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APPLICATION

NetworkExtinction: An R package to simulate extinction propagation and rewiring potential in ecological networks

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Abstract

1. Earth's biosphere is undergoing drastic reorganization due to the sixth mass extinction brought on by the Anthropocene. Impacts of local and regional extirpation of species have been demonstrated to propagate through the complex interaction networks they are part of, leading to secondary extinctions and exacerbating biodiversity loss. Contemporary ecological theory has developed several measures to analyse the structure and robustness of ecological networks under biodiversity loss. However, a toolbox for directly simulating and quantifying extinction cascades and creating novel interactions (i.e. rewiring) remains absent.
2. Here, we present *NetworkExtinction*—a novel R package which we have developed to explore the propagation of species extinction sequences through ecological networks and quantify the effects of rewiring potential in response to primary species extinctions. With *NetworkExtinction*, we integrate ecological theory and computational simulations to develop functionality with which users may analyse and visualize the structure and robustness of ecological networks. The core functions introduced with *NetworkExtinction* focus on simulations of sequential primary extinctions and associated secondary extinctions, allowing user-specified secondary extinction thresholds and realization of rewiring potential.
3. With the package *NetworkExtinction*, users can estimate the robustness of ecological networks after performing species extinction routines based on several algorithms. Moreover, users can compare the number of simulated secondary

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extinctions against a null model of random extinctions. In-built visualizations enable graphing topological indices calculated by the deletion sequence functions after each simulation step. Finally, the user can estimate the network's degree distribution by fitting different common distributions. Here, we illustrate the use of the package and its outputs by analysing a Chilean coastal marine food web.

4. *NetworkExtinction* is a compact and easy-to-use R package with which users can quantify changes in ecological network structure in response to different patterns of species loss, thresholds and rewiring potential. Therefore, this package is particularly useful for evaluating ecosystem responses to anthropogenic and environmental perturbations that produce nonrandom and sometimes targeted, species extinctions.

KEYWORDS
disturbance, extinction thresholds, food webs, mutualistic networks, network science, network topology, robustness

1 | INTRODUCTION

Biological systems are commonly represented as complex networks of interactions (i.e. links between nodes representing species) through which matter and energy flow in a structured way. Prominent examples of such structures are food webs (Benedek et al., 2007; Pascual & Dunne, 2006; Proulx et al., 2005) and mutualistic networks (González-Castro et al., 2021; Schleuning et al., 2016; Sebastián-González et al., 2015). A myriad of perturbations, such as those produced by climate change and/or direct human activities, lead to local and/or global extinction or severe reductions in the abundance of species (Barnosky et al., 2011; Costello et al., 2016; May et al., 1995; Pimm et al., 2019; Scheffer et al., 2001; Vitousek et al., 1997) hence altering the networks where these species exist. Such changes can deeply alter network-contained energy fluxes at different temporal and spatial scales (Donohue et al., 2016; Radchuk et al., 2019; Venter et al., 2016), modifying the ecological network components by adding or removing species and interactions, rewiring and changing interaction strengths. These impacts can be propagated through the ecological network and alter the stability and resilience of the ecosystem (Dunne et al., 2002b).

Whether cascading effects are observed or not following the removal or addition of a node depends, to some extent, on the complex structural attributes (also known as topological properties) that define the network (McWilliams et al., 2019) as well as the probability of each node to respond to the loss of its links (Baldock et al., 2019; Eklöf et al., 2013; Staniczenko et al., 2010). Since species extinction and/or modification of their interactions may directly induce the degradation of ecosystem services, affecting human well-being, anticipating the potential propagation of these effects is of paramount importance (Barnosky et al., 2011; Dirzo & Raven, 2003). Conclusively, the understanding of ecosystem stability and resilience to different perturbations inducing species extinctions has received considerable attention in the literature (Allesina & Pascual, 2009; Ávila-Thieme et al., 2021; Curtsdotter et al., 2011; Dunne et al., 2002a; Hastings et al., 2016; Jordan, 2009; Pimm et al., 2019; Ramos-Jiliberto et al., 2012; Roopnarine, 2006; Roopnarine et al., 2007; Valdovinos, 2019; Valdovinos et al., 2009).

1.1 | Measuring network stability/robustness with topological properties

The response of ecological networks to the selective loss of species is often referred to as network robustness. Within the context of the work we present here, network robustness is measured as the number of secondary extinctions spurred by individual primary extinctions (see Box 1 for definitions). In addition, we include complementary measures of robustness, the R_{50} and R_{100}, which respectively indicate the fraction of primary extinction events that cause 50% and 100% of all species in the network to go extinct through both primary removals and secondary extinctions (Bellingeri et al., 2013; Dunne et al., 2002b). The complexity of ecological networks imposes some challenges in developing an integrated framework and tools to study network perturbation processes and outcomes. Nevertheless, some general attributes that characterize the structure of networks do exist. These metrics are known as topological properties and have been linked extensively to network robustness, that is, how ecological networks respond to the selective loss of species. For example, the impact of species richness and connectance has been emphasized by several authors, but discrepancies persist. While some studies suggest that increasing the number of species and connectance among them delay the onset of cascades of secondary extinctions (Dunne et al., 2002b; Dunne & Williams, 2009; Estrada, 2007; Gilbert, 2009), others show the opposite relationship (Pires et al., 2015; Sauve et al., 2014; Staniczenko et al., 2010). Thébault and Fontaine (2010) propose that these discrepancies may be driven by the type of network (e.g. trophic vs. mutualistic networks), which necessitates a different treatment of mutualistic and trophic networks

BOX 1 Definitions relevant to the *NetworkExtinction* R package workflows.

- **Network robustness**—A measure of the maintenance of network structure in the face of perturbations and quantified here as the number of species (nodes) lost as a consequence of primary species extinctions (secondary extinctions).
- **Interaction type**—A link between two nodes reflecting the type of relationship involved. *NetworkExtinction* handles mutualistic (+/+) and trophic/parasitic (−/+) interaction types. For a more exhaustive overview of interaction types, consult Morales-Castilla et al. (2015).
- **Interaction strength**—The direct effect that nodes have on each other's demography (Morales-Castilla et al., 2015), fitness (de Santiago-Hernández et al., 2019) or resource acquisition/transfer of energy (Heymans et al., 2016). *NetworkExtinction* implicitly treats interaction strength as the effect that nodes have on each other's persistence.
- **Extinction threshold**—*NetworkExtinction* treats an extinction threshold as a percentage of interaction strength loss (relative to the total interaction strength at the onset of extinction simulation) which a vertex may lose before becoming secondarily extinct (Schleuning et al., 2016).
- **Rewiring capability**—Rewiring is the process by which a vertex may allocate interaction strength associated with a link which is removed due to a loss of interaction partner to an entirely new or already linked partner, thereby increasing the interaction strength of new or already existing links in a network (Fründ, 2021; Schleuning et al., 2016; Staniczenko et al., 2010).

when studying extinction cascades. Similarly, theoretical models show that ecological networks' degree distribution (i.e. distribution of links per node) is strongly associated with their robustness to species loss (Sole & Montoya, 2001). Usually, degree distributions follow a fat-tailed distribution (Bascompte, 2009; Dunne et al., 2008). However, power-law degree distributions where super-connected nodes are more common are more vulnerable to the removal of the most connected nodes (de Santana et al., 2013; Dunne et al., 2002a; Estrada, 2007; Sole & Montoya, 2001). More generally, a directed attack on the nodes with a higher degree can have more significant whole-scale consequences in the network (Albert et al., 2000; Albert & Barabási, 2002). Identifying the best model to describe an empirical degree distribution has been an active research area, with even different approaches generating controversial discussion in the literature (Clauset et al., 2009; Xiao et al., 2011). Although simultaneously evaluating the degree distribution with multiple approaches is a valuable contribution, there is a lack of a package to do so (Table S1). Here, we fit the degree distribution using linear versus nonlinear approaches.

