtinctionOrder (Network = chilean_intertidal, Order = c(67,37,69,...,97,106,107))
```

In this case, the function returns a data frame with the metrics of the food web after each removal step (Table 2) and a graph with the accumulated secondary extinctions after each removal

step (Fig. 1). The structure and nomenclature of this table is the same as the nomenclature of the Table 1. In the (Table 2), the last species removed was the species in the position 27. This is because the extinction functions stop when the network reaches a zero number of links.

The resulting plot (Fig. 1) represents the cumulative secondary extinctions (vertical axis) that were produced after each removal step (horizontal axis).

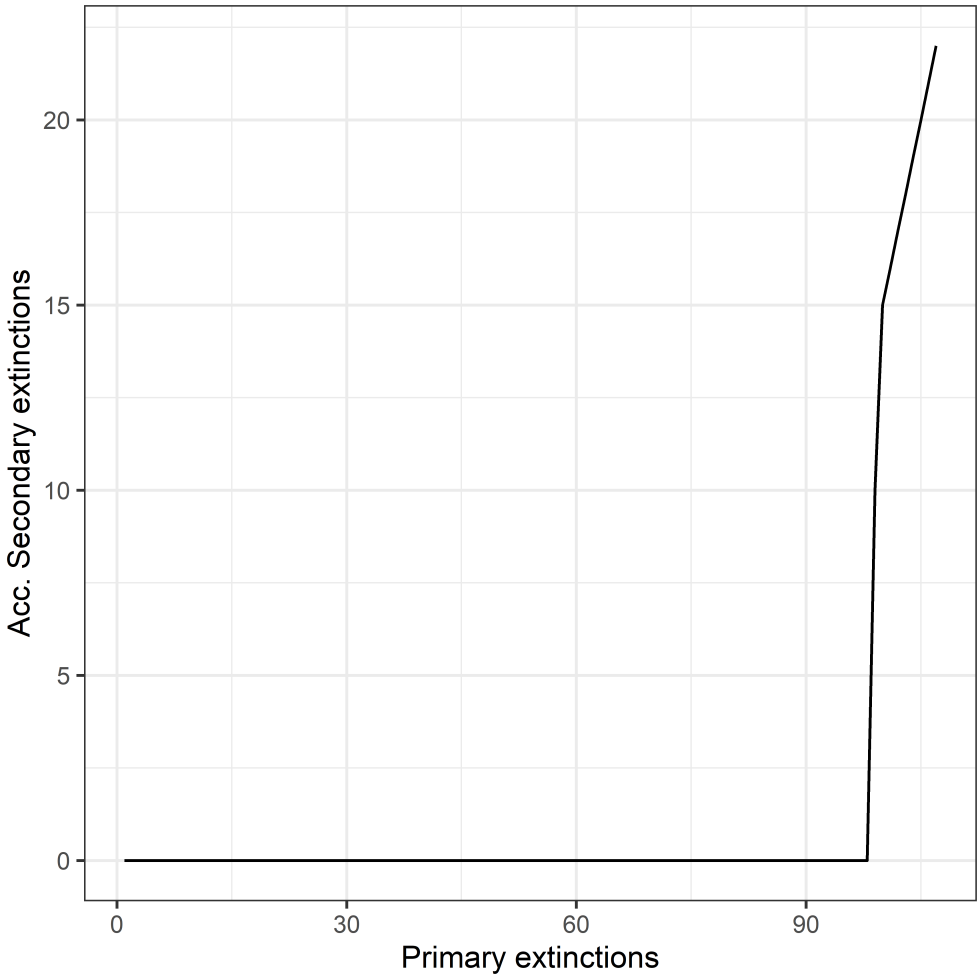

Figure 1: Cumulative secondary extinctions after each removal step (Primary extinctions) using the *ExtinctionOrder* function for the intertidal food web.

- `RandomExtinctions`

The `RandomExtinctions` function generates *nsim* independent random extinction sequences by bootstrapping. Each trajectory in *nsim* runs until all species are extinct. After all the trajectories were simulated, the function calculates the average and standard deviation of the number of secondary extinctions through *nsim* for each removal step.

