ROBUSTNESS THROUGH REGIME FLIPS IN COLLAPSING ECOLOGICAL NETWORKS

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Abstract There has been considerable progress in our perception of organized complexity in recent years. Recurrent debates on the dynamics and stability of complex systems have provided several insights, but it is very difficult to find identifiable patterns in the relationship between complex network structure and dynamics. Traditionally an arena for theoreticians, much of this research has been invigorated by demonstration of alternate stable states in real world ecosystems such as lakes, coral reefs, forests and grasslands. In this work, we use topological connectivity attributes of eighty six ecological networks and link these with random and targeted perturbations, to obtain general patterns of behaviour of complex real world systems. We have analyzed the response of each ecological network to individual, grouped and cascading extinctions, and the results suggest that most networks are robust to loss of specialists until specific thresholds are reached in terms of network geodesics. If the extinctions persist beyond these thresholds, a state change or 'flip' occurs and the structural properties are altered drastically, although the network does not collapse. As opposed to simpler or smaller networks, we find larger networks to contain multiple states that may in turn, ensure long-term persistence, suggesting that complexity can endow resilience to ecosystems. The concept of critical transitions in ecological networks and the implications of these findings for complex systems characterized by networks are likely to be profound with immediate significance for ecosystem conservation, invasion biology and restoration ecology.

Introduction

Interest in 'robust, yet fragile' nature of complex systems transcends disciplinary domains of biology, engineering, sociology and ecology, with much to be gained

through investigations into the behavior of complex dynamical systems like ecosystems that are robust by virtue of their continued existence in evolutionary time [1,2]. Structural attributes shared by these systems can provide clues about their stability and robustness, and here we focus on large scale free real world systems such as ecological webs, which are known to display an unexpected degree of tolerance or structural robustness to loss of specialist species [3,4]. Studies on mutualistic networks have highlighted that modularity; one of the emergent properties of networks, endows robustness to systems as diverse as fire prone savannahs, spread of infectious diseases or financial networks like the Fedwire[5]. Compartmentalization has been shown to render the much needed robustness to these systems, suggesting that dynamics of large complex networks formed by interacting species impact the way biodiversity influences ecosystem functioning[2,6]. Understanding the behavior of ecological networks, as envisaged in this work, is also central to understanding the response of biodiversity and ecosystems to perturbations.

Although there is adequate evidence to imply that structural and topological attributes of networks influence dynamics and function[7,8,9], the attributes of nodes and overall topological properties of networks that endow stability against perturbations are not sufficiently understood. The 'targeted extinction' approach for exploring the effects of node loss and associated co-extinctions has been well established over the last decade[3,10]. We have automated this conventional approach through development of an online interactive webserver called *NEXCADE* [11] that performs simulations of random or targeted primary extinctions on a network based on a user selected node attribute such as the number of links or 'degree'. The response of the network in terms of resulting secondary extinctions or other topological parameters can then be visualized and sequentially investigated to infer the significance of the node attribute being studied[4,12]. Extensive work on the robustness of ecological networks and attributes that enable species coexistence and diversity have revealed that these networks are highly robust to loss of specialists but are unable to withstand the targeted removal of generalists. This study was undertaken with the aim to understand how species persist in a collapsing mutualistic network following targeted extinctions and associated secondary coextinctions. The initial analysis was carried out using NEXCADE on primary frugivory data collected from Great Nicobar Island, India (GNIC) followed by exploration of response and behavior of the network, in terms of species richness, secondary extinctions, nestedness, fragmentation and diameter. The GNIC study led to the detection of alternate stable states that help sustain the integrity of the collapsing network. These states are identifiable in terms of two attributes of the Network Diameter. As a well-studied network attribute, the diameter is often interpreted to reveal the extent of internal communication within a network, both in terms of its exact size or pathlength (LDia), as well as the total number of diameters in a given network (NDia). In this work, we describe the GNIC frugivory network, our initial observations of alternate stable states in GNIC, followed by a large scale generalization and validation of our findings across eighty-five ecological networks of varying sizes. We report these data here, revealing that alternate states or flips may pervasively exist across all real world ecological networks, bestowing stability and robustness to ecosystems.