1.2 | The need for simulation approaches in extinction analyses

While the assessment of ecosystem robustness through topological metrics of ecological networks is computationally inexpensive (Table S1 presents a comparison of R packages for this purpose), relying on topological metrics alone may be misleading considering the different implications given network types (Thébault & Fontaine, 2010), and the potentially weak connection between these metrics and empirical network resilience to extinctions (e.g. Ávila-Thieme et al., 2021). Alternatively, assessments of the impact of species loss on ecological networks can be carried out by simulating a sequence of species removals and quantifying subsequent changes to the respective network. Such extinction simulations can render a more direct quantification of network robustness than the single-step calculation of topological metrics. However, throughout these sequential extinction simulations, some network metrics (e.g. node degree or connectance) change dynamically and need to be recalculated after each simulation iteration resulting in increasingly complex automation requirements for such analyses.

Previous attempts at such extinction consequence simulations have been made but largely fail to provide an easy-to-use toolbox which can be adapted for different types of ecological interactions while considering relevant coextinction dynamics such as extinction thresholds and formation of rewired interactions (Schleuning et al., 2016).

To fill this software and functionality gap, we present here a novel, open-source R package that facilitates the exploration of trophic and mutualistic ecological networks' robustness (see Box 1 for definitions) and changes in attributes following the removal or extinction of nodes in complex ecological networks. Here, we present the *NetworkExtinction* R package, which quantifies ecological network changes via topological metrics linked to network robustness (e.g. modularity, connectance and degree distributions) as well as through sequential simulations of extinction outcomes and effects. Finally, *NetworkExtinction* also makes available postextinction networks according to simulated extinction sequences and their consequences thus allowing forecasting of likely future ecological network constellations.

1.3 | Interaction types, extinction thresholds and network rewiring

Ecological network types are manifold and may be classified by the interaction type they encode (e.g. trophic or mutualistic), how many levels of organisms they represent (e.g. bipartite or multilayer networks), whether they quantify the strength of interactions or their presence/absence (i.e. weighted vs. binary networks) and whether they represent realized or potential interactions. To best represent network changes in response to node removal, coextinction simulation frameworks ought to account for the network-type specific changes in network cascade responses.

When considering simulations of extinction cascades, the core use of the *NetworkExtinction* package, it is thus critical to focus on three important aspects of networks (see Box 1 for definitions): (1) interaction types, (2) interaction strength introducing extinction thresholds and (3) potential rewiring of lost interactions enabling continued persistence of species.

Interaction types are the cornerstone of most ecological network research as they significantly impact how links between nodes are interpreted biologically and subsequently impact the consequences of loss of connections in extinction cascades. While recent work has identified a synergistic effect of differing interaction types on ecological communities (Simha et al., 2022), analyses using *NetworkExtinction* functionality are limited to network objects of homogeneous interaction types (i.e. mutualistic or trophic interactions), which have been the standard in ecological network research in contemporary literature (Ávila-Thieme et al., 2021; Bascompte & Jordano, 2007; Thébault & Fontaine, 2010). For example, in trophic networks, basal species may lose all associated predators, resulting in isolated nodes, but not in their extinction. In a mutualistic network, on the other hand, losing all connections will inevitably lead to the extinction of any node (given that the network encodes interactions required for survival; Carpentier et al., 2021; Schleuning et al., 2016).

However, a species does not necessarily have to lose all its interaction partners to be in danger of going extinct (Bascompte & Jordano, 2007; Eklöf et al., 2013). Such extinction thresholds may exist globally for all the nodes within a network or individually for each node. For example, a predator species may lose all except its main prey species and continue to thrive. In this case, as this package does, an extinction threshold ought to incorporate interaction strengths (i.e. link weights in network representation) which will indicate which interaction partner is most important for the target node. Alternatively, other techniques not contained in this package seek to incorporate complexity conditions of individual nodes using dynamic or Bayesian approaches to model the likelihood of secondary extinction (Baldock et al., 2019; Eklöf et al., 2013; Staniczenko et al., 2010).

Contrary to the discussion of extinction consequences so far, there is also potential for novel interactions or changes in established interaction strengths, which may manifest as the rewiring of networks in response to primary extinctions (Bartley et al., 2019; Ramos-Jiliberto et al., 2012; Staniczenko et al., 2010; Strona & Bradshaw, 2018; Valdovinos, 2019; Vizentin-Bugoni et al., 2020). Rewiring potential has recently received increased attention from the ecological network community as a possible mechanism by which the impacts of the Anthropocene may be abated. At its core, rewiring of interactions is a process by which links that are lost due to the removal of a node may be reallocated either to novel interaction partners or combined with existing interactions. Recalling the previous example of a predator losing access to its main prey item, when considering rewiring potential, this predator may shift to preying on other prey already contained in its diet or interact with entirely new prey instead of going extinct.

Most contemporary analyses of ecological networks and simulations of extinction consequences incorporate one or two of these considerations (interaction type, extinction threshold and rewiring), but rarely all three (Schleuning et al., 2016). We suggest that this is a consequence of the complexity of identifying appropriate thresholds of extinction risks and rewiring potential that can be realized and the complexity of analytic tools required to incorporate these mechanisms. To our knowledge, the *NetworkExtinction* package is the first implementation of all these considerations into one easy- and free-to-use software package.

2 | THE *NetworkExtinction* R PACKAGE

The *NetworkExtinction* package analyses ecological networks representing species as nodes and their interactions as links. The links within the networks can be weighted or binary. Using this input (formatted either as an adjacency matrix or a network object), the *NetworkExtinction* package simulates species extinctions sequences (SimulateExtinctions and RandomExtinctions functions). Nonrandom extinctions can be simulated as a static ('Ordered' method) or flexible ('Mostconnected' or 'Leastconnected' method) process. In doing so, the *NetworkExtinction* package interacts with other R packages, especially with the *network* package (Butts, 2008). *NetworkExtinction* also visualizes simulation results (ExtinctionPlot function) and compares them between the different methods (CompareExtinctions function). Finally, *NetworkExtinction* fits the network degree distribution (DegreeDistribution function). See Figure 1 for a visual representation of this functionality.

When executing simulations of extinction cascades using the *NetworkExtinction* package, users can specify (1) what interaction type (i.e. trophic or mutualistic) is being analysed (networks must contain exclusively one of these interaction types, not both), (2) whether to consider a species extinction threshold and (3) whether to simulate link rewiring.

In the case of trophic ecological networks, only bottom-up trophic cascades (Berg et al., 2015; Curtsdotter et al., 2011; Dunne et al., 2002b) are modelled (i.e. losing predator species does not affect the survival of a prey node although it may become disconnected from the network).