To run the `RandomExtinctions` function the following arguments are necessary:

- *Network*: Network class. The name of the network to analyze.
- *nsim*: is number of random extinction sequences chosen by the user.
- *parallel*: is an optional argument to run the simulation in parallel trough different cores to decrease the running time. if is TRUE, it will use parallel processing, if FALSE (default) it will run sequentially.
- *ncores*: number of cores to use if using parallel processing. To calculate the number of cores you can run:

```
R> ceiling(parallel::detectCores())
```

```
R> data("chilean_intertidal")

R> RandomExtinctions(Network= chilean_intertidal, nsim= 500, parallel = TRUE, ncores = 4)
```

The function returns a data frame and a plot with the mean of secondary extinctions for each removal step averaged through all the simulations. The resulting data frame contains five columns (Table 3). The first column incorporates the cumulative number of species removed (NumExt). The second column presents the cumulative 95% of confidence intervals (CI) of the secondary extinctions among all the simulations performed. The third column shows the cumulative average of the secondary extinctions among all the simulations performed. The fourth and

fifth column represents the lower and upper limit of the [mean + 95% CI], respectively.

The resulting plot (Fig. 2) shows the cumulative average number of secondary extinctions (± 95% CI) along with the number of primary extinctions.

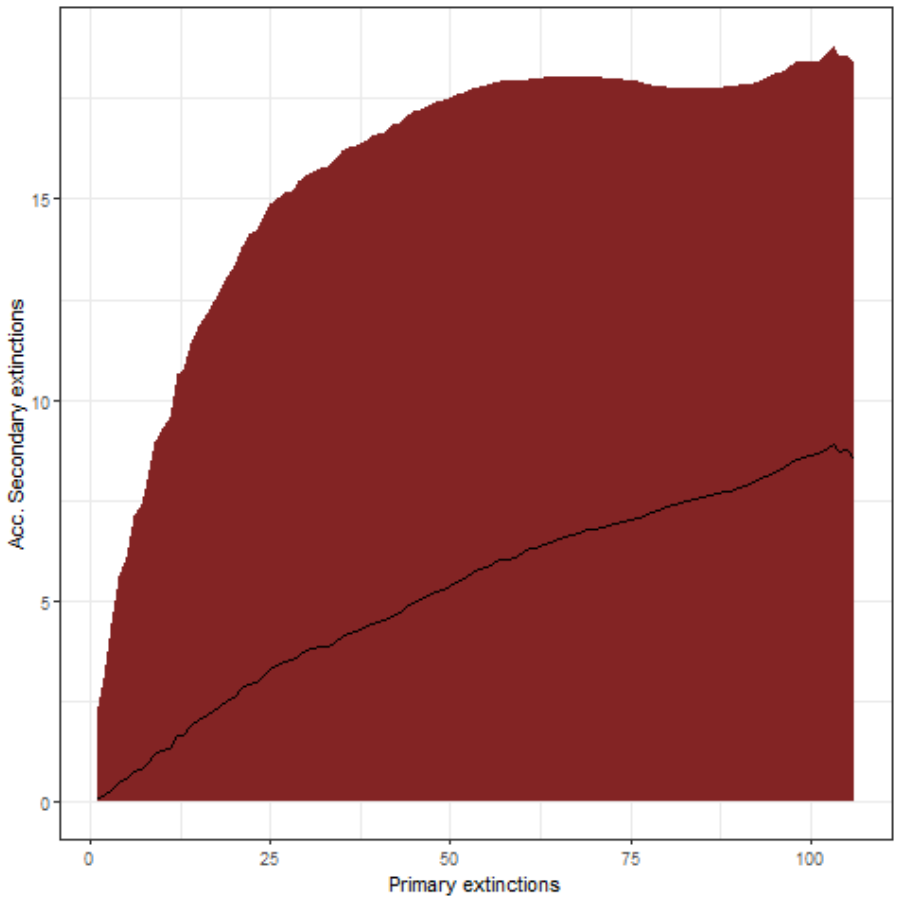

Figure 2: Cumulative secondary extinctions (Cumulative Secondary extinctions) after each removal (Primary extinctions, chosen by user) step using the *RandomExtinction* function for the intertidal food web.

