Network Robustness

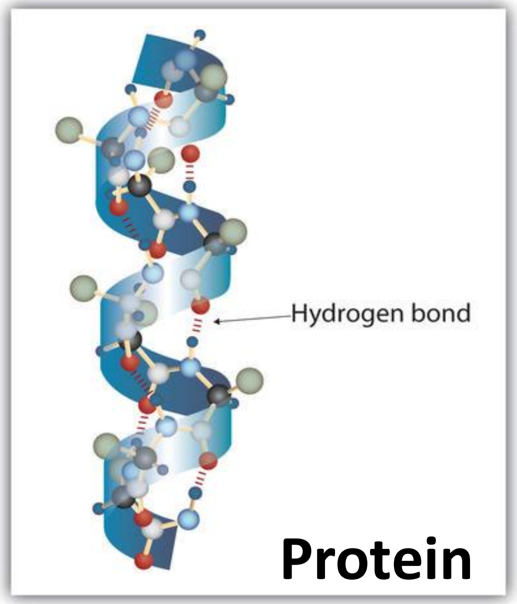
Fernando Gonçalves

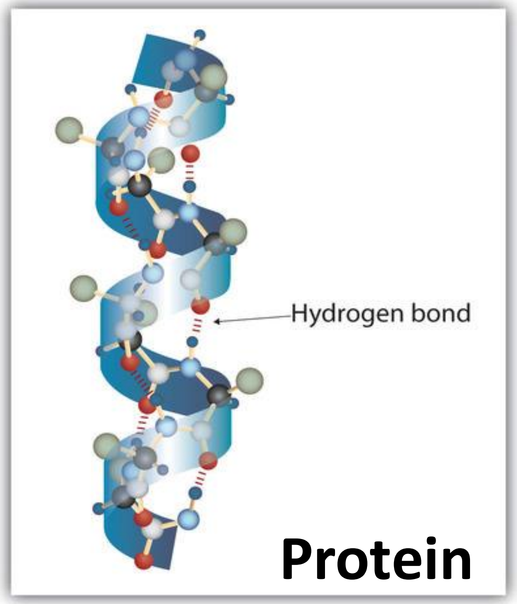
University of Zurich

Robustness, means “oak” in latim, being the symbol of strength and longevity in the ancient world

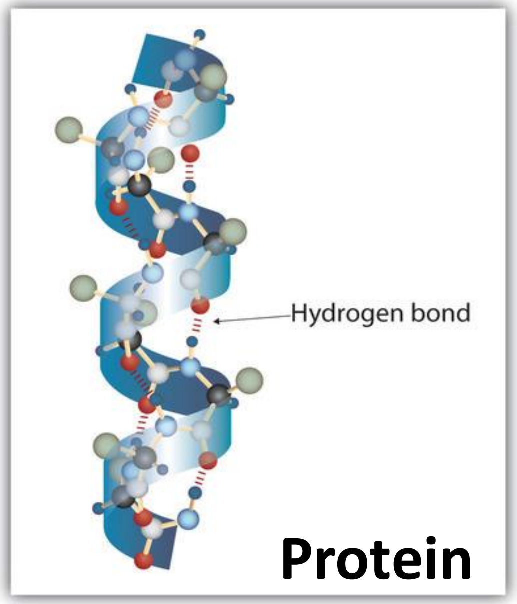
(of a process, system, organization, etc) Able to withstand or overcome adverse conditions

(of an object) Sturdy in construction: a robust metal cabinet

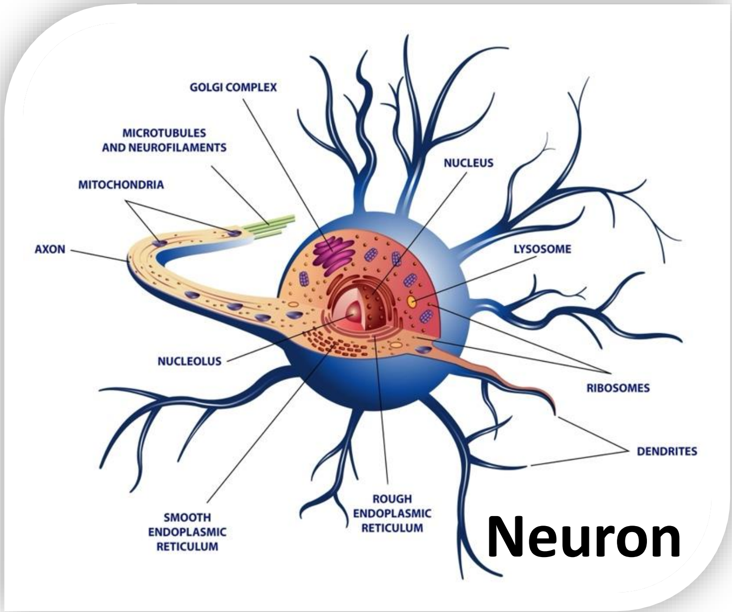

Hydrogen bond
Protein

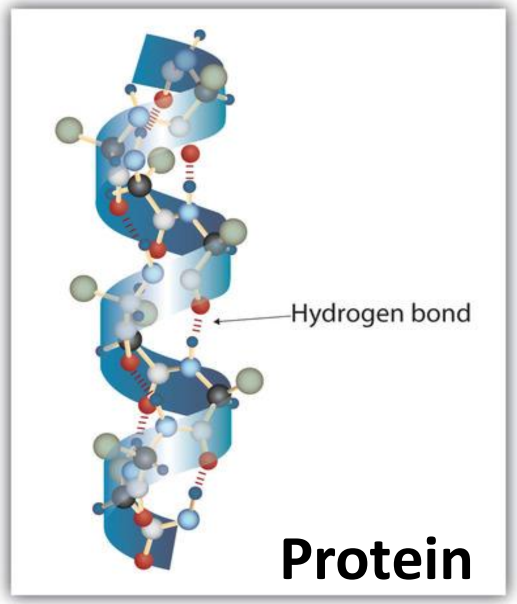

Hydrogen bond
Protein

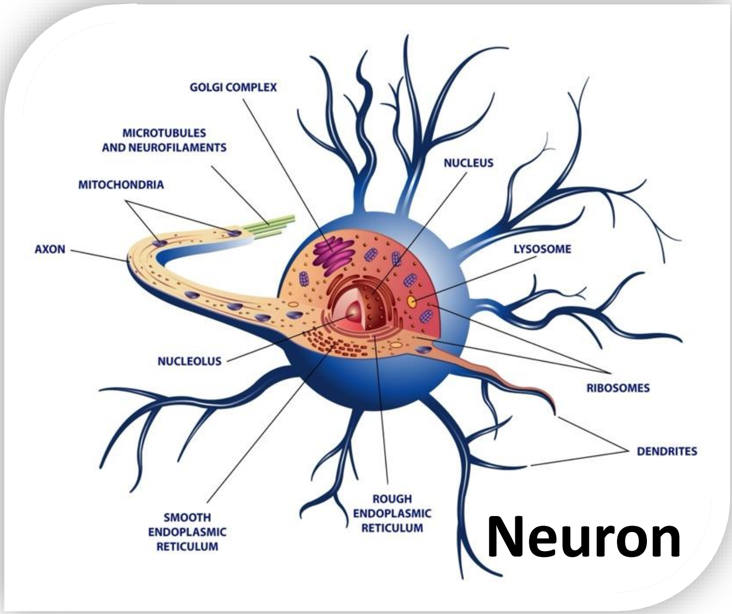

Internet

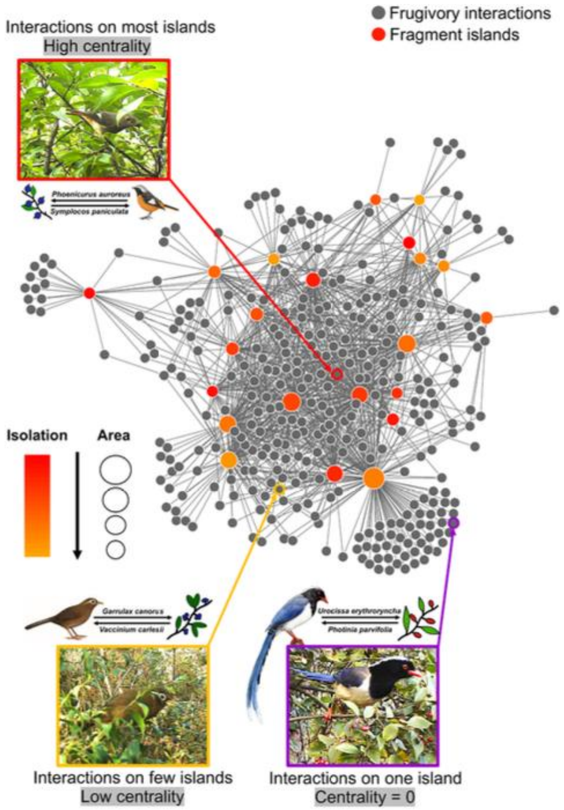

Hydrogen bond
Protein


Internet

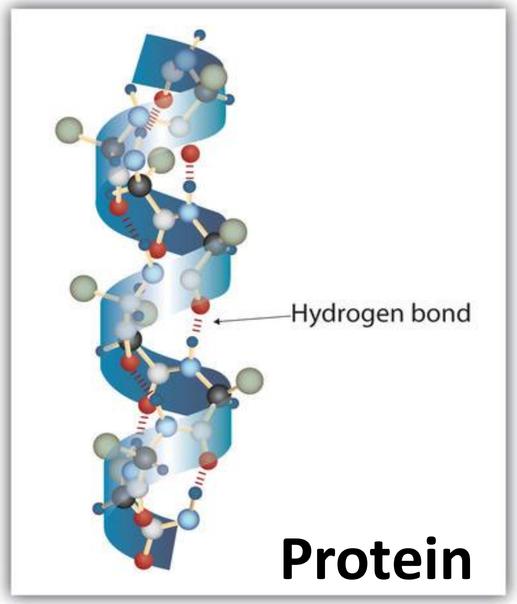

GOLGI COMPLEX
MICROTUBULES AND NEUROFILAMENTS
MITOCHONDRIA
AXON
NUCLEUS
LYSOSOME
NUCLEOLUS
RIBOSOMES
DENDRITES
SMOOTH ENDOPLASMIC RETICULUM
ROUGH ENDOPLASMIC RETICULUM
Neuron