Here, we demonstrate the functionality and outputs of the *NetworkExtinction* package using an empirical marine intertidal rocky shore trophic network (hereafter, 'chilean_intertidal'), which contains 107 species forming 1381 realized trophic interactions (Ávila-Thieme et al., 2021; Kéfi et al., 2015). For a use-case of mutualistic network analyses with the *NetworkExtinction* package, see Kusch and Ordonez (2023) or supplementary code chunk 12. In the following, we focus on implementing a basic workflow with the *NetworkExtinction* package and how to augment extinction simulations considering extinction thresholds and rewiring mechanisms. For a detailed overview of the functions within the R package, their inputs, arguments and outputs, please refer to the documentation of the R package directly.

2.1 | The basic workflow

The NetworkExtinction package is hosted on CRAN and can be installed and loaded thusly:

```
R> install.packages ("NetworkExtinction")
R> library (NetworkExtinction)
```

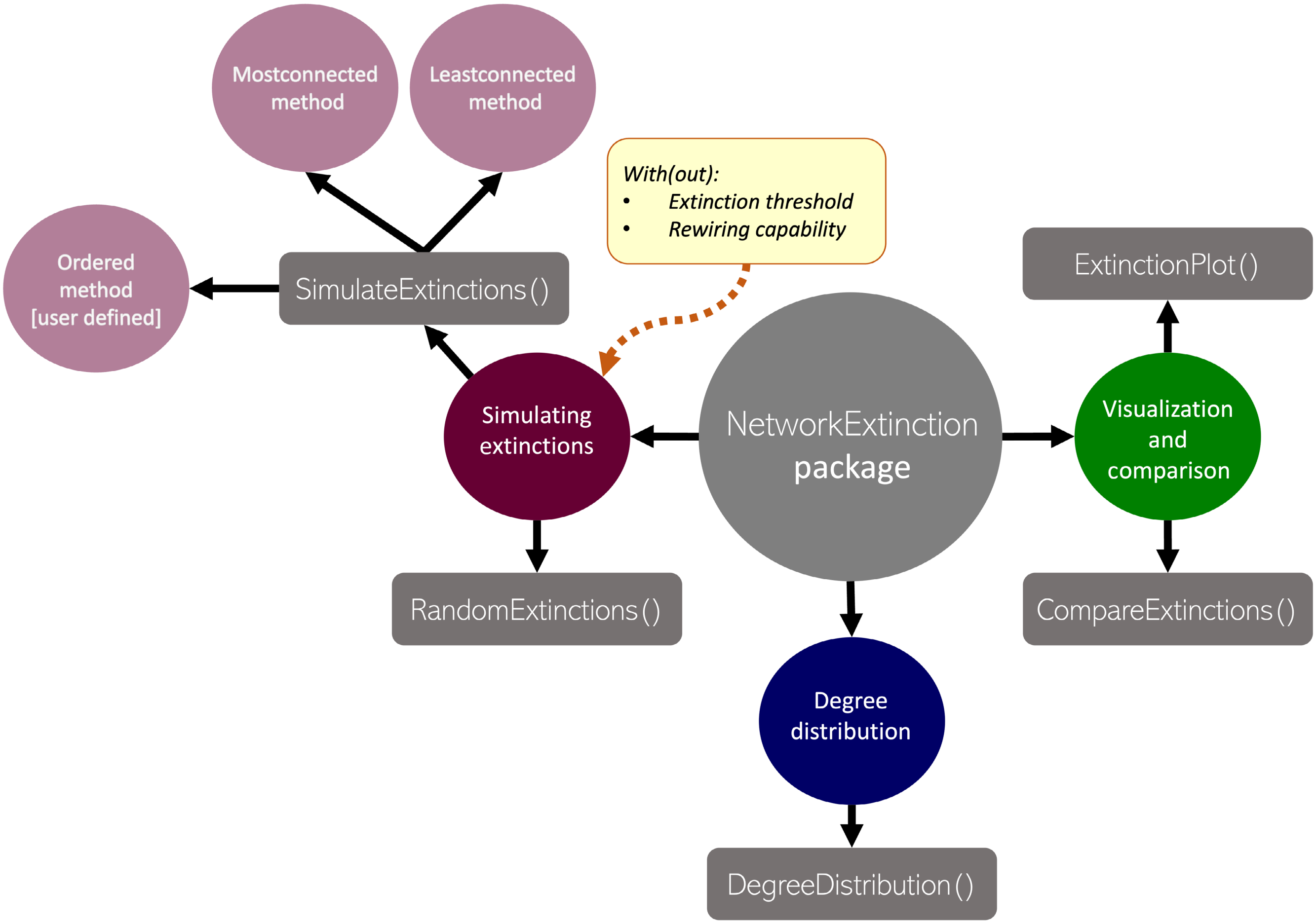


FIGURE 1 Synthesis and functions of the *NetworkExtinction* package and its functions.

2.1.1 | Extinction functions

Two of the five functions contained in the *NetworkExtinction* package are used to simulate extinction cascades and measure ecological network topology and robustness after simulating a given species deletion sequence corresponding to primary extinctions and identifying secondary extinctions. These functions are called SimulateExtinctions and RandomExtinctions.

The SimulateExtinctions() Function

SimulateExtinctions enables the user to remove nodes from the network based on the following two deletion sequences: (1) species' degree ('Mostconnected' or 'Leastconnected' method) and (2) a user-defined order ('Ordered' method).

Mostconnected and leastconnected extinction order. Using the 'Mostconnected' and 'Leastconnected' methods, users are encouraged to explore high- and low-impact primary extinction sequences, respectively. When executing a simulation with these specifications, the SimulateExtinctions function first identifies the most/least connected species via the degree of its corresponding node, that is, the number of links attached to the node. This node is then removed from the network, and the function checks whether other species are now going extinct according to user specifications of the function (having become completely unconnected, in the default case shown here). This step is repeated until the entire network is unconnected. At each step, SimulateExtinctions recalculates node degree for each extant species to reidentify the next most/least connected node up for primary removal (see Figure S1 and code chunk 2 in the Supplementary Material for an execution and visual representation of results of both approaches).

The SimulateExtinctions function returns four objects: (1) a data frame (…$sims) containing topological metrics of the network after every step of species removal (Table 1), (2) the R_{50} (…$R50), (3) the R_{100} (…$R100) robustness indexes and (4) the reduced network (…$Network) corresponding to the portion of the original network extant after removal of primarily and secondarily extinct species. The 'Mostconnected' method of SimulateExtinctions for the Chilean intertidal food web results in complete network annihilation after the primary removal of the 37 most connected species. Consequently, the reduced network is empty.