Methods

The GNIC Dataset: Primary data in the form of direct observations of foraging by vertebrates on fruits was collected from the tropical rainforests of Great Nicobar Island (spread from 6°45' to 7°15'N and 93°38' to 93°55'E, spanning a total area of about 1045km^2), the southernmost Island in the Andaman & Nicobar archipelago, India, spanning a period of seven years with field work being conducted on fifty nine transects, each 500m long, in various regions of the island from December 1999 to November 2006. This study was undertaken as part of a larger initiative by the Ministry of Environment and Forests, Government of India, under the Man and Biosphere (MAB) Programme on Great Nicobar (GNIC) Biosphere Reserve, India. Direct observations of instances of foraging by vertebrates on fruits were recorded as an interaction matrix consisting of 181 plant species and 38 frugivores (33 birds and 5 mammals). Plant and frugivore species were identified and the interaction data obtained was compiled for the entire island. The GNIC data is a binary interaction matrix where nodes are species and edges represent an frugivore relationship between two species. Preliminary analysis and visualization of network architecture was done using Cytoscape [13] version 2.6.2.

Co-extinction Analysis: Primary species loss was simulated on GNIC by carrying out cascades of directed species removals/extinctions, based upon degree (the number of links). These sequential extinctions were performed in two opposing directions, namely specialist-first (i.e least-linked to most-linked species) and generalist-first (most-linked to least linked species) cascades. Topological parameters of the resulting reduced networks were compared with random extinction cascades, following Memmott *et al*[3]. Random removals were analysed after averaging from 300 replicates. In all extinction cascades, upon removal of a given node, those species that are left without any interaction are assumed to undergo co-extinction. The network remaining after every primary extinction and subsequent co-extinction was assessed for various network attributes commonly used to summarise patterns in ecological webs, such as degree, species richness, secondary extinction, fragmentation, lost interactions, degree-distribution-gamma values, axes, length and number of diameters etc.

Network Attributes: All network indices were calculated using in-house fortran scripts and R CRAN packages IGRAPH[14] version 0.5, SNA[15] version 1.5, and BIPARTITE[16] version 0.91. Detailed description of each of the indices can be found within the respective package manuals. We examined the exponential, power law and truncated power law models to cumulative distributions for each network. Nestedness was calculated using the recently proposed nestedness metric NodF[17] using the ANINHADO program[18]. To assess the significance of nestedness values, the observed NodF was compared with benchmarks provided by three different null models. For each network, a population of n = 300 random networks was generated for each null model. As a statistic indicating significance, we estimated the probability, p, that a randomization was equally or more nested than the real matrix. Only the significant NodF values were used for further analysis. Comparison of nestedness across reduced networks was done without normalizing these values for

variation in species richness or number of interactions, since each reduced network is essentially a subset of the original unperturbed network.

Robustness and Regime Flips: For any given network, the retention of connectivity between any two pairs of nodes is considered as the most important feature in terms of communication or information flow[2,9]. Accordingly, in all our comparative assessments, networks that preserve a single connected character are treated as more stable, as compared to networks that undergo fragmentation, since a connected web enables flow of information between any two nodes. This ability to communicate between network nodes is further measured in terms of the diameter of the network. The shortest paths (also called geodesics) were calculated by using breadth-first search in the graph. The diameter (LDia) of a graph is defined as the length of the longest geodesic. The number of diameters (NDia) was calculated as the sum of all diameters between every pair of nodes separated by a distance equivalent to the diameter (LDia). The NDia value, representing the total number of longest geodesics shortest in the entire network is used as a proxy for assessing network robustness and stability. The higher this number, the greater the interconnectivity or communication between any two nodes of the network. A regime flip is considered to have taken place when the network abruptly increases its NDia by reducing its LDia value.

Open Access Source Code: A Unix program was designed to automate the entire analysis. This code takes a given binary network as input, simulates different co-extinction sequences and evaluates the sub-network remaining after every subsequent species removal, for its stability and robustness, and then extracts the attributes required for detection of regime flips or alternate stable states. For each reduced network, it creates a list of extinct and co-extinct species and calculates seven network level indices, namely species richness, secondary extinction, lost and remaining interactions, number of fragments, LDia and NDia and compares these indices across and between the different extinction sequences, and finally plots the results into vector format files. The entire source code has been developed into an online interactive open source web server, namely NEXCADE, available freely at www.nipgr.res.in/nexcade.html [11].