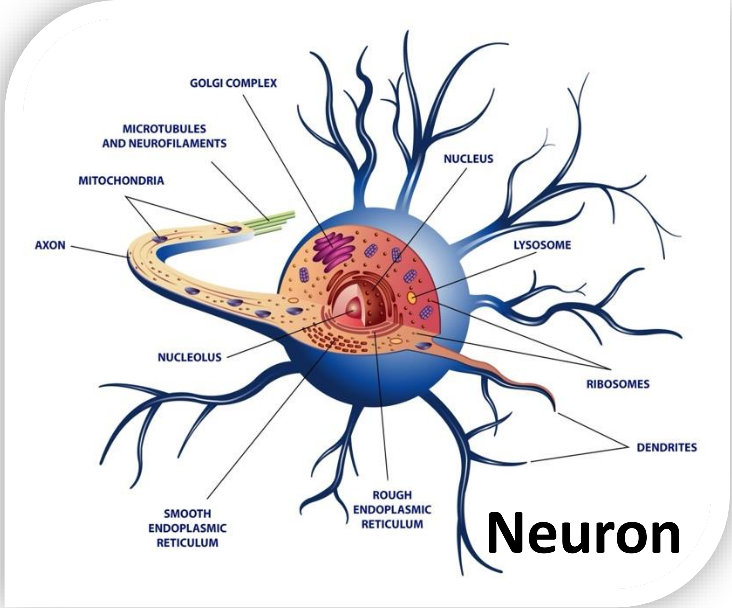


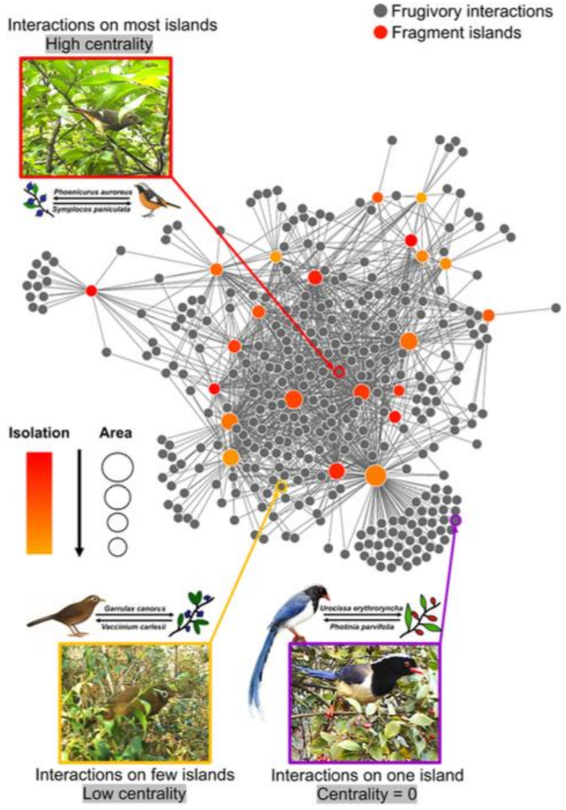




Zhu et al. 2025. *PNAS*







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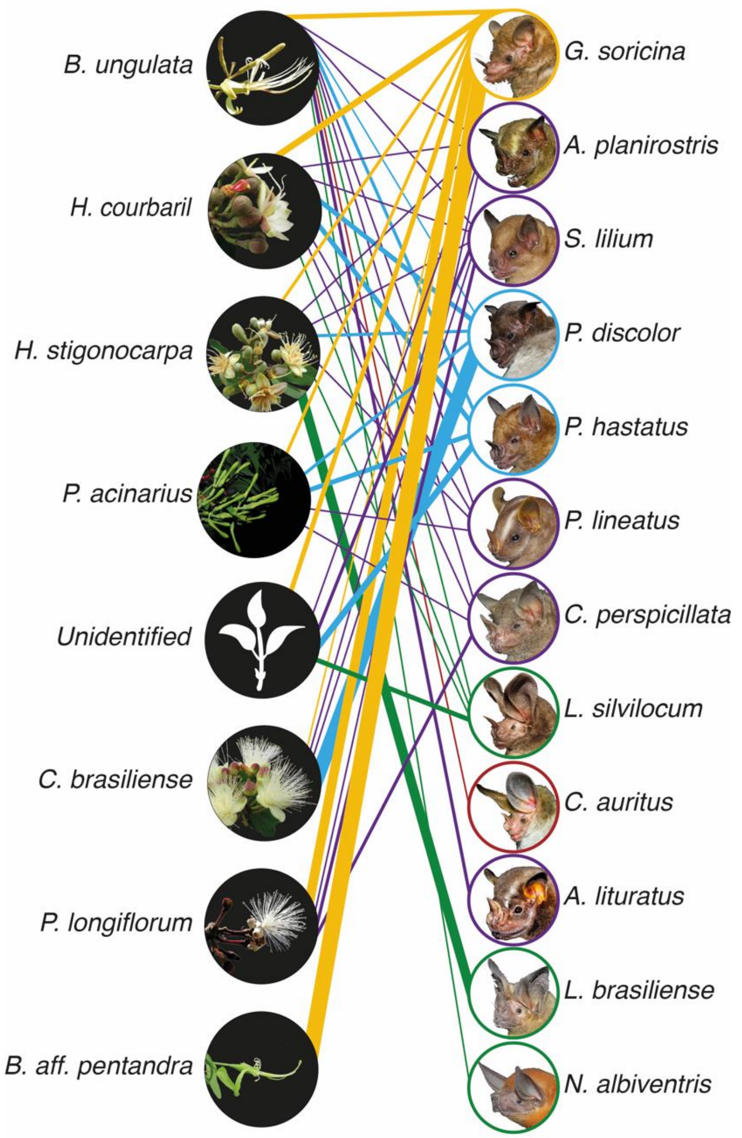
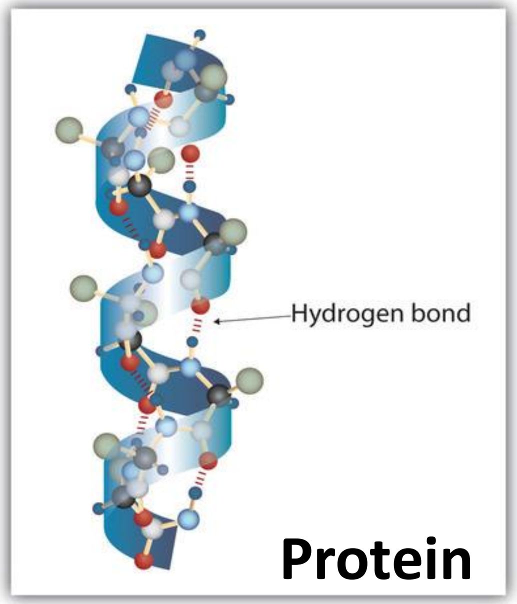
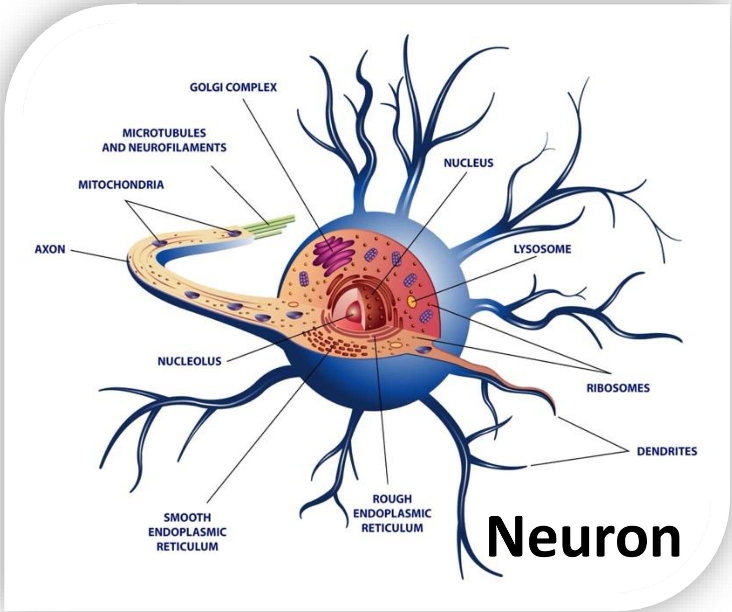
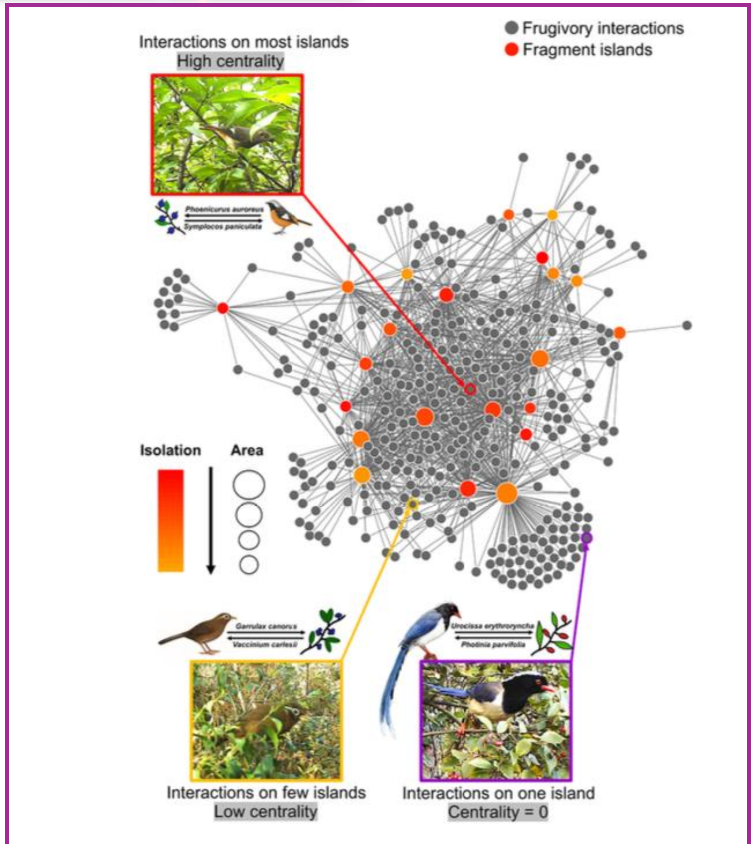