Within the data frame of topological metrics (…$sims) are contained 12 columns, in which each row corresponding to a primary extinction. The first column (Spp) identifies the vertex position of the removed species (i.e. the primary extinction), expressed as the index of the original adjacency matrix. The second through sixth

TABLE 1 *Summarized results of the SimulateExtinctions function with the 'Mostconnected' method for the intertidal food web, showing the first and last three rows of the original data frame (see full results in Table S2). Spp: node removed as a primary extinction, S: richness, L: number of links, C: connectance, Link_density: link density, SecExt: secondary extinctions, Pred_release: cumulative number of nodes that resulted with an outdegree = 0 after each primary extinction (predation release in trophic networks only), Iso_nodes: cumulative number of isolated nodes (totaldegree = 0) after each primary extinction, AccSecExt: cumulative number of secondary extinctions, NumExt: cumulative number of primary extinctions, TotalExt: number of total extinctions (primary plus secondary extinctions). See code chunk 2 in the Supplementary Material to produce this output.*

Spp	S	L	C	Link_density	Modularity	SecExt	Pred_release	Iso_nodes	AccSecExt	NumExt	TotalExt
15	106	1314	0.12	12.4	0	0	0	0	0	1	1
13	105	1252	0.11	11.92	0	0	0	0	0	2	2
4	104	1192	0.11	11.46	0	0	0	0	0	3	3
.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.
106	58	19	0.01	0.33	0.36	0	41	41	15	34	49
67	57	10	0	0.18	0.39	8	41	47	23	35	58
107	48	1	0	0.02	0	1	46	46	24	36	60

columns represent the following topological indexes: species richness (S), number of links (L), network connectance ($C = L / S^2$), link density ($\text{Link\_density} = L / S$) and modularity (calculated according to user specification of the 'clust.method' argument). The seventh column (SecExt) indicates the number of secondary extinctions produced after each removal step, which is quantified as the number of nodes (except for the basal nodes, in trophic networks) that meet the extinction threshold (IS, discussed in more detail later) after producing a primary extinction. The eighth column (Pred_release) represents the cumulative number of species that were released from predation after each removal step (i.e. nodes with zero predators after a primary extinction). The predation release index does not consider the initial top predators in their calculation and is only quantified for trophic networks. Finally, from the 9th to the 12th column, …$sims presents the number of nodes that result with a total degree of 0 (Iso_nodes), the cumulative number of secondary extinctions (AccSecExt), the cumulative number of primary removals (NumExt) and the total number of extinctions ($\text{TotalExt} = \text{NumExt} + \text{AccSecExt}$).

User-defined extinction order. Supplying a user-defined order to SimulateExtinctions is particularly useful when knowledge about extinction risks of species exists or is inferred from species' traits (e.g. size, trophic position). In contrast to the 'Mostconnected'/'Leastconnected' method of the SimulateExtinctions function, the 'Ordered' method does not change the initial extinction order but treats it as static. Note that, throughout the process of sequential extinction simulations with the SimulateExtinctions function, any primary extinction which is already included within the set of secondary extinctions will be skipped thus potentially resulting in shorter simulation runs than indicated by the initial order supplied by the user. Additionally, SimulateExtinctions, by default, only considers first-order secondary extinctions at each simulation step. To circumvent this behaviour and ensure secondary extinction cascades are tracked to their ultimate conclusion, the user may use the optional argument forceFULL as demonstrated in supplementary code chunk 12.

For our example here, we supply the 60 most connected species that are not top predators in the Chilean intertidal network (see code chunk 3 in the Supplementary Material and Table S3 for the full extinction sequence). Regardless of the selected method, the SimulateExtinctions function returns the same kind of output previously described. However, having supplied a primary extinction order that does not include all nodes in the original network and whose extinction simulation did not lead to total network annihilation, we can also assess the postextinction simulation network (Figure 2).

Random extinctions

The second extinction simulation function—RandomExtinctions—allows users to simulate the removal of a number of nodes based on random deletion sequences. The output of this function is particularly useful for establishing effect sizes of nonrandom deletion

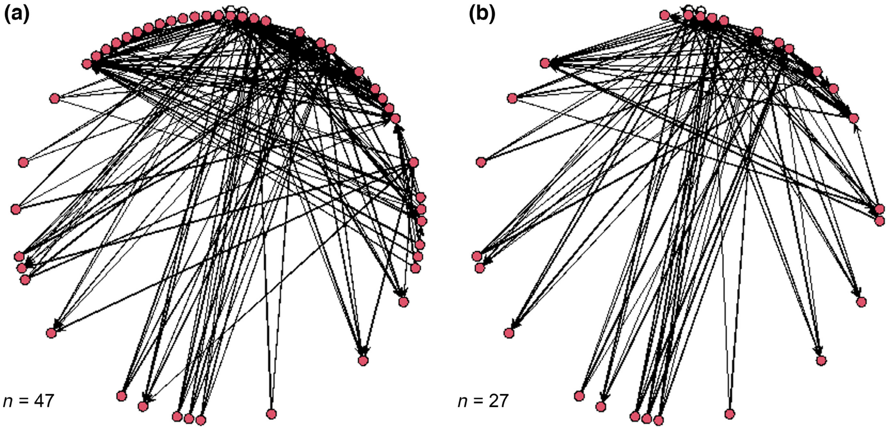


FIGURE 2 Postextinction network representative of removal of the 60 most connected nontop predator species from the Chilean intertidal network. (a) Reduced network following removal of only primary extinction nodes. (b) Reduced network obtained via the *SimulateExtinctions* function which also accounts for secondary extinctions. n = number of remaining nodes. See code chunk 4 in the Supplementary Material for the generation of these networks and plots.

TABLE 2 Summarized results of the *RandomExtinction* function for the intertidal food web, showing the first and last three rows. NumExt: cumulative number of primary extinctions, AccSecExt_95CI: cumulative 95% CI of the secondary extinctions among all the simulations performed, AccSecExt_mean: cumulative average of secondary extinctions among all the simulations performed, Upper and Lower: lower and upper limit of the [mean + 95% CI] respectively. nsim: Number of active simulation runs (i.e. runs which have not resulted in a fully disconnected network yet). See the full results in Table S4 and the code to produce this output in code chunk 5 in the Supplementary Material.

NumExt	AccSecExt_95CI	AccSecExt_mean	Upper	Lower	nsim
1	0	0	0	0	100
2	2.94	0.15	3.09	0	100
3	2.94	0.15	3.09	0	100
4	4.93	0.44	5.37	0	100
.	.	.	.	.	.
.	.	.	.	.	.
.	.	.	.	.	.
103	2.26	2	4.26	0	4
104	1.39	1.5	2.89	0.11	2
105	NA	1	NA	NA	1

sequences (see code chunk 5 in the Supplementary Material). This randomness, in our implementation, is generated via a call to the SimulateExtinctions function with a randomly generated Order containing a user-defined number of nodes (SimNum). This primary extinction sequence is subsequently treated as static. To execute several such random extinction sequence simulations, users may use the nsim argument to specifies how many random extinction simulations to run.

The function returns at a data frame (Table 2) and a plot (when the optional plot argument is set to TRUE) with the mean of secondary extinctions for each removal step averaged through all the simulations. Also, it returns the mean and 95% confidence intervals (CIs) of the R_{50} (…$R50result) and the R_{100} (…$R100result) robustness indexes.

2.1.2 | Analysis and visualization functions

Two more functions contained in the *NetworkExtinction* package are used to visualize and analyse ecological networks and their extinction sequences beyond simulations of extinction cascades. These are called ExtinctionPlot and CompareExtinctions.

The ExtinctionPlot() function

The ExtinctionPlot function is particularly useful for visualizations of extinction simulation outcomes as obtained through SimulateExtinctions. Using this function, users can plot any of the topological metrics that SimulateExtinctions calculates at each simulation step against the progress of the extinction simulation along the extinction order (see code chunk 6 in the Supplementary Material). As such, this function can visualize all columns displayed in the standard SimulateExtinctions output (Table 1). As an example, we plot the link density of the intertidal food web at each removal step using the ‘Mostconnected’ deletion sequence of the SimulateExtinctions function (Figure 3).