Validation through Meta-Analysis: In addition to GNIC, data records were obtained from a set of 85 ecological networks using previously published reports as well as the Interaction Web Database repository at the National Centre for Ecological Analysis and Synthesis (NCEAS) website (http://www.nceas.ucsb.edu/interactionweb). These 85 webs include one Anemone Fish network, four plant-herbivore, four ant-plant, seven host-parasite, one Predator-prey, 25 Seed dispersal or Frugivory networks and 43 Pollination networks. Each network was analysed using the NEXCADE code described above and subsequently examined for the occurrence of regime flips, as they appeared on plots of N_{Dia} and L_{Dia} with primary extinctions. Statistical analyses on the results across networks were carried out in R (V 2.11.0).
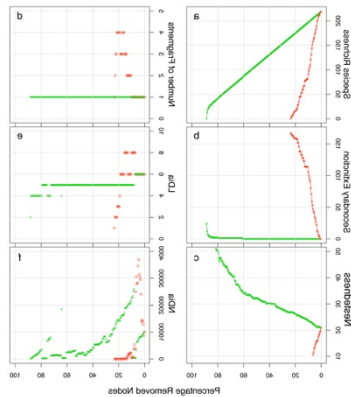
Results

Primary Data: The GNIC is a bipartite network having 812 interactions between 38 frugivores and 181 tree species, as shown in Figure 1. GNIC has highly asymmetric interactions, a characteristic path length of three, and a diameter of six (LDia = 6). Several diameters are highlighted in the Figure, and the unperturbed network contains 10065 such diameters i.e independent shortest paths of length six, between a given pair of nodes (NDia =11065). As expected of ecological networks, species interact with nested subsets of partners as shown for one mammal visiting thirteen different trees (Figure 1). The nestedness of GNIC is high (NodF value 21.02) and its degree distribution showed best fit to a truncated power law distribution. In comparison with other frugivory webs reported to date, GNIC has higher links per species (L/S), greater density, asymmetry and specialization, and a comparatively lower Connectance (L/S²).
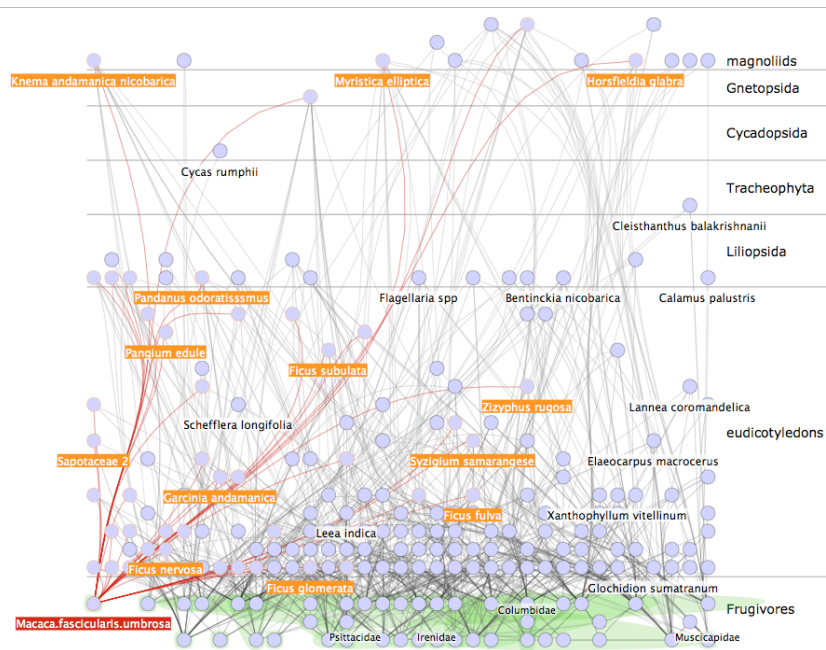
Figure 1: Illustration of the bipartite GNIC frugivory network from Great Nicobar Island, India. Nodes represent species (green- plants; pink- birds, blue- mammals); Edges are interactions. Plants have been arranged horizontally into major taxonomic classes.