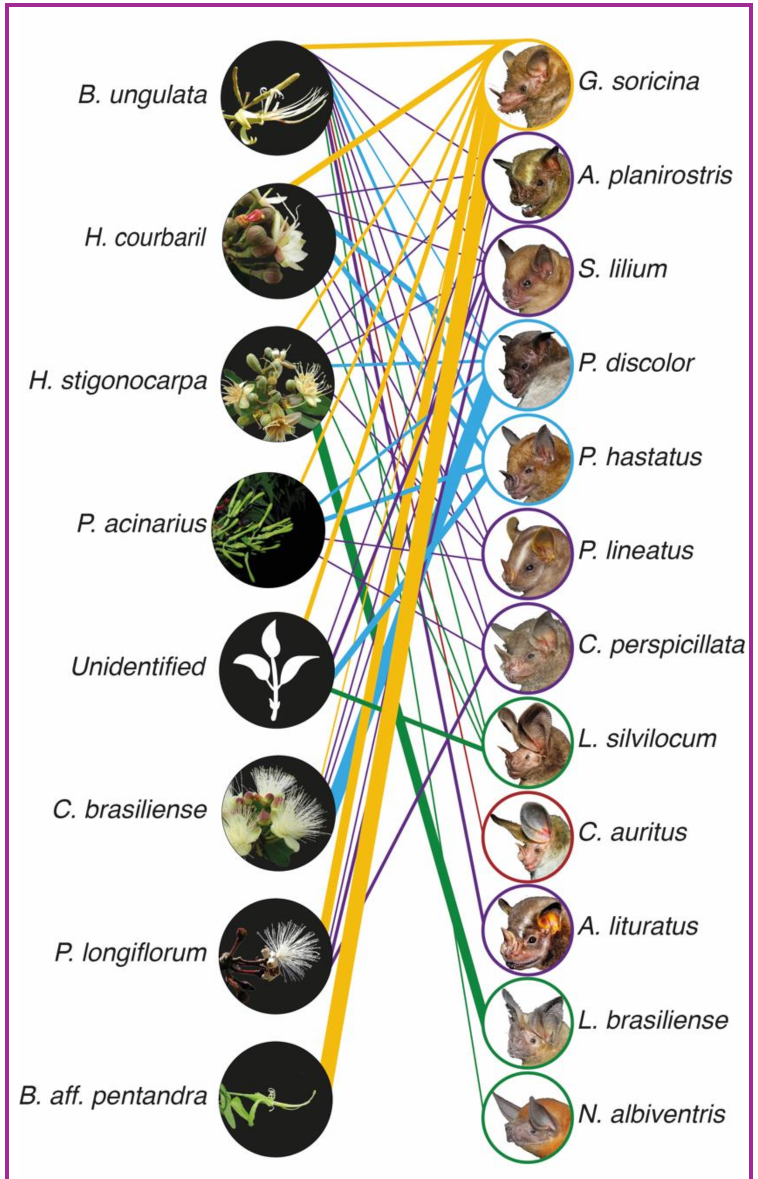
Gonçalves et al. 2025. *Funct. Ecol.*





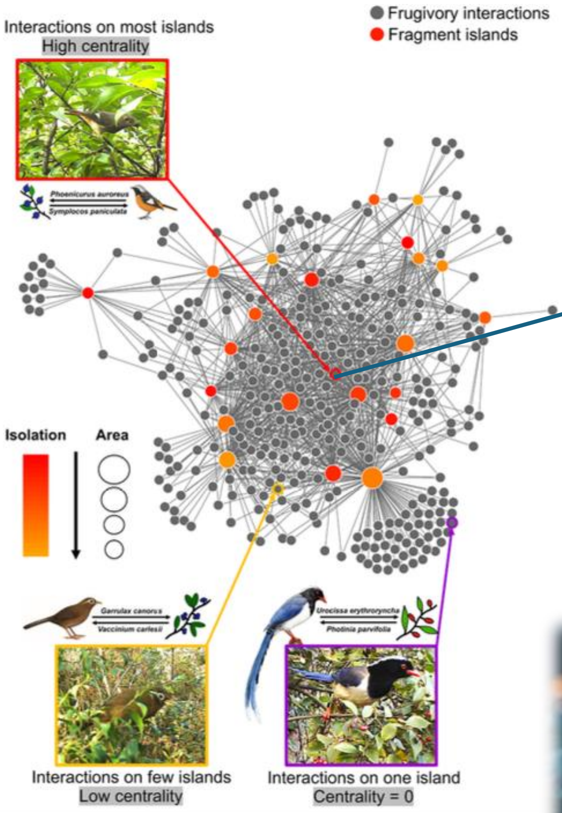


Zhu et al. 2025. *PNAS*



Gonçalves et al. 2025. *Funct. Ecol.*

* It is important to understand under which conditions they are fragile to external perturbations and/or internal failures



Zhu et al. 2025. *PNAS*

The interconnected nature of networks can be either beneficial or detrimental to disturbances

* It is important to understand under which conditions they are fragile to external perturbations and/or internal failures

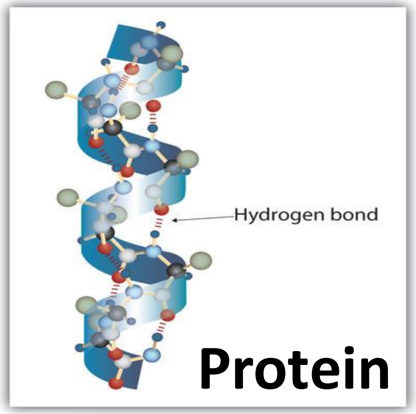
CNN World

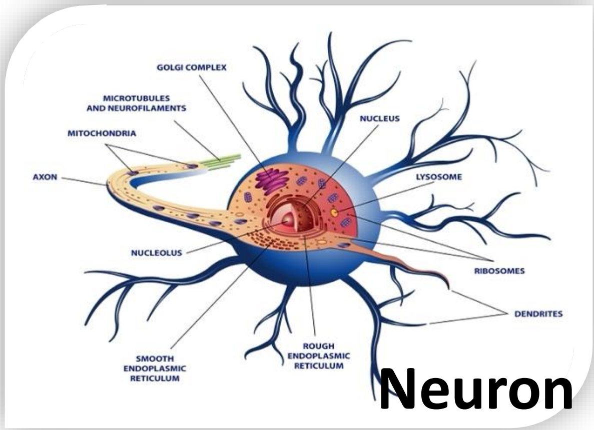
World / Europe

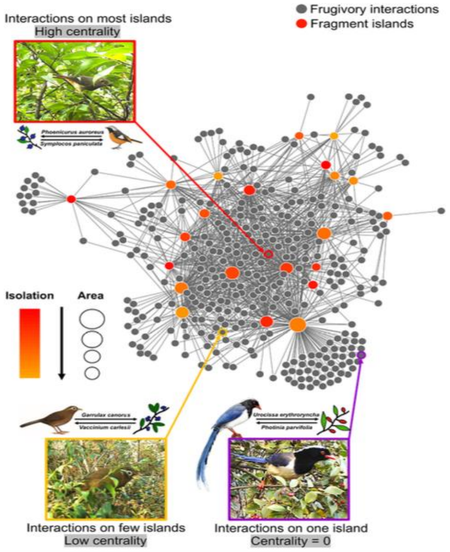
Global travel is disrupted by Heathrow's closure. Here's what we know

"The impact of this incident can cascade over several days, as aircraft, crew, passengers are out of place, with limited spare aircraft and seats available to recover passengers," says the analytics firm.

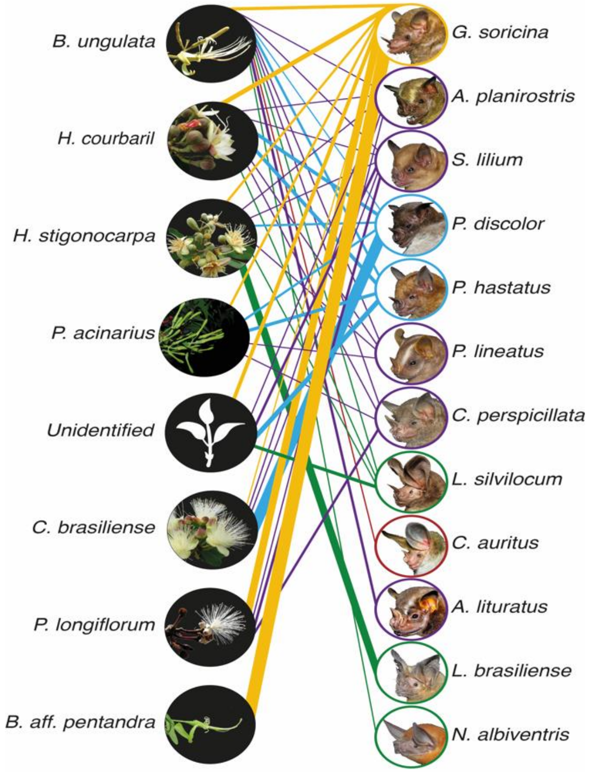
* The robustness and resilience of complex networks are defined by various types of phase transitions. The nature of these transitions depends on the system's structural features, such as whether it is spatially embedded, interdependent with other systems, or multiplex, as well as its dynamics.