The CompareExtinctions() function

The CompareExtinctions function compares the number of secondary extinctions produced by either of the two options of the SimulateExtinctions function, against a set of random deletion sequences (see code chunk 6 in the Supplementary Material). This comparison is returned as a figure (Figure 4). Here, we compare

FIGURE 3 Link density after each removal step (primary extinctions) in the intertidal food web using the '*Mostconnected*' method of the *SimulateExtinctions* function and visualized using the *ExtinctionPlot* function.

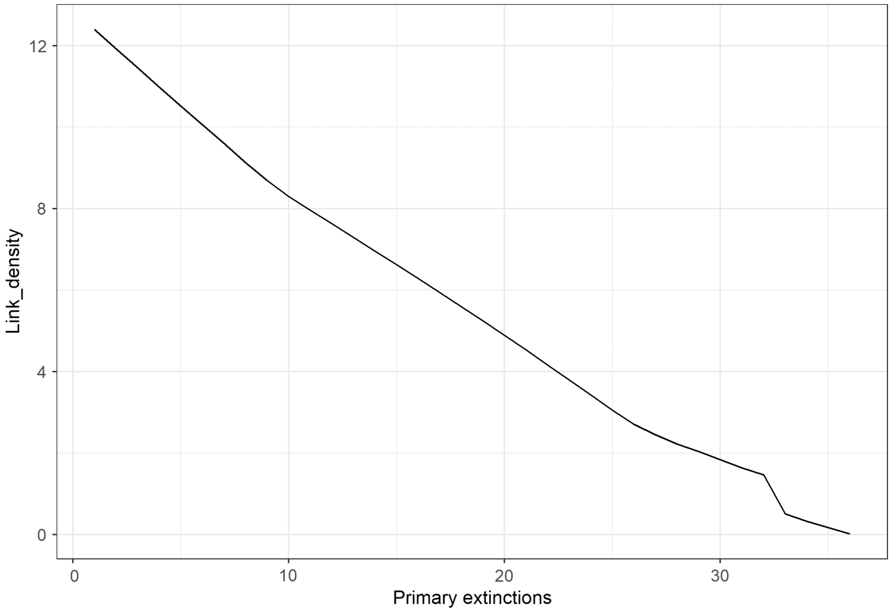
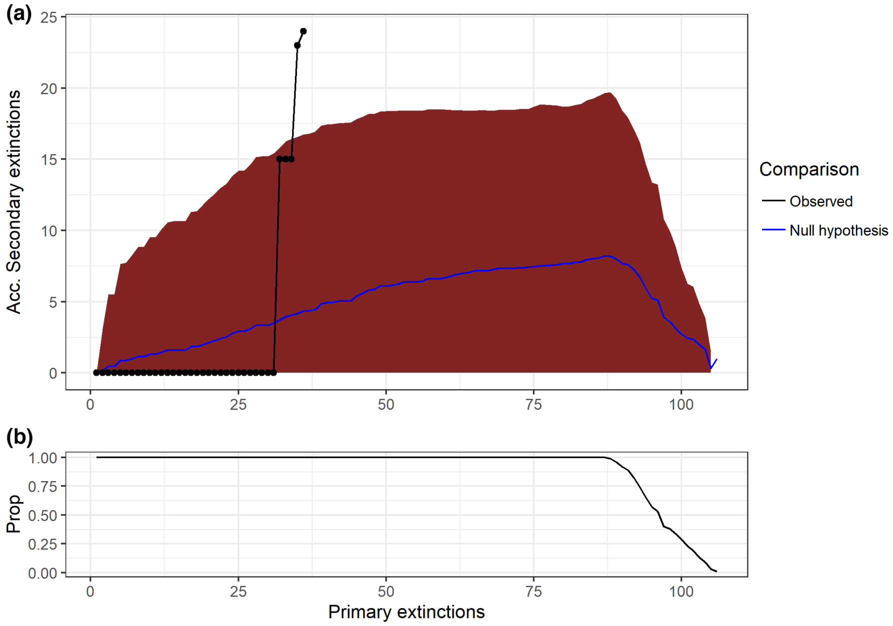


FIGURE 4 (a) Comparison of the cumulative secondary extinctions after each removal step (Primary extinctions, defined by user) between the random (Null hypothesis) and '*Mostconnected*' (Observed) deletion sequence in the intertidal food web using the *CompareExtinctions* function. The blue line is the average (±95% CI [red area]) of secondary extinctions of the null model and the black line following the dots represents the secondary extinctions of the observed model. (b) Proportion of active simulation runs defining the trend line and shading of the null hypothesis.



the secondary extinctions produced by the random deletion sequences (RandomExtinctions) with the extinctions produced by the 'Mostconnected' deletion sequence of the SimulateExtinctions function. In this example, Figure 4 shows clearly that the primary extinction of the most connected species has a more drastic effect on the rate of secondary extinction accumulation than would be expected following random primary extinctions.

2.1.3 | Degree distribution

The final function contained in the *NetworkExtinction* package—DegreeDistribution—fits the degree distribution of the network using two approaches: linear (on log-transformed data) and nonlinear regression (see code chunk 7 in the Supplementary Material).

Different statistical approaches have been proposed to fit the degree distribution, such as maximum likelihood (Clauset et al., 2009), ordinary least squares or linear versus nonlinear regression (Xiao et al., 2011). As in other fields, the use of linear and nonlinear 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 nonlinear regression methods (Xiao et al., 2011). In part, this is because when using linear regressions (LRs) on log-transformed data the error distribution may not meet the assumptions needed to statistically compare across different models; hence, a second group of approaches considers the use of nonlinear regression using general least squares, in combination with Akaike's information criteria to select the best model that fits the degree distribution.

DegreeDistribution incorporates these considerations in its three data frame outputs (models, params and DDvalues) with:

- models: Comparison of the AIC and normal distribution of the residual assumption test between the different distributions tested (Table 3).
- params: The statistical parameters of each model (Table 4) corresponding to $P_{(k)} = ck^{\beta}$ (nonlinear power-law models), $\log P_{(k)} = \beta \log k + c$ (linear power-law models) and $P_{(k)} = e^{\lambda k + c}$ (nonlinear exponential distribution models), $\log P_{(k)} = \lambda k + c$ (linear exponential distribution models).
- DDvalues: The degree distribution with the observed values and the value of each fitted model (visualized automatically by the function as seen in Figure 5).

In our example, the best model is the exponential degree distribution obtained from nonlinear regressions (NLRs) with an AIC = −160.30 (see Table 3). 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 (Figure 5).

TABLE 3 Model parameters and normal distribution tests.

logLik	AIC	BIC	Model	Normal.Resid	Family
83.15	−160.30	−153.64	Exp	No	Exponential
13.39	−20.77	−14.20	Power	No	PowerLaw
−27.48	60.96	67.53	LogExp	No	Exponential
−80.84	167.68	174.25	Logpower	No	PowerLaw

TABLE 4 Statistical parameters of the models.