By default this function does not record the result of each nsim simulated,

By default, this function does not record the result of each simulated nsim. If you require the result of each nsim, you can add the argument records = T in the `RandomExtinctions` function

- `CompareExtinctions`

The `CompareExtinctions` function compares the accumulative observed extinction generated by the *ExtinctionOrder* function or by the *Mostconnected* function against a null model of the expected accumulative secondary extinctions developed by the *RandomExtinctons* function.

To run the `CompareExtinctions` function is necessary the following arguments:

- *Nullmodel*: A data frame. The object returned by the *RandomExtinctons* function.
- *Hypothesis*:A data frame. The object returned by the *Mostconnected* function or the *ExtinctionOrder* function.

In this case, we compared the secondary extinctions produced by the *random* deletion sequence with the extinctions produced by the *Mostconnected* deletion sequence.

```
R> data("chilean_intertidal")
R> Random <- RandomExtinctons(Network= chilean_intertidal, nsim= 500,
parallel = TRUE, ncores = 4)
(see RandomExtinctions function to arguments information)
R> MC <- Mostconnected(Network = chilean_intertidal)
(see Mostconnected function to arguments information)
R> CompareExtinctions(Nullmodel = Random, Hypothesis = MC)
```

This function returns a figure comparing the number of secondary extinction between the two deletion sequences performed (Fig. 3).

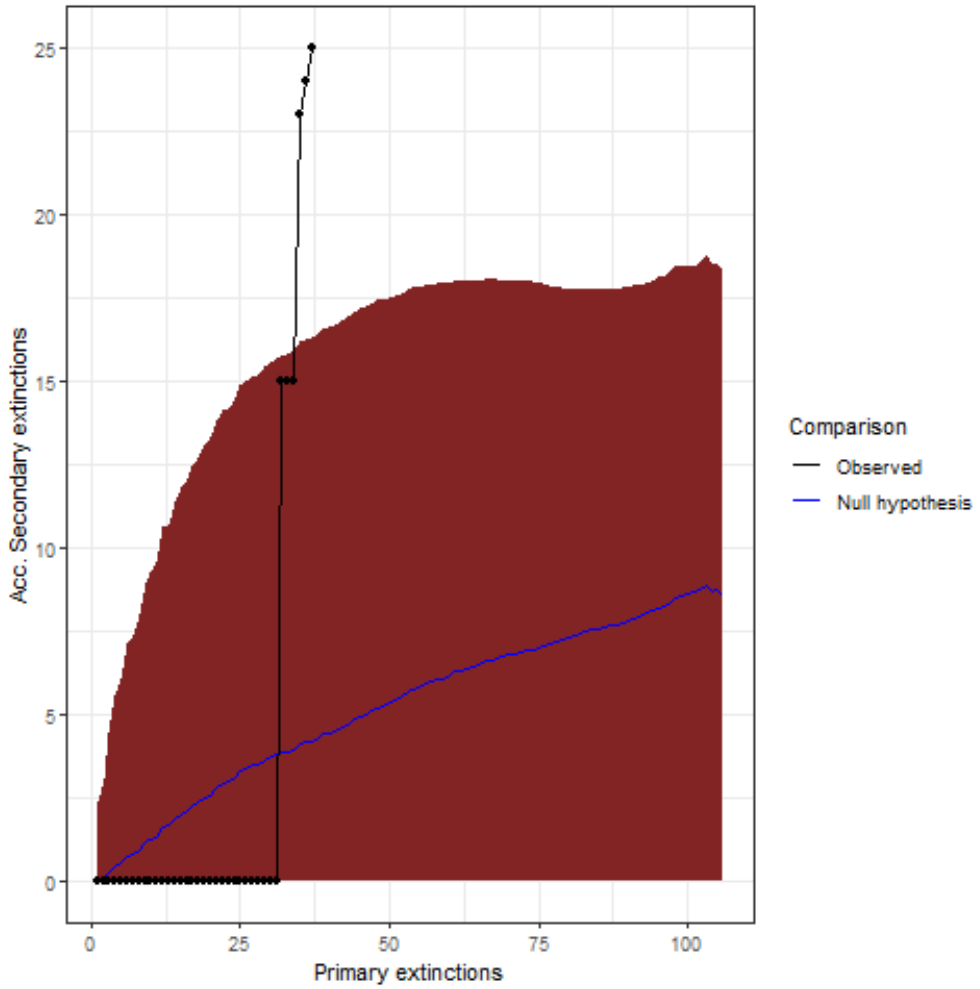

Figure 3: Comparison of the cumulative secondary extinctions (Cumulative Secondary Extinctions) after each removal step (Primary extinctions, defined by user) between the random (Null hypothesis) and *Mostconnected* (Observed) deletion sequence in the intertidal food web using the *CompareExtinctions* function. The solid blue line is the average ($\pm 95\% CI$) of secondary extinctions of the null model and the solid black line, the secondary extinctions of the observed model.