Sequential Co-extinctions and Network Robustness: Degree based co-extinction simulations were carried out for GNIC, in two opposing degree-based sequences, as described in Methods, in order to investigate the contrasting ability of mutualistic networks to withstand attacks on specialists as against generalists, the former a more realistic extinction threat. Distinct responses were observed: Generalist first extinction cascade of GNIC caused the species richness to plummet due to steep rise in secondary coextinctions, whereas the specialist first cascade shows a linear decrease in species richness as it does not involve the loss of associated species, as shown in

Fig 2a-b. A similar effect was observed in case of Nestedness, one of the most significant and widely observed non-random pattern in networks of ecological interactions, that is known to greatly affect the robustness of mutualitsic networks[19]. As specialists are removed, nestedness of the resulting networks tends to increase, while the removal of generalists triggers a rapid loss of nestedness in the corresponding reduced webs (Figure 2c), supporting the notion that nestedness provides alternate routes for system responses after perturbations such as link removals, and that extinctions of specialists improves the robustness of the reduced networks. Interestingly, in the specialists-first cascade, the graph does not fragment unless at the very end (Fig 2d), whereas, the reverse sequence (generalist first extinction) results in catastrophic network fragmentation into many disconnected sub-webs and complete collapse within the first 23% primary species removals. Our hypothesis was that in the specialist-first scenario, network attributes 're-wire' to make the reduced network more compact, thereby maintaining optimal communication between the remaining nodes, and we explored this further as described below.

Figure 2: GNIC response to targeted extinction in terms of six attributes resulting from generalists-first (red) and specialists-first (green) extinction sequences are plotted against the fraction of nodes removed. These six attributes are (a) Species richness (b) Secondary Extinctions (c) Nestedness (d) Fragmentation (e) LDia and (f) NDia.

***Emergent Properties of Collapsing networks:*** In order to understand the observed robustness of GNIC to loss of specialists, a detailed examination of both cascades was performed, in terms of bipartite network attributes such as degree-distribution exponent gamma, density, asymmetry, connectance, generality, specialisation, C-score, V-ratio and various aspects of geodesics, including number, length and unique sets of shortest paths. Only two of these properties, showed significant patterns and these two represent mutually independent attributes describing internal network communication (LDia and NDia), as shown in Figure 2e and f. Most prominently, these two attributes show a coordinated response when specialists are removed, revealing a characteristic pattern that is absent in case of generalists-first extinctions. Defined as the longest geodesic of the network, the diameter has been relatively less studied in mutualistic webs, despite being a well established measure of topological robustness of several complex communication systems, ranging from cells to social, civilian networks and the Internet[10]. For a given network, a low diameter is considered advantageous as it can contribute to greater interconnectedness, shorter communication paths and lower load on links, or edges. As described in methods, we examined two aspects of the diameter: (a) its length or 'LDia', and (b) the number of diameters or 'NDia', and detected a topological re-adjustment between LDia and NDia in the specialist-first extinction scenario, presumably an internal compensation that endows the perturbed network with the ability to avoid fragmentation. Every instance of a very low NDia value coincides exactly with a

corresponding single unit change in the LDia value, leading to a reversal of NDia reduction. Recovery of sufficient number of NDia in the collapsing network presumably enable it to maintain communication between remaining nodes, which stay connected despite the sustained perturbations. Such a coupling was not observed in the generalist-first extinction sequence, where the perturbed network undergoes multiple fragmentations, driven by an excessive decline of NDia.

Alternate Stable States circumvent Network Fragmentation: As can be seen in Figure 2e-f, in the generalists-first extinction sequence, LDia and NDia both undergo a steep decrease and rapid collapse, a trend that corresponds with NDia curves; loss of generalists leads to a brief but drastic increase in NDia (to over 36900 at just under 5% primary extinctions), after which it steeply drops (to 455 by 10% deletions). This low number of diameters (NDia) corresponds to a failure of internal communication and subsequently the network undergoes fragmentation. Juxtaposition of plots 2d and e shows that the first instance of fragmentation in the collapsing network occurs at about 10% deletions, coinciding exactly with the lowest value of NDia. Further node deletions rapidly result in more fragments and the network collapses by 23% removals. In contrast, when specialists are removed first, LDia remains constant and NDia decreases steadily. By about 8% deletions, NDia reaches its lowest value of 436. However, the plot in Figure 2d shows that despite minimal internal communication, the single unit connected character of the collapsing network is preserved. Interestingly, the lowest value of NDia corresponds to a single unit reduction in the LDia, which in turn, results in a steep recovery of NDia values (from 436 to 25966). Subsequently this pattern repeats itself iteratively, i.e, NDia decreases at pace with loss of specialists till about 80% extinctions. At its lowest value, it drastically rises again - corresponding to a further unit change in LDia. Evidently, the coordinated response between NDia and LDia and the associated renewal of internal communication, makes it possible for the reduced network to make a stable transition to a new state and remain unfragmented, all through the specialist-first extinction sequence. Such a compensatory 'flip' response between two mutually exclusive network attributes, specific to the specialist-first scenario, and absent in the generalist-first scenario, has not been reported before. Complete details of this analysis for all 86 webs, along with the number of fragments, co-extinctions, LDia and NDia measured after every consecutive species deletion are in Nexcade.