Term	Estimate	Std.error	Statistic	*p*-value	Model
c	2.25	0.38	5.84	0	LogPower
Beta	−1.20	0.11	−10.44	0	LogPower
Beta	−0.45	0.04	−11.17	0	Power
c	1.54	0.15	10.27	0	Power
c	0.67	0.09	7.25	0	LogExp
Lambda	−0.07	0.00	−28.41	0	LogExp
Lambda	−0.04	0.00	−26.98	0	Exp
c	0.16	0.03	6.63	0	Exp

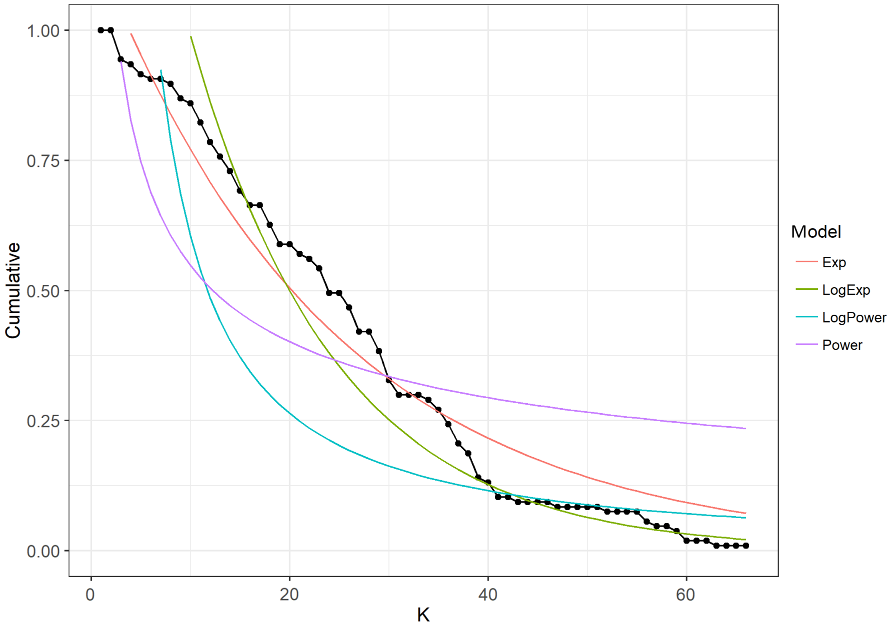


FIGURE 5 Cumulative probability distribution for a given degree (k) using the DegreeDistribution function. The plot shows two different model fits (lines). Note that since the fitted lines are regression models, their predicted values can sometimes start in values over one. Dots are the observed values.

2.2 | Extinction thresholds—Using weighted networks

Biological interactions may be expressed either as present or absent, or quantified via a host of measures such as interaction frequency (González-Castro et al., 2021), diet composition proportion (Cuff et al., 2021) or handling time of food items (Sentis et al., 2021), among others. Such weighted interactions are used to create weighted ecological networks and establish a spectrum of the importance of interaction partners for each node. For example, the loss of a prey comprising 70% of a predator diet constitutes a much greater risk to its own continued existence than the loss of a prey item accounting for only 5%.

Using the argument IS (short for 'interaction strength') in the SimulateExtinctions and RandomExtinctons functions, users may define what proportion of original interaction strength each node is required to retain before being considered secondarily extinct. The default value is 0, denoting that a node has to become fully unconnected from the network to be considered secondarily extinct. The IS argument may be used to either set a global extinction threshold or index local extinction thresholds for each individual node (see

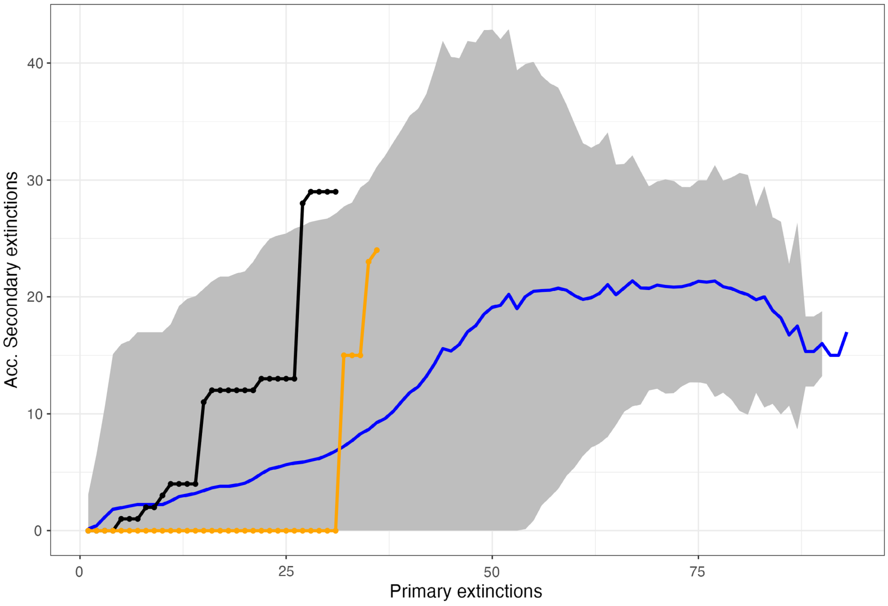


FIGURE 6 Comparison of the cumulative secondary extinctions after each removal step (Primary extinctions) between the random (Null hypothesis) and '*Mostconnected*' (Observed) deletion sequence in the weighted intertidal food web assuming an extinction threshold of 0.75. The blue line is the average (±95% CI [grey area]) of secondary extinctions of the null model and the black line following the dots represents the secondary extinctions of the observed model. The orange line represents the observed model assuming an extinction threshold of 0 using an unweighted network representation (Figure 4). See code chunk 8 in the Supplementary Material for the generation of the deletion sequences and visualization.