- `ExtinctionPlot`

The *ExtinctionPlot* function takes an output data frame from any of the extinction functions

and plots the indicator of interest after each primary extinction step. By default, this function plots the number of accumulated secondary extinctions after every primary extinction, but any of the indices (e.g., link density, or predation release) can be plotted with the function by changing the *Variable* argument.

To run the `ExtinctionPlot` function is necessary the following arguments:

- *History*: A data frame. The object returned by the *Mostconnected* function or the *ExtinctionOrder* function.
- *Variable*: is the name of the dependent variable of interest to be plotted against the number of extinctions.

As an example, we plot the link density of the intertidal food web at each removal step using the *Mostconnected* function (Fig. 4)

```
R> data("chilean_intertidal")
R> MC <-Mostconnected(Network = chilean_intertidal)
R> ExtinctionPlot(History = MC, Variable = "Link_density")
```

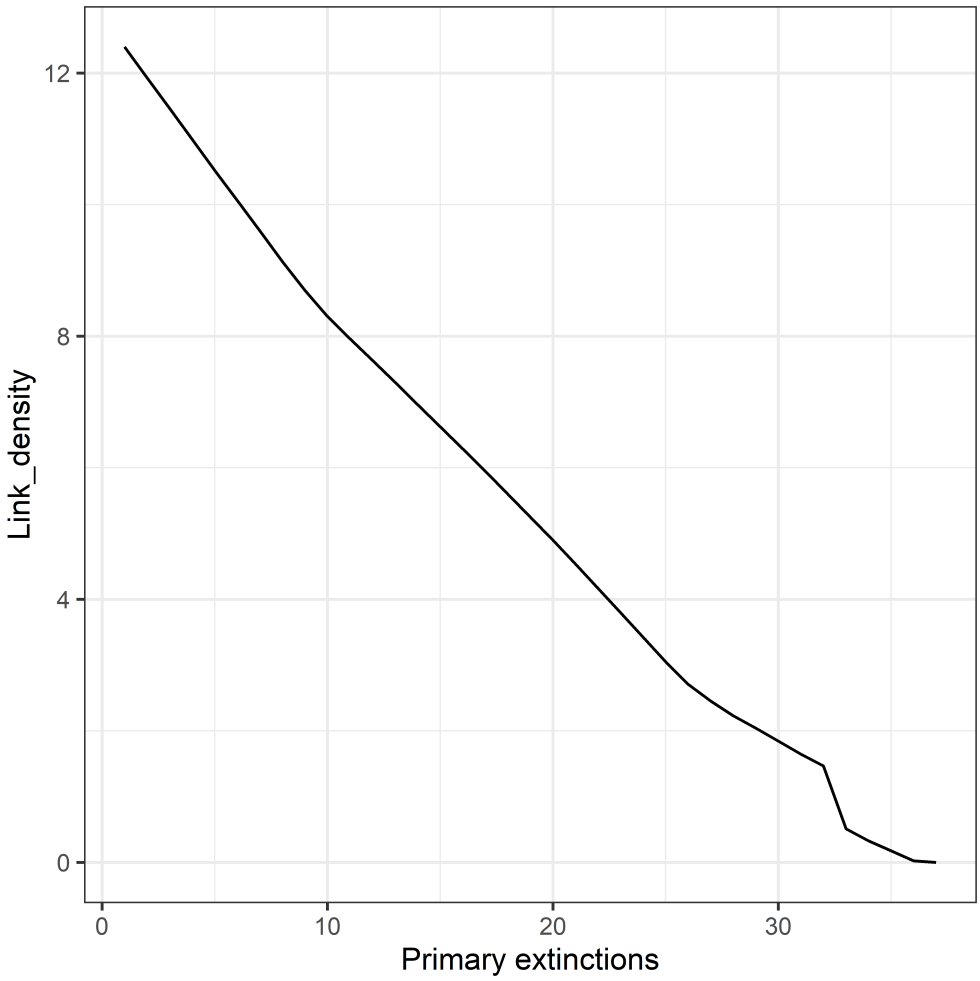

Figure 4: Links density (Link_density) after each removal step (Primary extinctions) in the intertidal food web using the *ExtinctionPlot* function.