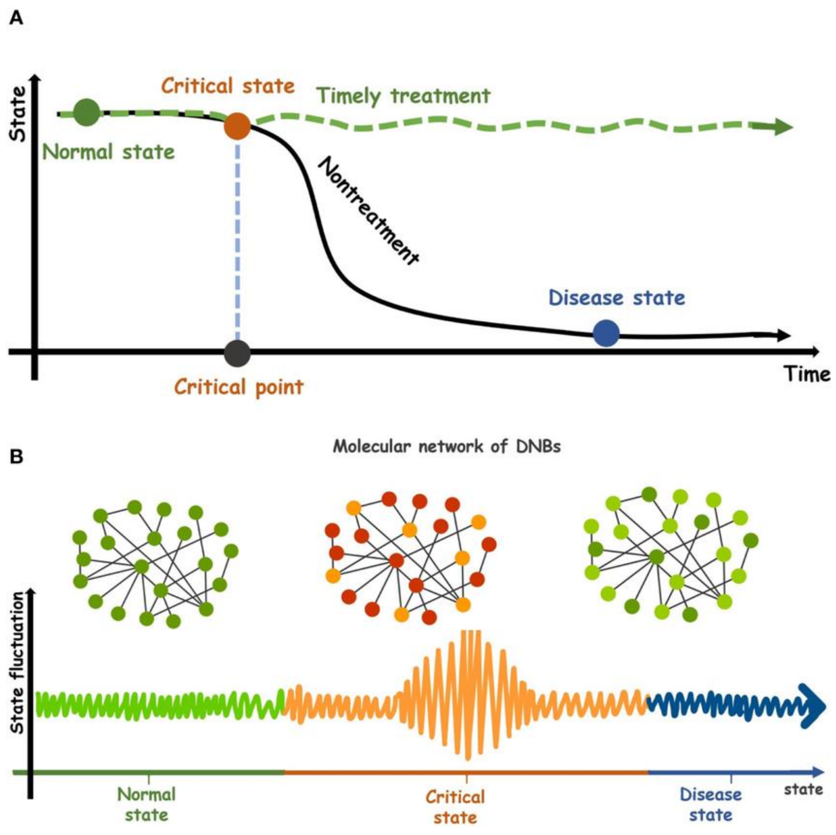


Zhu et al. 2025. *PNAS*



Gonçalves et al. 2025. *Funct. Ecol.*

* The study of a system's response to perturbations (in terms of structural and dynamical stability) is crucial because it can be used to anticipate critical transitions



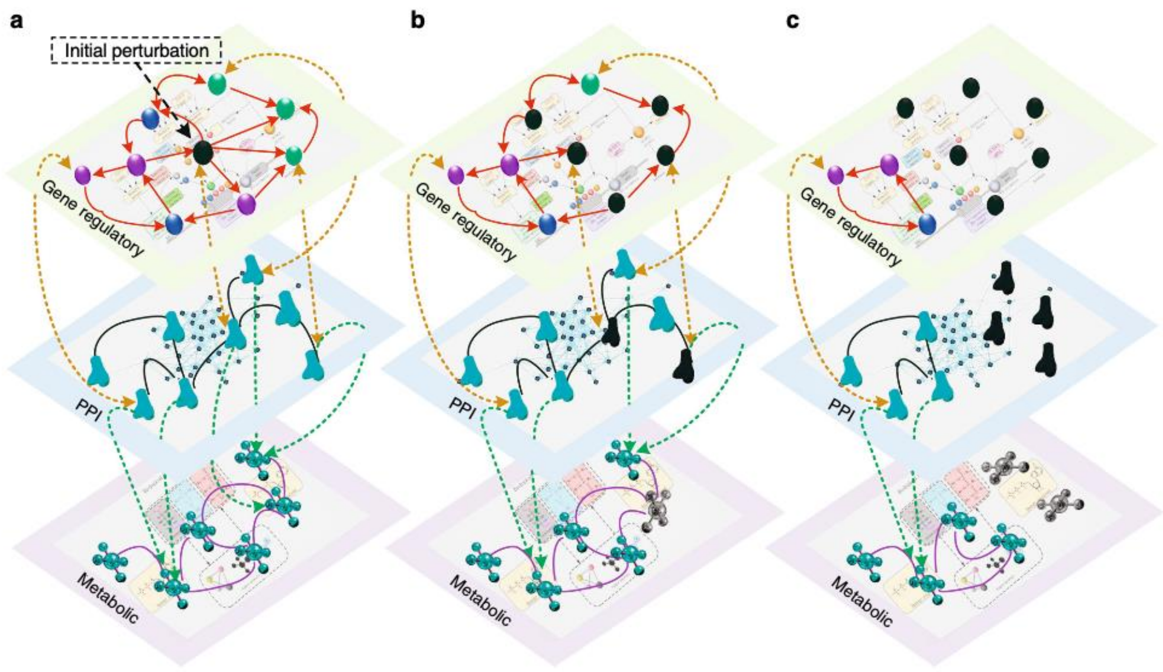
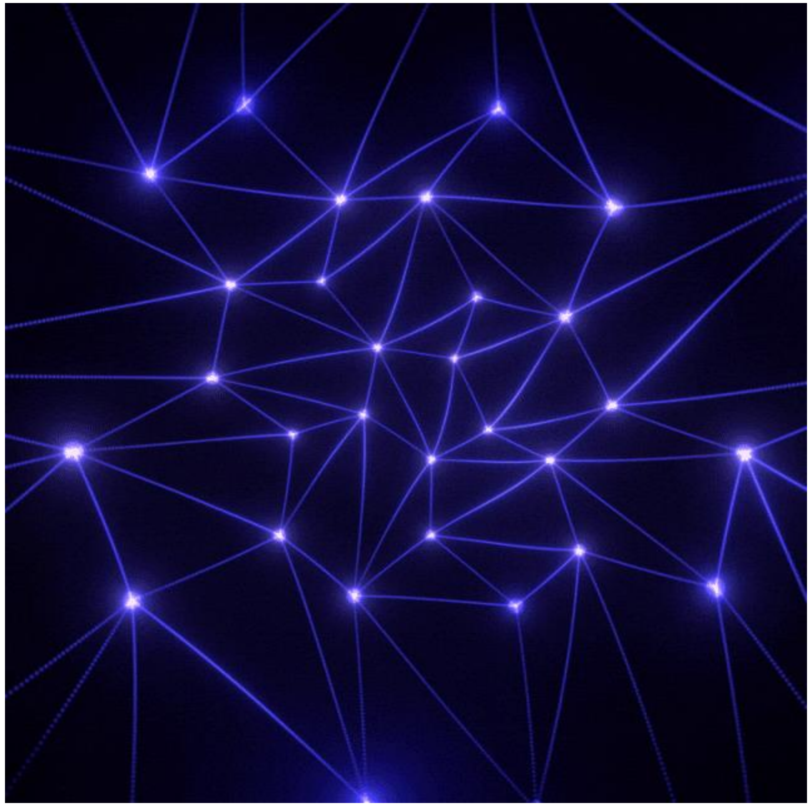
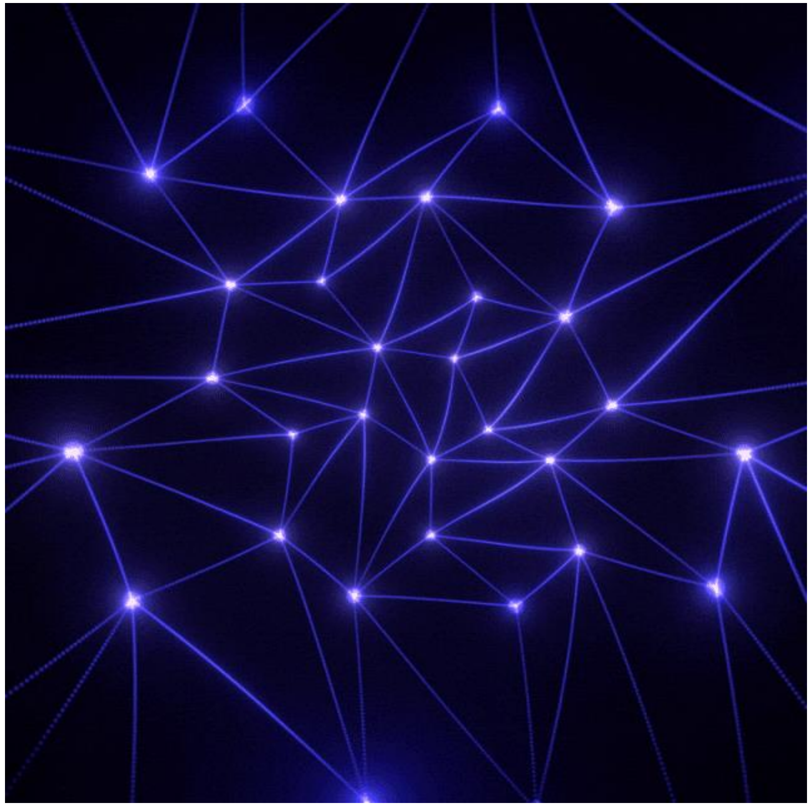


Fig. 1 Schematic demonstration of the cascading failure process in multilayer biological molecular networks. The multilayer model includes a gene regulatory network in which the genes (ellipses) are linked by regulatory relations (red directed links), a PPI network in which proteins (bone shapes) are linked by physical interactions (black undirected links), and a metabolic network in which metabolites (molecule shapes) are connected by chemical–chemical interactions (purple undirected links). The gene regulatory and PPI networks are connected by bidirectional interdependency links (yellow dashed lines). From the PPI to metabolic networks, there are multiple supporting links (green dashed lines). **a** Initially perturb a gene in the gene regulatory network causing such gene to stop functioning (represented by a black ellipse). **b** The target genes of the perturbed genes fail (black ellipses), and their corresponding proteins stop functioning, represented by black bone shapes. **c** The proteins that disconnected from the largest connected component fail (black bone shapes), and the metabolites losing all supports from the PPI network stop functioning (black molecule shapes).