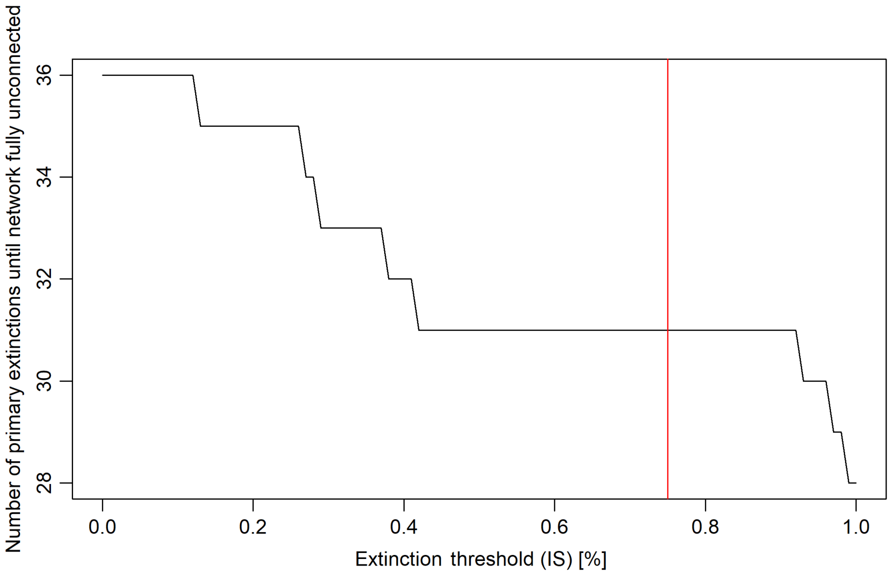
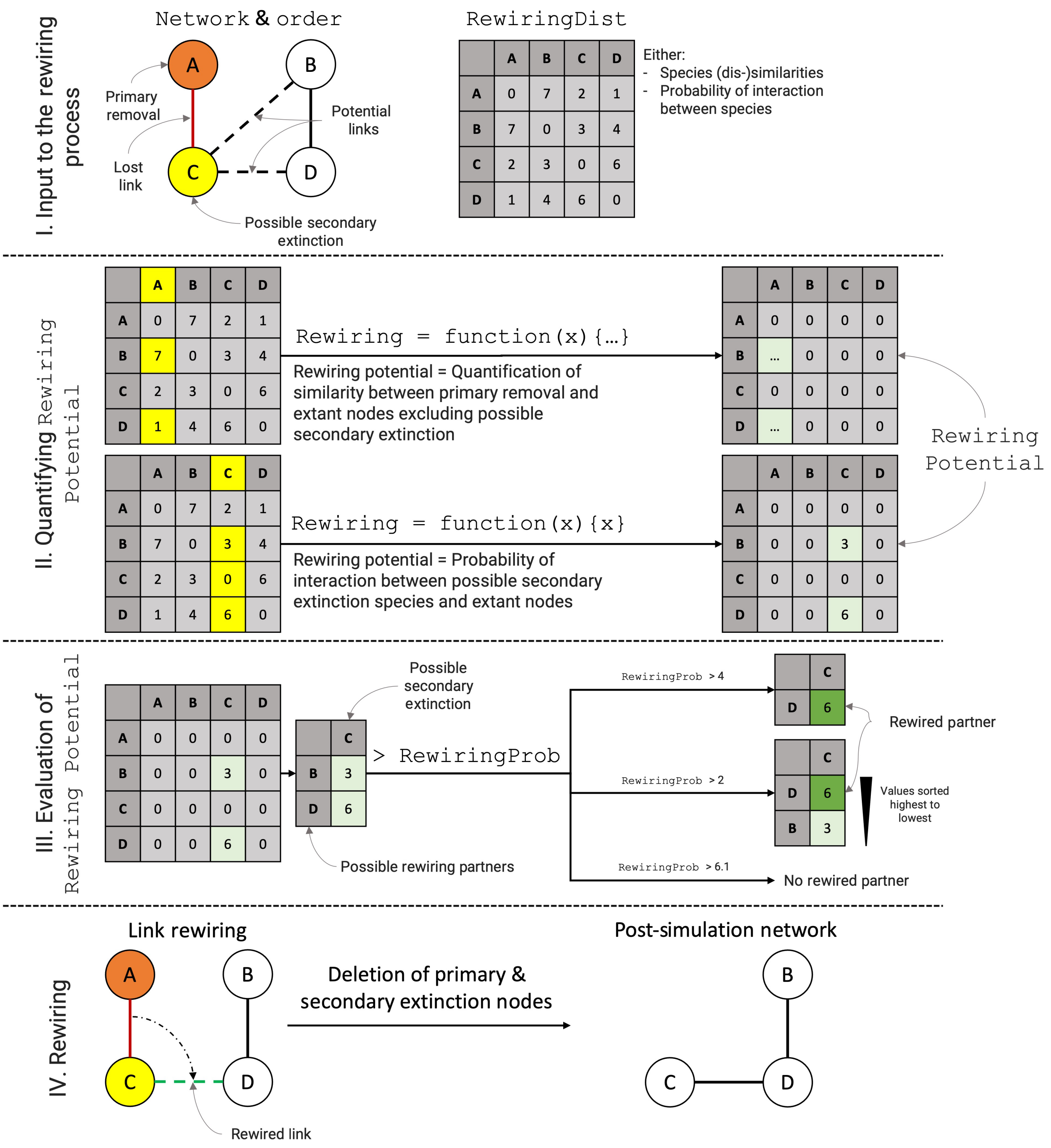


FIGURE 7 Network robustness (network of primary extinctions required to produce total disconnection of the network) over the value space of the extinction threshold parameter. The red line indicates the extinction simulation depicted in Figure 6. See code chunk 9 in the Supplementary Material for this computation.

code chunk 11 in the supplement for an example). Here, we demonstrate the extinction threshold argument with a global threshold of 0.75—each node goes secondarily extinct when it loses more than 75% of its original interaction strength. To do so, we use the 'chilean_weighted' data object supplied with the *NetworkExtinction* package (see code chunk 8 in the Supplementary Material). Figure 6 shows how the accumulation of secondary extinctions can change when accounting for extinction thresholds, particularly when compared to Figure 4.

To highlight the relevance of the chosen extinction threshold to the output obtained by the *NetworkExtinction* package, we have run the SimulateExtinctions function with the 'Mostconnected' method for all possible values of IS between its minimum of 0 and maximum of 1 in steps of 0.01. We extracted the primary removal step



	A	B	C	D
A	0	7	2	1
B	7	0	3	4
C	2	3	0	6
D	1	4	6	0

	A	B	C	D
A	0	0	0	0
B	…	0	0	0
C	0	0	0	0
D	…	0	0	0

	A	B	C	D
A	0	0	0	0
B	0	0	3	0
C	0	0	0	0
D	0	0	6	0

	C
B	3
D	6

	C
D	6

	C
D	6
B	3

FIGURE 8 The process of identification of possible rewiring in response to a primary extinction, evaluation of rewiring likelihood and selection of rewiring partners as executed by the *NetworkExtinction* package using the optional *RewiringDist*, *Rewiring* and *RewiringProb* arguments.

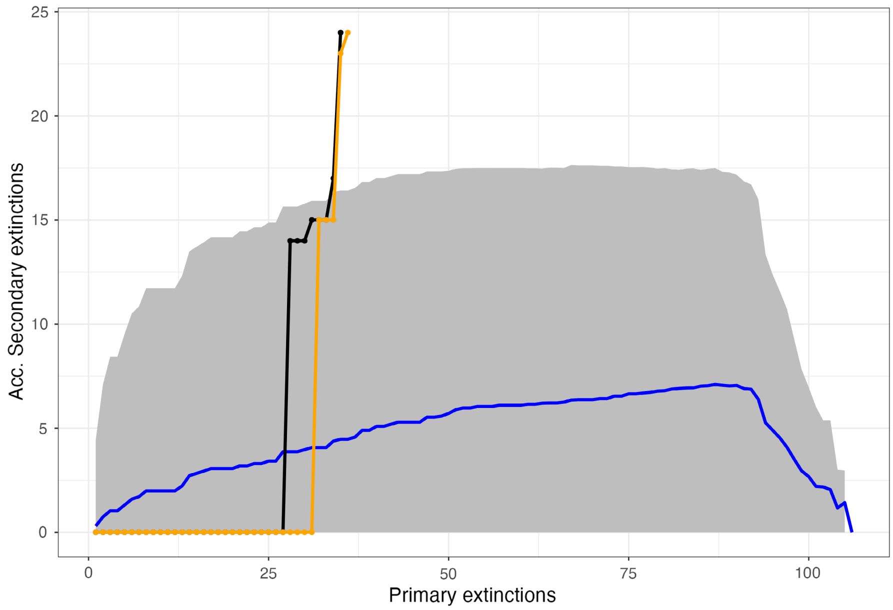


FIGURE 9 Comparison of the cumulative secondary extinctions after each removal step (Primary extinctions) between the random (Null hypothesis) and '*Mostconnected*' (Observed) deletion sequence in the intertidal food web assuming rewiring as indicated in the main text. The blue line is the average (±95% CI [grey area]) of secondary extinctions of the null model and the black line following the dots represents the secondary extinctions of the observed model. The orange line represents the observed model assuming no realization of rewiring potential (Figure 4).

at which the entire network had become unconnected/fully extinct and visualize the results in Figure 7 which shows the drastically increased rate of secondary extinctions as IS approaches 1.