Meta-Analysis of Ecological Networks: A comparative analysis of 85 additional ecological networks showed these patterns in LDia, NDia and fragmentations to be consistent and pervasive across all networks during the specialists-first breakdown scenario, and not limited to mutualistic webs only. As with GNIC the coordinated variation between NDia and LDia values endowed robustness to the perturbed networks and they persisted as single connected units during the attacks. In several cases, the different states were more pronounced than observed for GNIC. At least two and upto six flips were observed across the networks. In networks with low interaction density (< 1.35), the transition between states was not very clear. In cases where the initial network was disconnected, the specialist-first extinction sequence began with the removal of the smaller unit/s, and eventual persistence of the single largest unit. Figures 3a and 3b depict the synchronised behaviour observed in two of the 25 frugivory webs studied (codes SILV and JOR1). Figure 3c shows the flips

observed in MEMO, a pollination network with 299 interactions among 104 species. Figures 3d and e depict similar plots for an anemone-fish network (ANEM), and an ant-plant network (BLUT) respectively. Figures 3f-h depict the LDia-NDia plots for a host-parasite, plant-herbivore and a predator-prey network (LAKE, JEOM and MART) respectively.
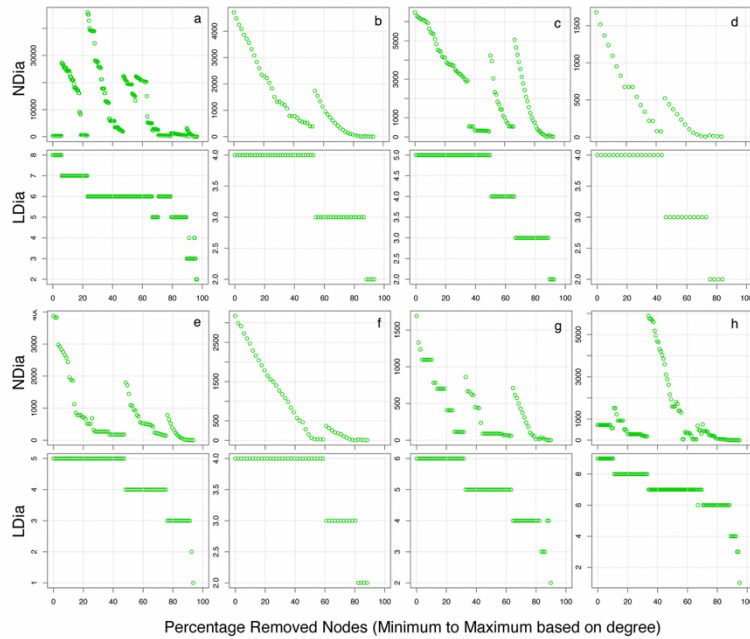

Figure 3: Variation between NDia and LDia in eight representative ecological networks following extinction cascades, resulting in flips and alternate stable states. For each network, the panels contain the corresponding NDia and LDia plots arranged vertically below each other. Details in Supp Data A2.