- `degree_distribution`

The `degree_distribution` function computes the degree distribution of a network, calculating $P(k)$, i.e, the probability that a node in the network is connected to k other nodes (Estrada, 2007). Then, the observed distribution is fitted to the exponential and power-law models using two different approaches, non-linear least squares (Godfrey et al., 1998), and linear models on

log-transformed data (Xiao et al., 2011). A complete set of model fitting techniques is already available (Clauset et al., 2009).

We used a two-step model selection approach to decide between the two models fitted to the network degree distribution. Firstly, it select the best way of fitting the models (non-linear, NLR vs log-transformed linear approach, LR) in terms of providing good estimates of precision for hypothesis testing; and secondly, after one approach has been selected for the exponential and the power-law distribution, it is selected to which distribution form the data fits better. To select the method for fitting each distribution, exponential or power-law, we fit each the model of each distribution using both methods (LR and NLR) (Table 4). Following Xiao et al. (2011), we used maximum likelihood fitting for testing the normal distribution of residuals, and calculated *AICc* values for each method. To do that, we compared the ΔAICc between both methods (LR and NLR) to each distribution model. If, the ΔAICc between LR and LNR is larger than 2 (like it is in example below), we used that method as the best for fitting the distribution, otherwise, a model average is used between both methods using Akaike weights following (Burnham and Anderson, 2002).

After the linearized or non-linear approach has been selected, a comparison is made between the exponential vs the power-law distributions using AIC comparison (Burnham and Anderson, 2002). By doing this, we only select the best model describing the degree distribution, since there is no way of doing model averaging between both models (for more details about the model selection see Xiao et al. (2011)).

To run the `degree_distribution` function is necessary the following arguments:

- *Network*: Network class. The name of the network to analyze.
- *scale*: a character stating if the graph is on a log-log scale ("LogLog") or arithmetic

scale ("arithmetic")

Here, we will exemplify using a log-log scale. Thus,

```
R> data("chilean_intertidal")

R> degree_distribution(chilean_intertidal, scale = "LogLog")
```

The results of this function are three data frames (models, params, and DDvalues) with:

- *models*: The comparison of the AIC and normal distribution of the residual assumption test between the different distribution tested (Table 5)
- *params*: The statistical parameters of each model (Table 6).
- *DDvalues*: The degree distribution with the observed values and the value of each fitted model.

To recognize which model better explains the observed data, it is necessary to analyze the output data frame *models* (Table 5). The data frame contains five columns with the fitted model information in the rows ordered by descending AIC, that is, from the best to the least agreement between data and model distribution. The first column shows the relative likelihood of the error structure. The second and third column shows the AIC and BIC information criteria measures. The fourth column indicates whether or not the normal distribution of the errors and log-normal errors assumptions is met. The last column represent the family distribution of the model fitted to data.