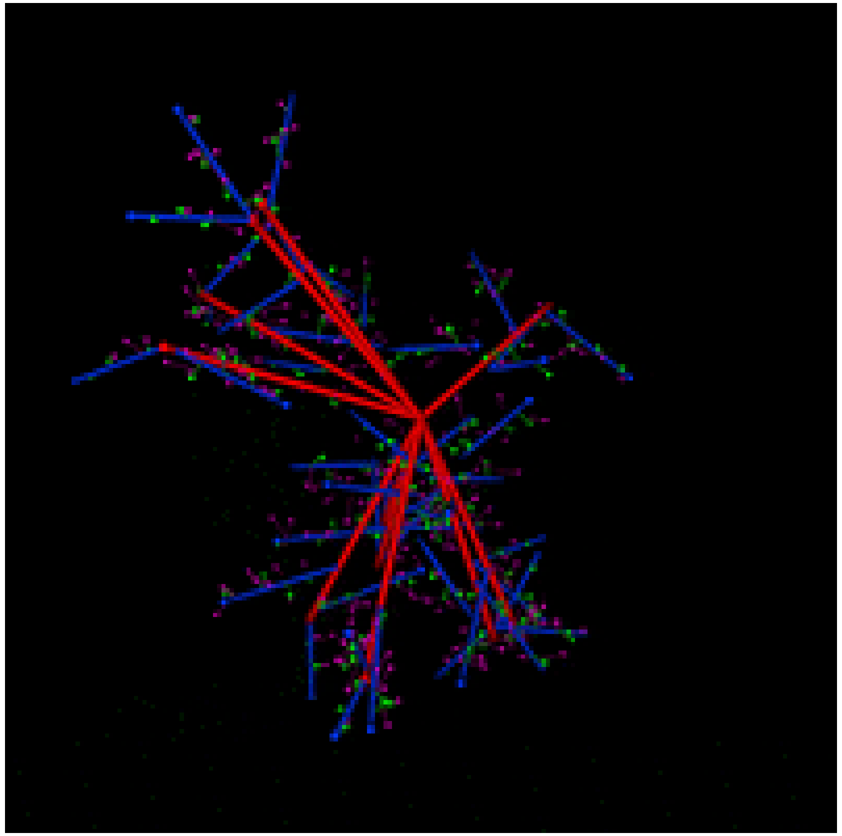
The boundaries of the safe operational space preserving all species



The boundaries of the safe operational space preserving all species



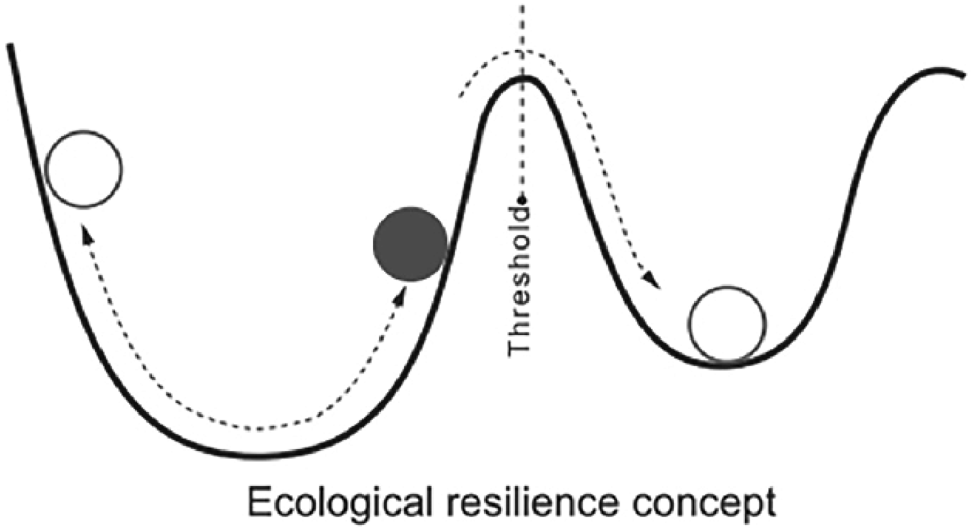
The rate and shape of network collapse once the boundaries of such a space are crossed



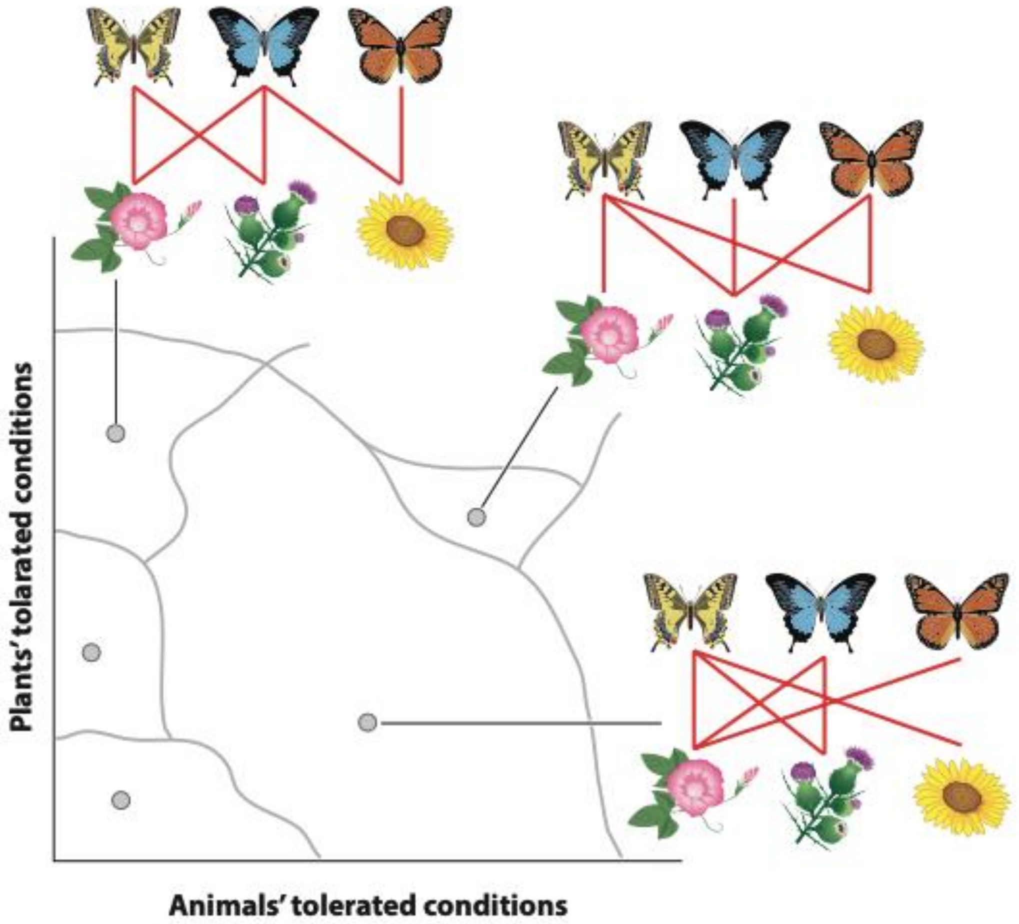
The structural stability of mutualistic networks