2.3 | Realizing rewiring potential—Escape from cascades

So far, we have demonstrated the use of the *NetworkExtinction* package under the assumption of static links. However, this assumption rarely holds in nature, where networks have been demonstrated to be capable of rewiring to new or pre-existing partners (Baldock et al., 2019; Bartley et al., 2019; Schleuning et al., 2016; Staniczenko et al., 2010). We have implemented functionality to account for rewiring potential in the *NetworkExtinction* package through three optional arguments to the SimulateExtinctions and RandomExtinctons functions. These are:

- RewiringDist—this must be a matrix of the same dimensions as the adjacency matrix defining the Network argument and contain either species-(dis)similarities or rewiring probabilities.
- Rewiring—this argument must be a function that calculates rewiring probabilities from the species-(dis)similarities stored in the RewiringDist object. This argument can be defined much like the IS argument either globally or separately for each species.
- RewiringProb—this global threshold determines what level of rewiring probability must be exceeded for rewiring potential to be realized.

Following a primary extinction, the *NetworkExtinction* package identifies all links which are being lost due to the removal of the primary extinction node. Then it identifies all the nodes involved in these interactions that still remain in the network. Calculating rewiring probability from RewiringDist matrix using the Rewiring function, the *NetworkExtinction* package then identifies which potential rewiring options are realized by evaluating the computed rewiring probabilities against the RewiringProb threshold. Any of the previously identified links for whom a realization of rewiring potential has been identified are then transferred to the new interaction partner. If there exists a pre-existing link between these two, the rewired link's weight is added to the pre-existing link's weight (Figure 8). Notice, however, that this approach does not take into account properties of potential rewiring partners, for example, the abundance of potential partners, beyond the information contained within the RewiringDist argument as do other approaches (Eklöf et al., 2013).

Here, we demonstrate the use of the *NetworkExtinction* package with already identified rewiring probabilities, thus specifying the Rewiring argument such that the extinction cascade simulation evaluates the values stored in RewiringDist against the RewiringProb argument without further transformation. To identify potential links (i.e. rewiring potential), we assigned each species into functional groups and subsequently assume that a predator preying on any item of a specific functional group may also predate each other member of the same functional group. This results in a binary matrix of potential trophic interactions in the Chilean intertidal ecosystem. These data are available via the *NetworkExtinction* package as the chilean_potential object. See code chunk 10 in the supplementary material for the computation. As Figure 9 indicates, accounting for the rewiring potential of ecological networks leads to higher network robustness and longer runs of primary extinction simulations until full network annihilation is reached. Additionally, Figure 9 highlights that the realization of rewiring potential may lead to the concentration of links on a small subset of species which incur a large number of secondary extinctions when they are removed.

We realize that the implementation of the rewiring capabilities in this package may be too simplistic for some purposes as interactions may not be rewired at a large scale but only incrementally and split among multiple partners rather than just one rewiring partner. Although there are other ways to implement rewiring, such as considering the establishment of establishing interactions with new species or reweighting the interactions (Bartley et al., 2019; Ramos-Jiliberto et al., 2012; Schleuning et al., 2016), we suggest that the capability to analyse the realization of rewiring potential in the first place represents a step-change improvement for the field of ecological network analysis and subsequent considerations of more nuanced rewiring processes may be implemented in the *NetworkExtinction* package due to its open-source nature.

3 | CONCLUDING REMARKS

With the *NetworkExtinction* package, we have developed an easy-to-use package to visualize and assess the structure and robustness of the ecological network to different sequences of loss of species. The package lowers drastically the barrier of entry into extinction consequence forecasting models for a wide user-basis of ecologists and conservation practitioners, and we expect its applicability will be wide-ranging given the ubiquity of ecological networks.

AUTHOR CONTRIBUTIONS

M.Isidora Ávila-Thieme, Derek Corcoran and Pablo A. Marquet. conceived the study. M.Isidora Ávila-Thieme and Derek Corcoran produced initial code for analyses of degree distributions, visualizations and simulations of binary trophic networks. Erik Kusch produced additional code and added functionality to incorporate extinction thresholds, rewiring potential and support for weighted networks as well as mutualistic network types. Sergio A. Navarrete provided the data for the intertidal food web. Fernanda S. Valdovinos provided conceptual and technical support. M.Isidora Ávila-Thieme, Derek Corcoran and Simón P. Castillo wrote the first draft of the manuscript. Erik Kusch made substantial revisions to the manuscript and produced the final draft. All authors contributed to the final version of the paper.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The code for the R package can be found in Zenodo (Kusch et al., 2023) and in the project repository (github.com/derek-corcoran-barrios/NetworkExtinction).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Comparison of the package properties between the most common package that analyze food webs with the NetworkExtinction package. We compare three categories according to the food web attributes that accept, the network metrics that calculates and the type of network analysis that performs. PP: primary producers.

Table S2. Full results of the *SimulateExtinctions* function with the *Mostconnected* method for the intertidal food web. Spp: node removed as a primary extinction, S: richness, L: number of links, C: connectance, Link density: link density, SecExt: secondary extinctions, Pred release: cumulative number of nodes that resulted with an outdegree = 0 after each primary extinction (predation release in trophic networks only), Iso nodes: cumulative number of isolated nodes (totaldegree = 0) after each primary extinction, AccSecExt: cumulative number of secondary extinctions, NumExt: cumulative number of primary extinctions, TotalExt: number of total extinctions (primary plus secondary extinctions).

Table S3. Full results of the *SimulateExtinctions* function with the *Ordered* method for the intertidal food web. See column names in Table S2. Note that primary extinction of nodes 20, 36, 21, 9, 22 and 39 has been skipped as these went secondarily extinct before their sequential primary extinctions.

Table S4. Full results of the *RandomExtinction* function for the intertidal food web. NumExt: cumulative number of primary extinctions, AccSecExt 95CI: cumulative 95% of confidence intervals of the secondary extinctions among all the simulations performed, AccSecExt mean: cumulative average of the secondary extinctions among all the simulations performed, Upper & Lower: lower and upper limit of the [mean + 95% CI], respectively. nsim: number of active simulation runs.

Figure S1. Secondary extinction simulations within the Chilean Intertidal network following Mostconnected and Leastconnected orders. (A) Accumulated secondary extinctions following Leastconnected approach spike earlier than Mostconnected but level out thereafter. (B) Taking into account predation release and accummulated secondary extinctions, we find that, in our example, the Mostconnected approach leads to more drastic loss of nodes/links from our study network resulting in a fully unconnected network much quicker than the Leastconnected method. This behaviour is rooted in our specific study network being dominated by well-connected predator species which are removed initially by the Mostconnected method, whereas the Leastconnected method targets producers due to their relatively low connectedness in our network. See code chunk 2 in the supplementary material for the generation of these extinction sequences.

Figure S2. Network robustness (primary extinctions required to produce total disconnection of the network) as driven by IS-threshold of apex predator. See code chunk 11 for this computation.

Figure S3. Demonstration of the effect of primary extinction of node 3 from the package-contained 10-node mutualistic network. The resulting network is highly dependant on setting of the IS and forceFULL argument. Orange node = primary removal, red node(s) = secondary extinctions, red edge = lost interactions.

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