In our example, the best model is the exponential degree distribution obtained from NLR with a AIC = -160.30 (see Table 5). If we calculate the difference between the AIC value obtained from NLR (Exp model) with the AIC value obtained from LR (LogExp) (-160.30 - 60.96 = -221.26),

it is $<$ -2, which means that we proceed with the results obtained from NLR. Thus, the intertidal food web follows an exponential degree distribution (Fig. 5).

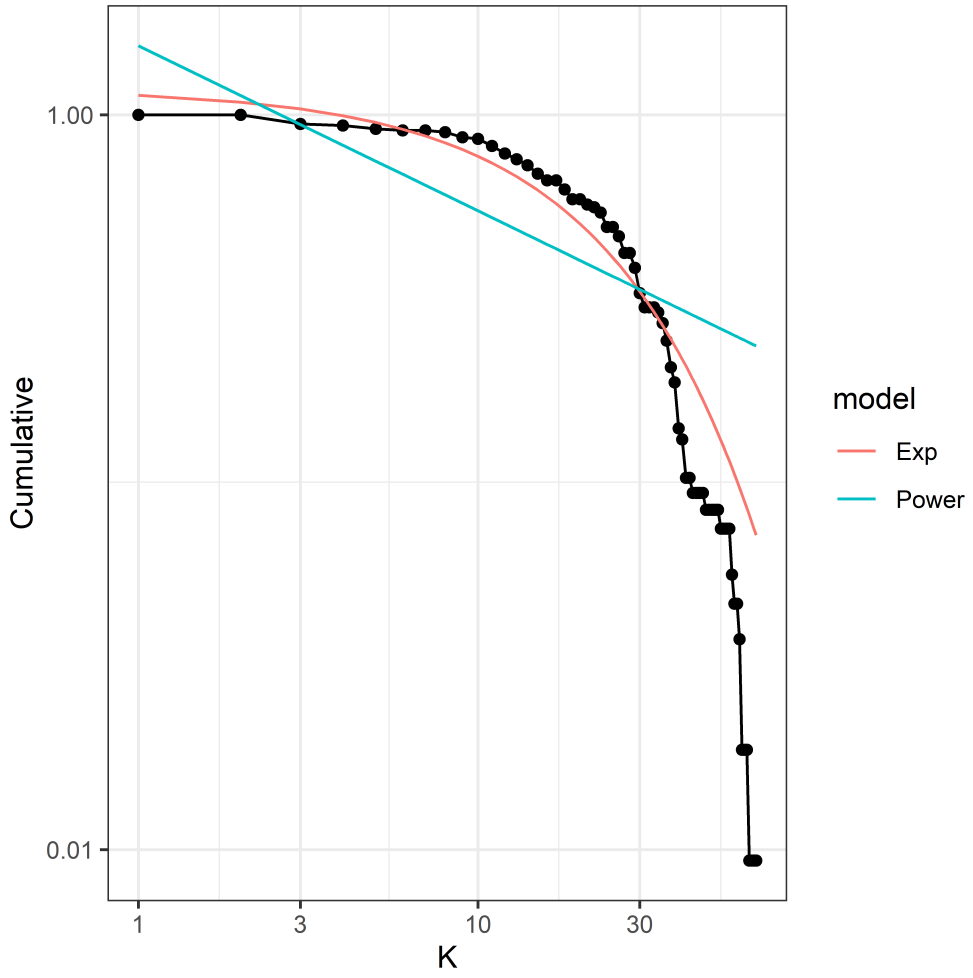

Figure 5: Cumulative probability distribution (Cumulative) for a given degree (k) using the degree_distribution function. The plot shows two different model fits (lines) note that since the fitted lines are regression models, their predicted values can sometimes start in values over one. Dots are the observed values

Finally, the statistical parameters of the models are presented in Table 6). The data frame contains the parameters of the power-law and exponential models and their log-transformed

versions. The first column represents the term of the models presented in Table 5. From the second to the fourth columns are the statistical parameters obtained with Kolmogorov Smirnov test. The sixth column indicate the model fitted to data.