The structural stability of mutualistic networks

The concept of linear stability



Bascompte & Scheffer 2023



Highest nested network

Highest robustness

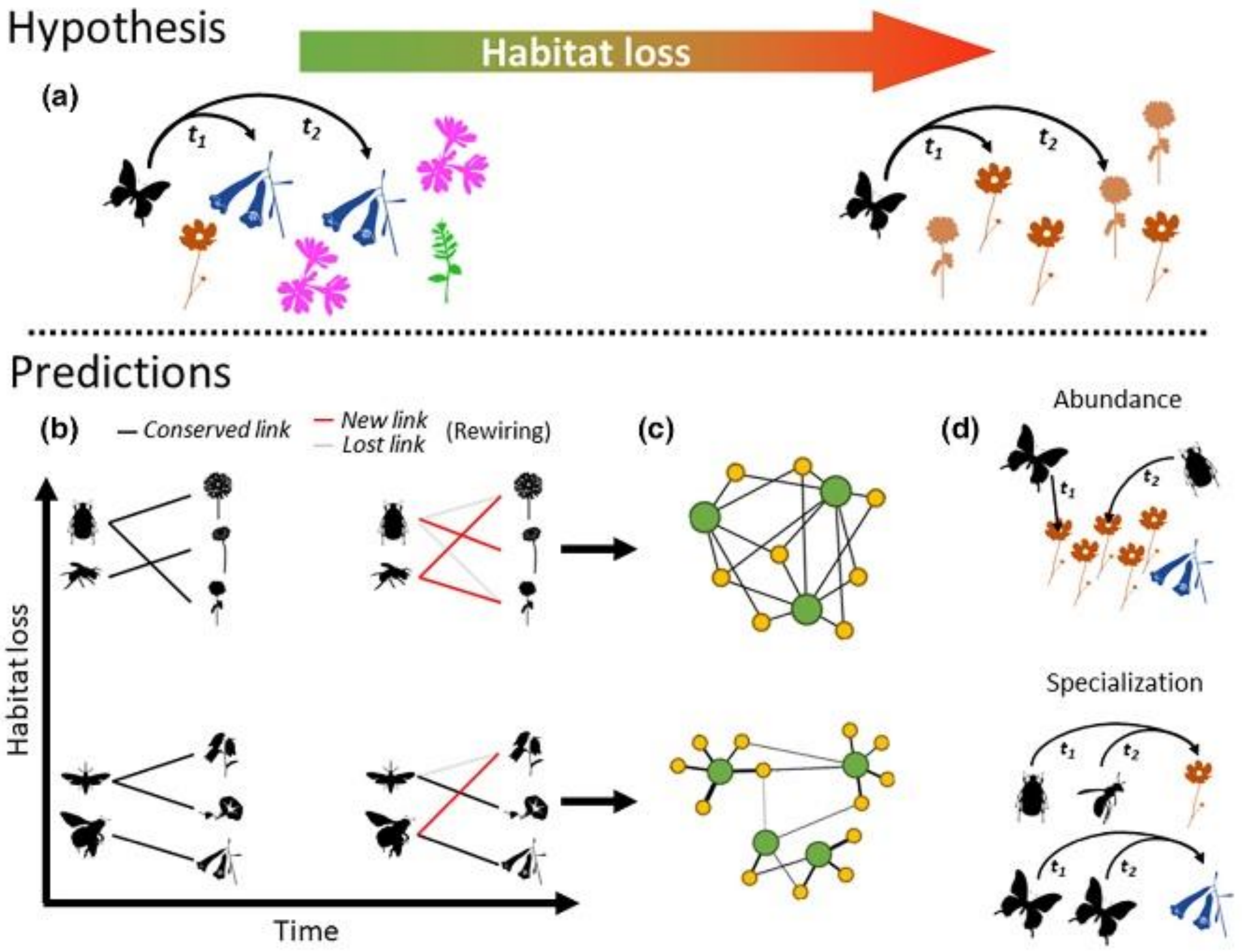
Figure 3

Network resilience can be measured through the concept of structural stability, which refers to the volume of parameter space compatible with the stable coexistence of all species. Different network architectures have different levels of resilience, with the highest corresponding to the nested network at the bottom. Figure

Bascompte & Scheffer 2023

Rewiring the Network

2.1. Rewiring the Network



2.1. Rewiring the Network

Why is it important to consider "rewiring" when estimating the robustness of mutualistic networks?

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Why is it important to consider "rewiring" when estimating the robustness of mutualistic networks?

Because species may not go extinct immediately after losing a partner, but there is likely to be some fitness reduction or population decline. Empirical evidence shows that secondary extinctions can be buffered through the rewiring of interactions with surviving partners.

2.1. Rewiring the Network

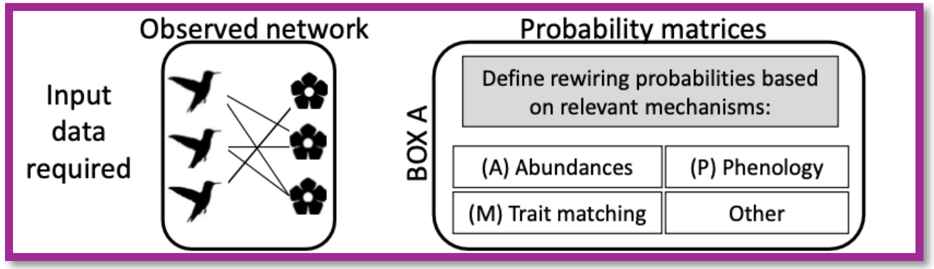
RESEARCH ARTICLE

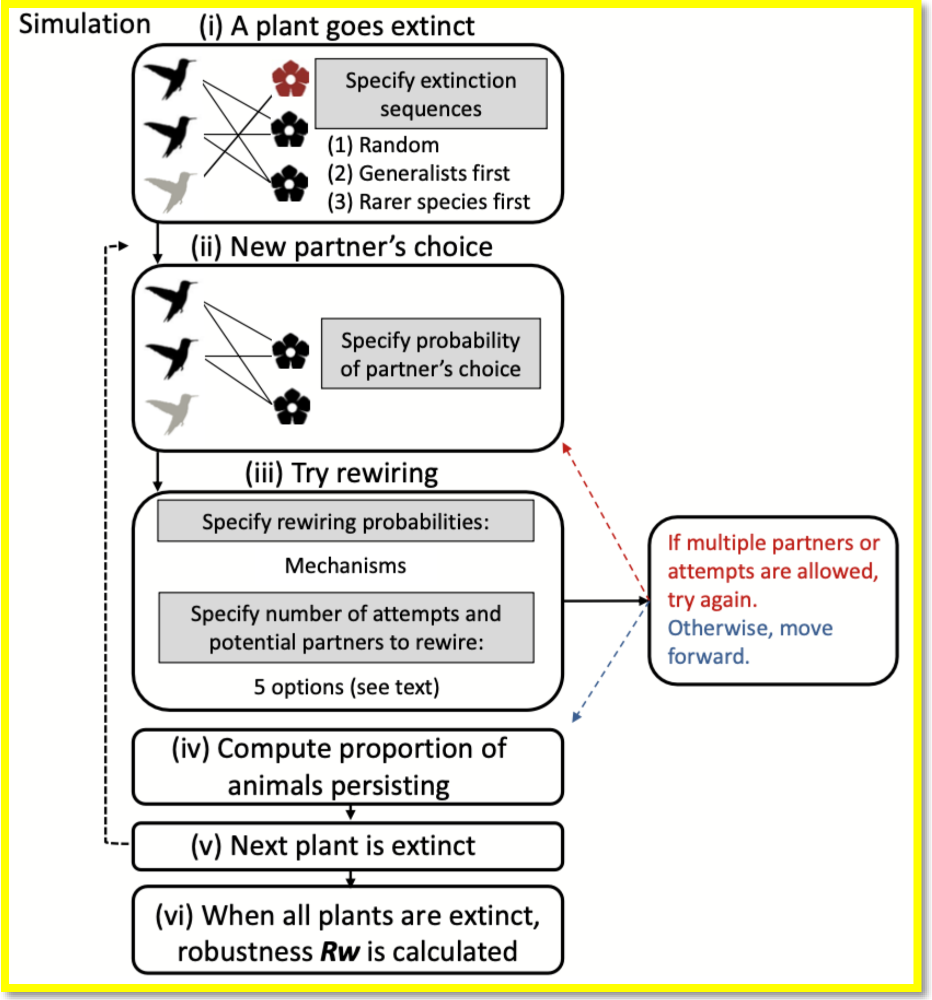
Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

Including rewiring in the estimation of the robustness of mutualistic networks

Jeferson Vizentin-Bugoni[1,2] | Vanderlei J. Debastiani[3] | Vinicius A. G. Bastazini[4] | Pietro K. Maruyama[5] | Jinelle H. Sperry[1,2]