Evidence for generalised regime flips: For all networks, 'resistance to flip' was estimated in terms of percentage of primary species extinctions after which the first flip was observed. Therefore 'resistance to flip' is higher if a large number of species deletions are required before the flip is observed, and lower if fewer node deletions cause the state change. Figure 4a shows the relationship between the 'resistance to flip' and initial LDia across the 86 ecological networks. Compact networks with small diameters require over 70% primary extinctions for a flip in their state (Figure 4a). Networks with initial diameters of 6 or more require a much smaller proportion of primary extinctions to switch to lower diameters. A linear regression of 'resistance to flip' on initial LDia indicates a significant negative relationship (Adjusted R^2= 0.3598, ß= -7.455, df=84, p-value: 6.288e-10). However a Loess plot of the same indicates a curvilinear rather than a linear relationship between the variables, when examined at different spans (Figure 4b). The data was found to meet the assumptions of homoscedasticity and normality of errors. It was also observed that a positive, nearly linear relationship exists between the likely number of flips and the initial diameter of the network (Linear model; Adjusted R^2

= 0.5981, ß = 0.559, df =84, p-value: < 2.2e-16). Results of the entire analysis of 86 ecological networks are available from the NEXCADE website.
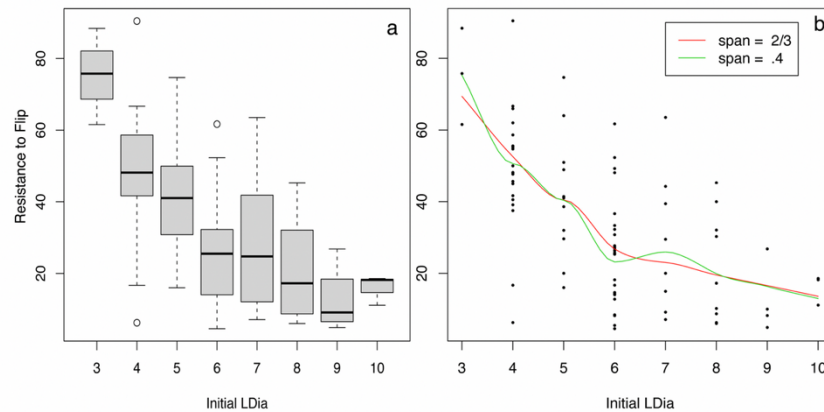
Figure 4: Influence of initial LDia of a network on its 'resistance to flip' or the primary extinctions required for a flip. The box plot provides a summary of the observations for 86 networks analysed in this study (a), while (b) Loess of the same.

Discussion

Co-extinctions are now recognized as a major driver of global biodiversity loss, along with habitat destruction, species invasion and overkill [20]. Since more than half of all known species and a large proportion of unnamed ones are involved in host specific relationships in atleast some stage of their life, specialists face a greater risk due to secondary extinctions[21,22]. There is added relevance of re-examining the threats of extinction knowing that interacting species may exist in alternate states. Besides broad implications on our understanding of bipartite networks in general, our findings have significance in conservation biology, invasion biology, and restoration ecology. Based on the present positioning of an interaction network along an extinction cascade, it may be possible to predict the proximity of the system to a catastrophic change and model real time stability indicators of networks. In addition to the dynamics associated with 'critical slowing down[23], this may be an alternate approach to predict the likelihood and proximity of a system to regime flips. Conservation programmes could benefit from directly identifying the most threatened systems, requiring immediate attention or prioritization.

The iterating pattern of gradual decrease in NDia till a threshold of extinctions is reached, followed by a sudden transition to a new high value at a lower LDia, resembles the behaviour of ecosystems that can exist in multiple states characterized by unique sets of conditions[24]. The theory of alternate stable states suggests that the discrete states are separated by thresholds and the system remains in one state unless perturbation is large enough to tip it over to the next state[16]. In case of GNIC, the network retains its integrity by flipping between alternate levels

of communication and complexity expressed in terms of LDia. However for the reduced network, the increased NDia now endows the system with high resilience, as the threshold required for the next flip or shift in LDia requires over 60% primary extinctions. The state with the widest stability basin, characterized by the maximum range of NDia at a given LDia, provides much of the robustness of the network. Figure 5 depicts this in a schematic representation.
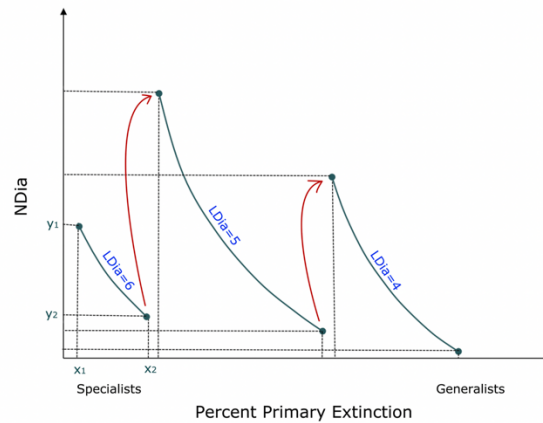

Figure 5: A schematic framework for GNIC explaining alternate states in ecological networks. The X-axis corresponds to percentage primary extinctions with specialists being removed first along a special-ist-generalist continuum. The Y-axis corresponds to NDia. Each state is depicted as a grey arc.