Conclusions

We developed an easy-to-use package to visualize and assess the food web structure and robustness to different sequences of species loss. This package is useful since releases the researcher from the high computational demand that is required after removing a node from the food-web to recalculate: (1) each of the network properties, (2) the number of secondary extinctions, and (3) the next species that has to be removed in those extinction sequences in which the identity of the node to be removed is dynamic. Although our package considered purely network topology methods, in which unweighted trophic links may mask important dynamics, we considered that assessing the potential robustness that structure may confer on an ecosystem is an important first step to identify. We expect this package will particularly benefit researchers who have low programming experience.

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Author's contributions

M.I.A. D.C. and P.M. conceived the study. M.I.A. and D.C. wrote the code. S.A.N. provided the data for the intertidal foodweb. M.I.A.T., D.C. and S.P.C. wrote the first draft of the manuscript. All authors contributed to the final version of the paper.

Data and code availability

Additional information can be found in the R vignette (https://rdrr.io/cran/NetworkExtinction/man/) and in the project webpage (https://derek-corcoran-barrios.github.io/NetworkExtintion).

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TABLES

Table 1: Summarised results of the *Mostconnected* function for the intertidal food web, showing the first and last three rows.

Spp	S	L	C	Link_density	SecExt	Pred_release	Iso_nodes	AccSecExt	NumExt	TotalExt
15	106	1314	0.12	12.40	0	0	0	0	1	1
13	105	1252	0.11	11.92	0	0	0	0	2	2
4	104	1192	0.11	11.46	0	0	0	0	3	3
.			.	.	.	.	.	.	.	.
.			.	.	.	.	.	.	.	.
.			.	.	.	.	.	.	.	.
67	57	10	0.00	0.18	8	41	47	23	35	58
107	48	1	0.00	0.02	1	46	46	24	36	60
33	46	0	0.00	0.00	1	45	46	25	37	62

Spp: node position of the extinct species, S: richness, L: number of links, C: connectance, Link_density: link density (L/S), SecExt: secondary extinctions, Pred_release: predation release, Iso_nodes: isolated nodes, AccSecExt: accumulative secondary extinctions, NumExt: number of primary extinctions, TotalExt: number of total extinctions

Table 2: summarised results of the ExtinctionOrder function for the intertidal food web, showing the first and last three rows of the original data frame.

Spp	S	L	C	SecExt	Pred_release	AccSecExt	NumExt	TotalExt
67	106	1345	0.12	0	0	0	1	1
37	105	1309	0.12	0	0	0	2	2
69	104	1275	0.12	0	0	0	3	3
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
1	6	7	0.19	0	0	37	80	117
4	5	2	0.08	3	1	40	81	121
27	2	0	0.00	1	1	41	82	123

Spp: vertex position of the specie deleted, S: richness, L: number of links, C: connectance, SecExt: secondary extinctions, Pred_release: predation release, AccSecExt: cumulative secondary extinctions, NumExt: number of primary extinctions, TotalExt: number of total extinctions

Table 3: summarised results of the *RandomExtinction* function for the intertidal food web, showing the first and last three rows

NumExt	AccSecExt_95CI	AccSecExt_mean	Upper	Lower
1	2.28	0.09	2.37	0
2	2.93	0.15	3.08	0
3	4.12	0.30	4.42	0
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
104	9.81	8.72	18.53	0
105	9.82	8.76	18.58	0
106	9.83	8.55	18.37	0

Table 4: Formulas for the different distributions

Distribution	Non-linear Model	Linear Model
Power-law	$P_{(k)} = ck^{\beta}$	$\log P_{(k)} = \beta \log k + c$
Exponential	$P_{(k)} = e^{\lambda k + c}$	$\log P_{(k)} = \lambda k + c$

Table 5: Model parameters and normal distribution tests

logLik	AIC	BIC	Normal.Resid	family
83.15	-160.30	-153.64	No	Exponential
13.39	-20.77	-14.20	No	PowerLaw

Table 6: Statistical parameters of the models

term	estimate	std.error	statistic	p.value	model
y	-0.45	0.04	-11.17	0	Power
a	1.54	0.15	10.27	0	Power
lambda	-0.04	0.00	-26.98	0	Exp
c	0.16	0.02	6.63	0	Exp