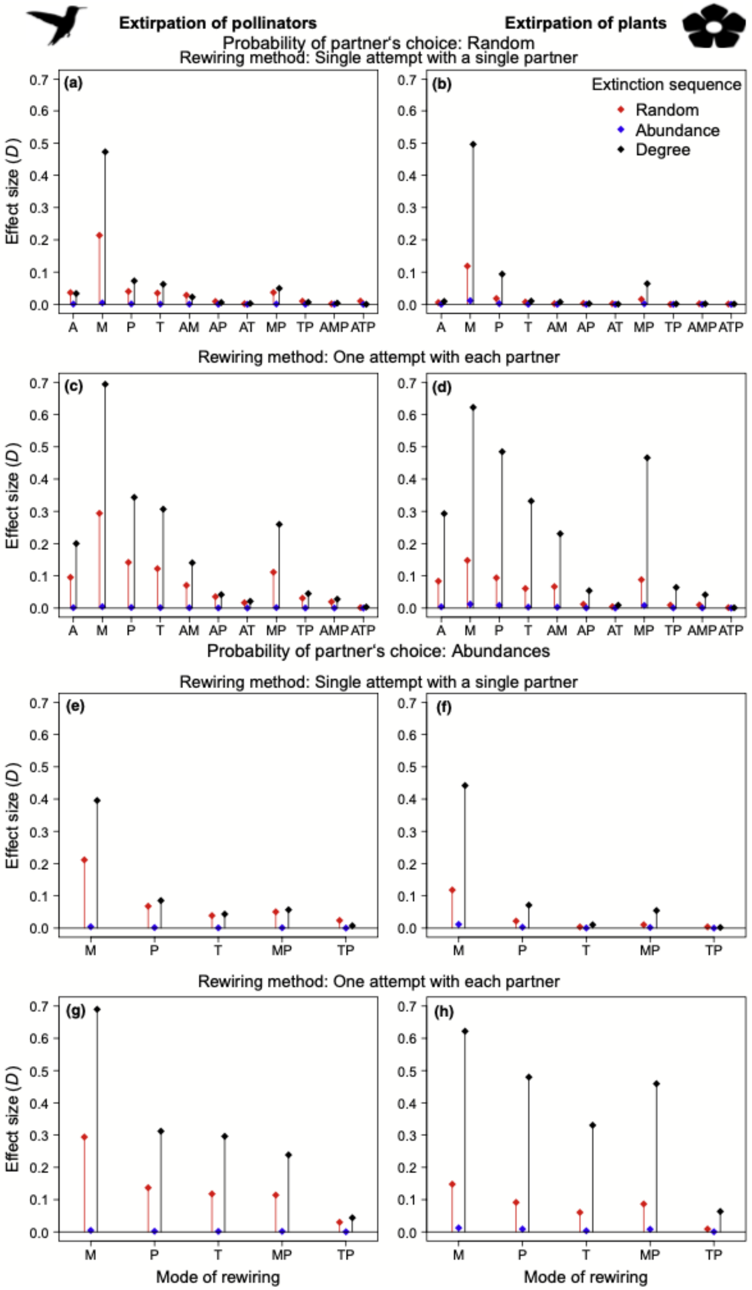
2.1. Rewiring the Network





Vizentin-Bugoni et al. 2019

2.1. Rewiring the Network



Vizentin-Bugoni et al. 2019

2.1. Rewiring the Network

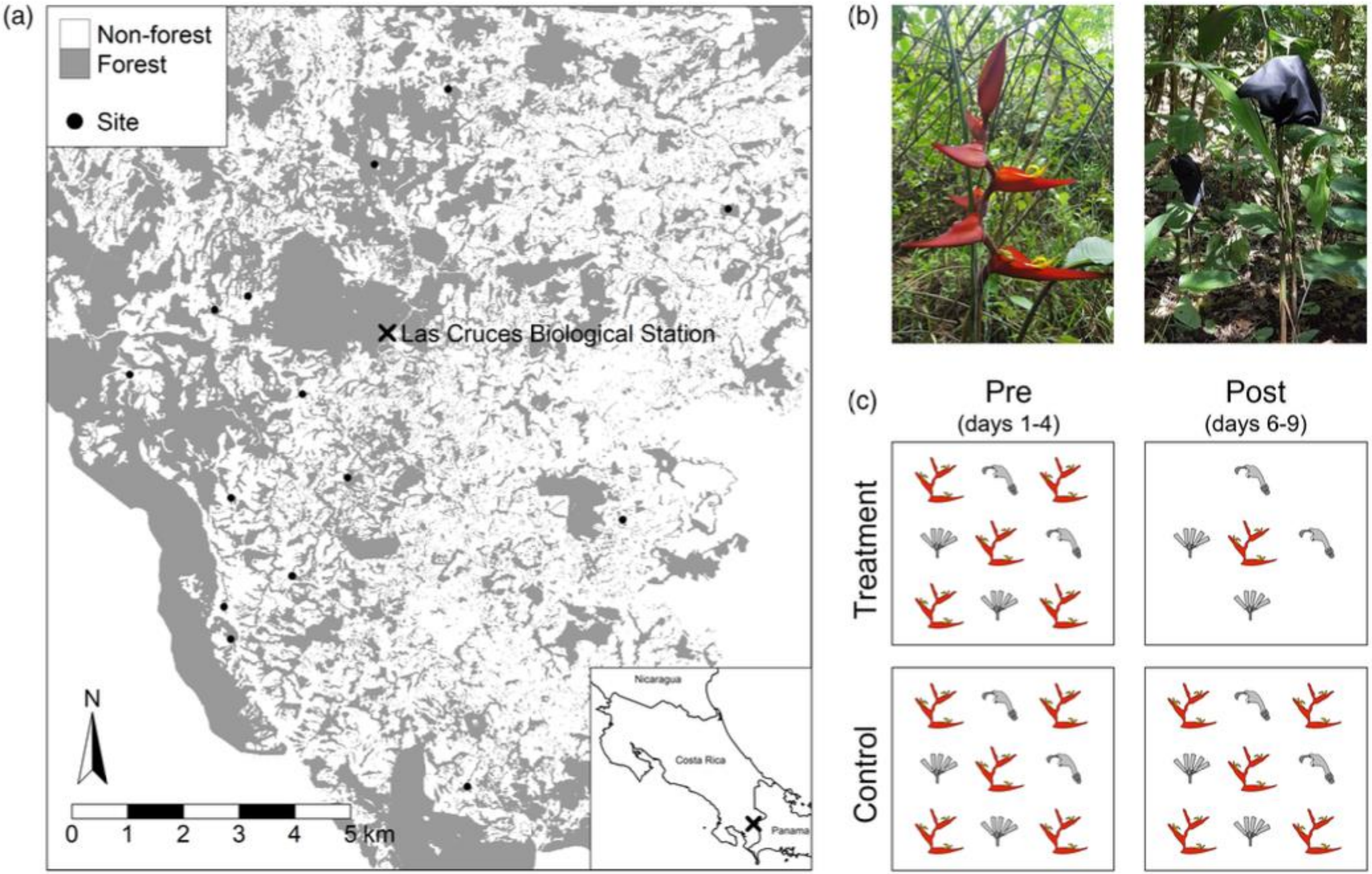
Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Plant–hummingbird pollination networks exhibit limited rewiring after experimental removal of a locally abundant plant species

Kara G. Leimberger[1] | Adam S. Hadley[1,2] | Matthew G. Betts[1]

2.1. Rewiring the Network



Leimberger et al. 2022

2.1. Rewiring the Network

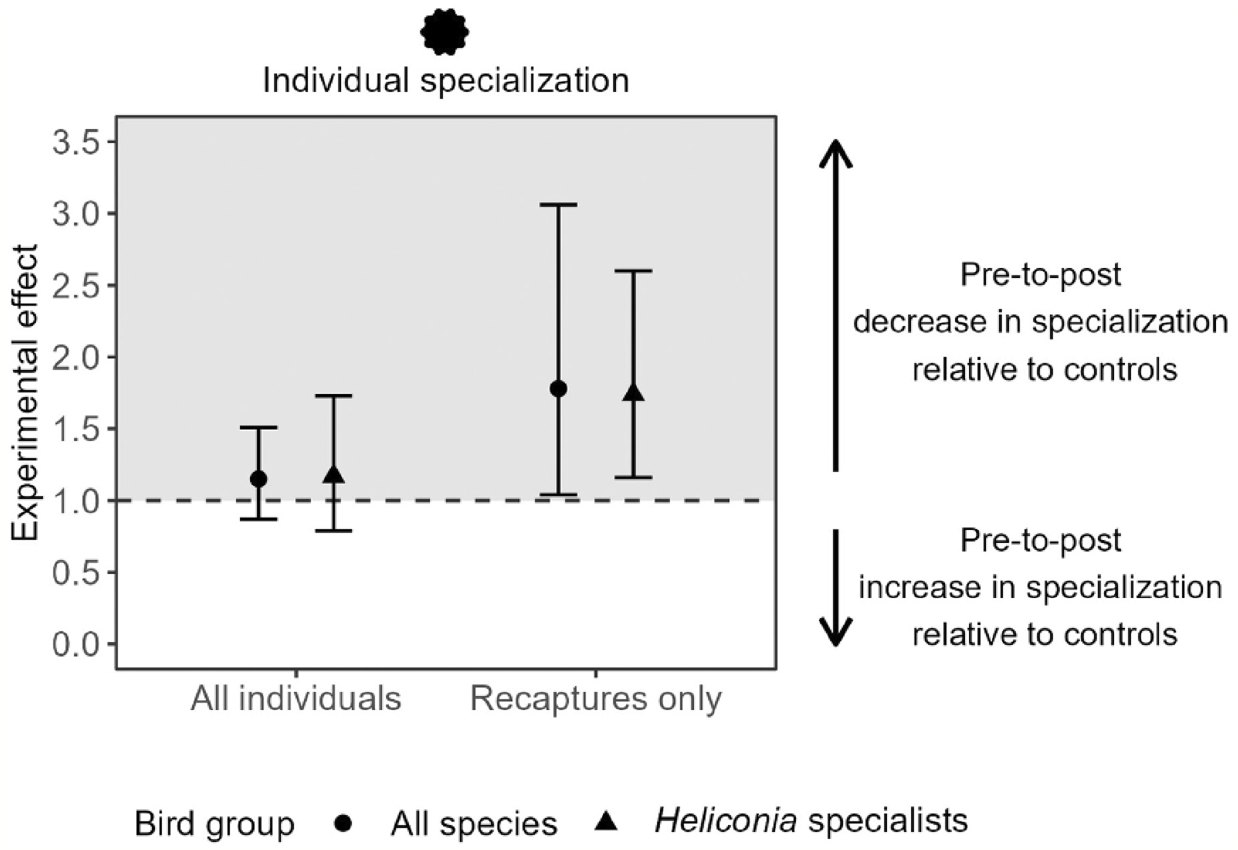
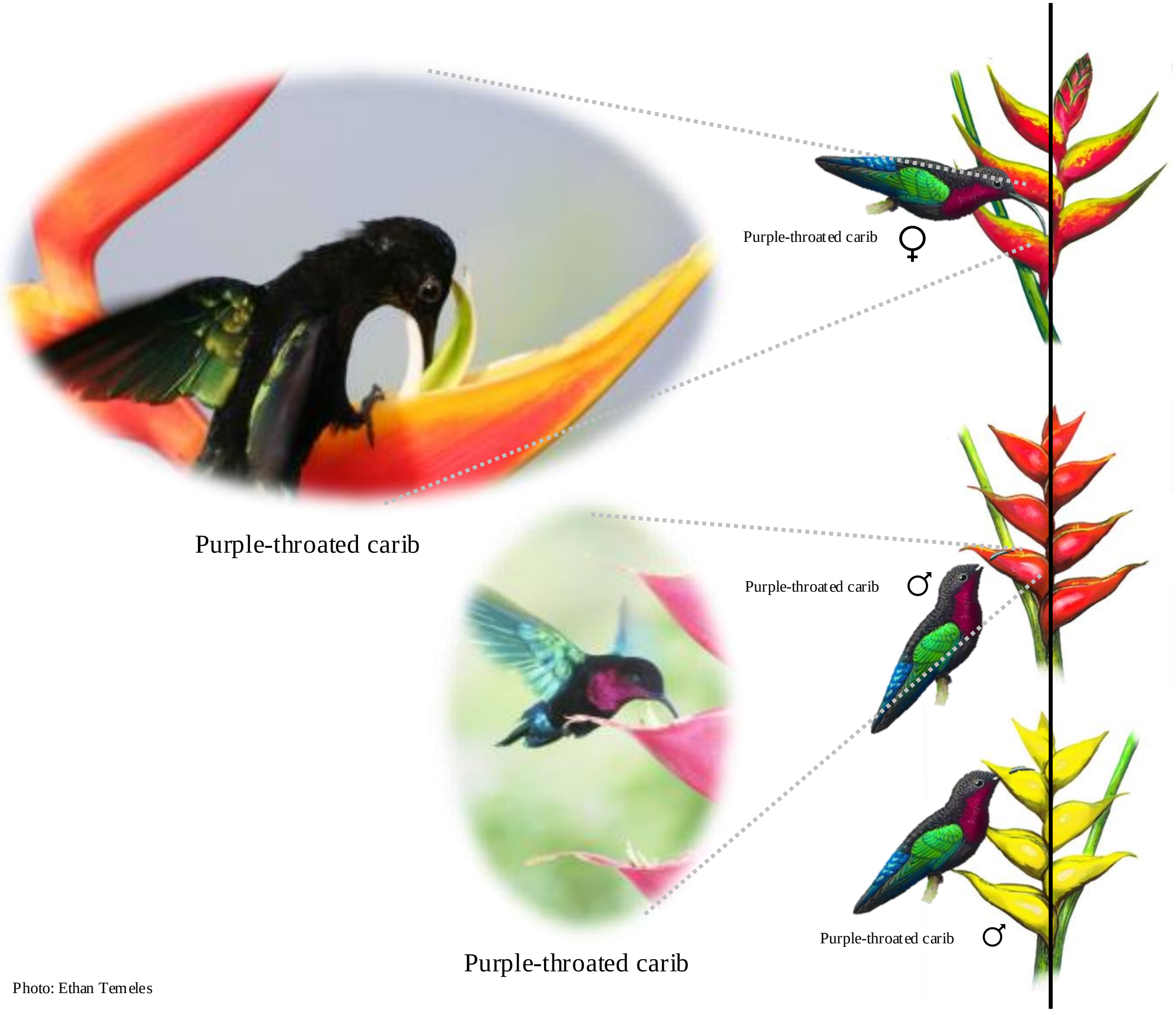