Hysteresis or path dependency, characteristic of alternate equilibria, becomes evident once a flip in LDia has occurred. If the lost node were to be returned to the network at this stage, it may not bring the system back to the previous state. Rather, it would lead to an increase in the NDia within the current state, i.e at the new value of LDia. This is likely because of the increasingly nested pattern of the reduced networks (Figure 2c) a new species is likely to preferentially attach to the 'hub' nodes or generalists[6]. Attachment to a hub node does not lead to an increase in LDia; it can only result in additional alternate paths or NDia. As a result, the system will not return to its previous state just by a simple reversal of extinction, or re-introduction of lost species. This observation may have wide implications in the area of restoration ecology and invasion biology, as we discuss later.

The following generalizations emerge from our observations on GNIC: (a) total number of alternate paths or diameters (NDia) decrease with loss of specialists, (b) for a given network, reduction in the diameter (LDia) increases the NDia, (c) the LDia reduction occurs only at, or beyond, a critical loss of specialists, (d) the network precludes fragmentation, with the loss of specialists across the entire cascade and (e) for a given network, there may be several alternate stable states that can spring surprises against slow moving perturbations which can be masked by internal adjustments of the network. The generality of these observed patterns in LDia-NDia was established by a comparative analysis across 85 additional ecological networks including mutualisms as well as antagonistic. webs. Our results show that the collapsing network sustains its connected or un-fragmented nature during the loss of

specialists by internal structural readjustments in terms of LDia and NDia, which is not evident during the loss of generalists, thereby leading to immediate collapse. We also find that initial network size corresponds to the number of flips observed. Larger networks are likely to have more number of alternative stable states to cope with uncertainties in evolutionary time. For example, a small network like the anemone-fish network has only 36 species and an unperturbed LDia of 4, resulting in only one alternate stable state which may restrict its ability to withstand perturbations (Figure 3d). Larger networks like the Brazilian Amazon (code SILV) and GNIC have several possible alternate stable states and are more likely to persist under long periods of adversity. Smaller perturbations tend to flip larger, more complex networks to alternate states (Figure 4a and b) and since they have several such possible states, the network architecture endows resilience to such networks. The smaller, less complex networks do not show any state changes under small perturbations indicating resistance. However, since smaller networks also have very few possible alternate states, they are low on resilience. The width of stability basins and the number of possible stable states that accompanies the loss of specialists progressively shrinks, as the network size reduces, thus affecting its overall resilience. Therefore there may be an evolutionary advantage in making ever larger webs of interactions that facilitate long-term persistence of species rich communities, a finding that complements a recent study[9] as to how mutualistic communities can enhance co-existence of species.

Implications of alternate states in ecological networks: Our results provide empirical evidence for the direct link that exists between topological heterogeneity and system dynamics. We show by means of detailed analysis of eighty-six ecological networks of varying nature that the networks can exist in alternate diameters and levels of communication. The outwards stability and unfragmented nature of these networks against perturbations often mask the internal re-wiring that progressively reduces their resilience resulting in sudden flips or transitions to lower levels of communication. This study shows that the continuous loss of specialists leads to significant loss of resilience for the networks, which is irreversible - something impossible to demonstrate experimentally. On one hand these findings hint at an evolutionary advantage in building ever-larger interaction networks (moving to higher levels of robustness), and on the other hand also highlights the inability of heavily damaged networks to respond to restoration in tangible amounts of time. The increased likelihood of an invasive species attaching to generalists in an impoverished native network partly explains its success in invaded ecosystems. The robustness of scale free networks could disguise enhanced percolation of disturbances across the network. This study establishes a prevailing pattern across known complex ecological networks and open ups possibilities for empirically driven dynamical modelling of these networks. We expect our findings to be the starting point for an array of investigations into the importance of alternate states in ecological networks in particular and other kinds of networks in general.

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