FIGURE 4 Effects of experimental *Heliconia* removal on individual-level specialization, quantified as the number of pollen morphotypes per hummingbird, using a dataset of 302 pollen samples. Following the Before-After-Control-Impact experimental design, the *y*-axis reflects the pre-to-post change in treatment replicates relative to pre-to-post change in control replicates. Estimates and 95% confidence intervals were calculated using the 'contrasts' function of 'emmeans' (Lenth, 2020). No change is indicated by the dashed line at 1, and grey shading indicates support of the *rewiring hypothesis* (i.e. decrease in specialization). Results are shown for all hummingbird species and for the two species considered *Heliconia* specialists: Green Hermits (*Phaethornis guy*) and Violet Sabrewings (*Campylopterus hemileucurus*). Additionally, results are shown for all individuals ($N_{\text{all species}}=275$, $N_{\textit{Heliconia}\text{ specialists}}=110$) and for a subset of individuals captured during both experimental periods (i.e. 'recaptures'; $N_{\text{all species}}=27$, $N_{\textit{Heliconia}\text{ specialists}}=16$).

Leimberger et al. 2022

2.1. Rewiring the Network

Before Hurricane



Purple-throated carib

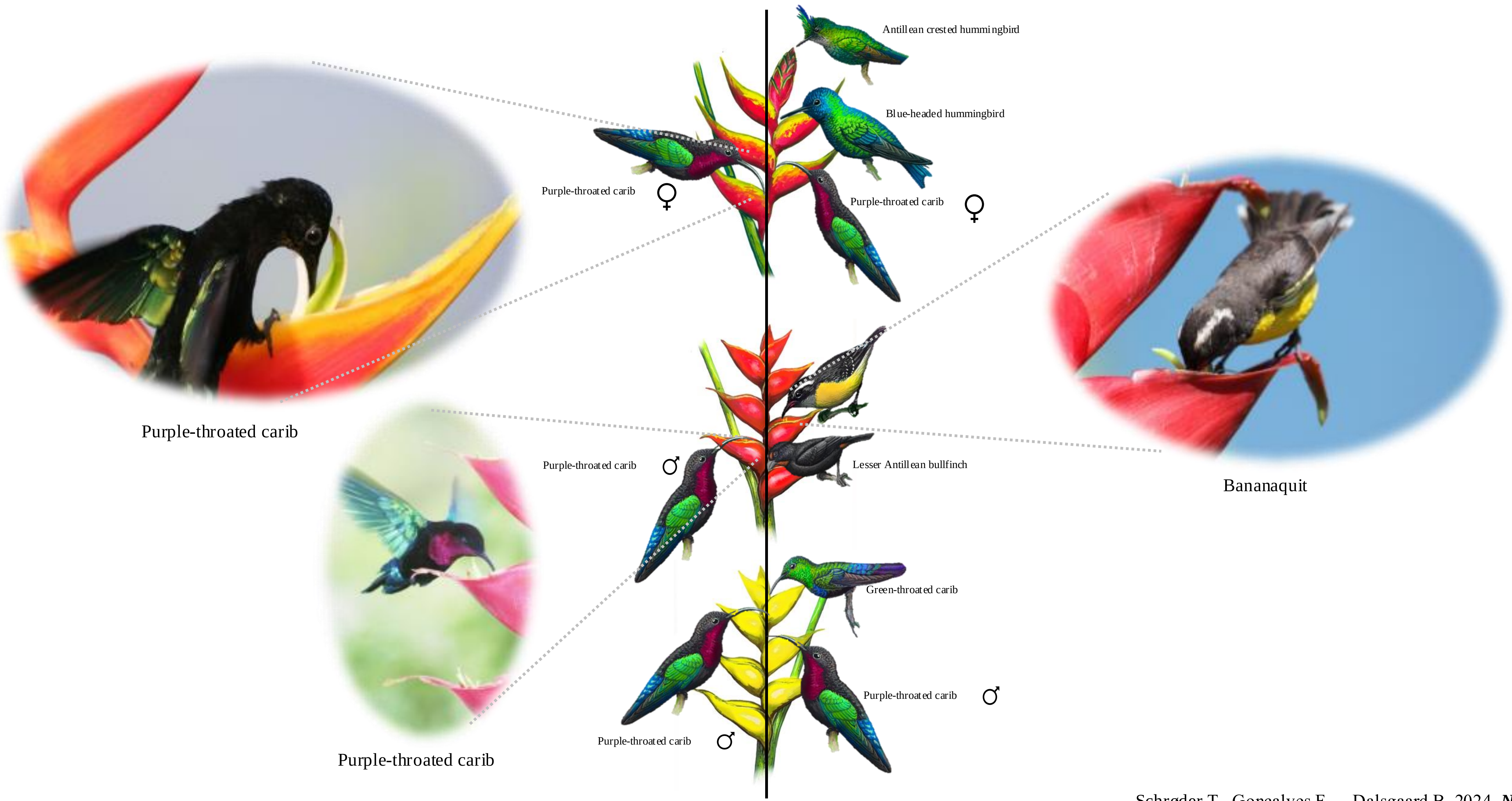
Purple-throated carib

Photo: Ethan Temeles

Schrøder T., Gonçalves F.,…Dalsgaard B. 2024. ***New Phytologist***

2.1. Rewiring the Network

After Hurricane

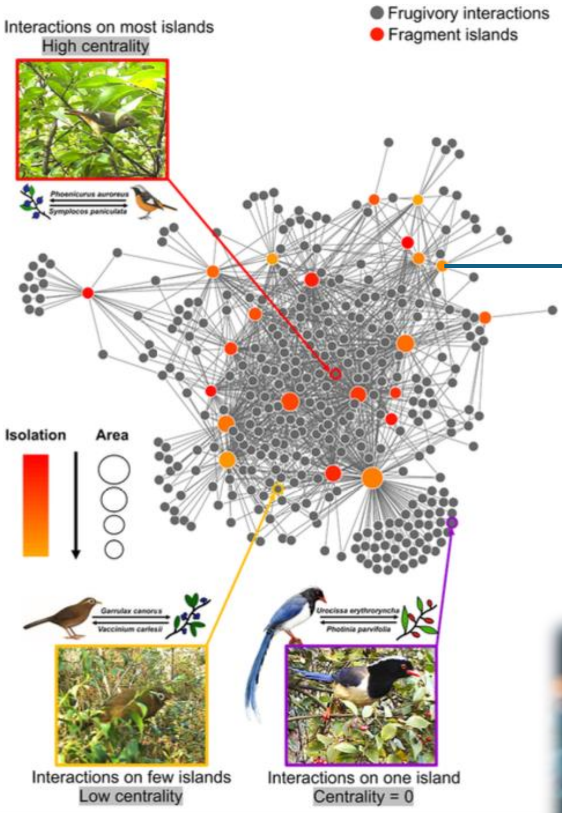


Schrøder T., Gonçalves F.,…Dalsgaard B. 2024. ***New Phytologist***

Increasing Heterogeneity

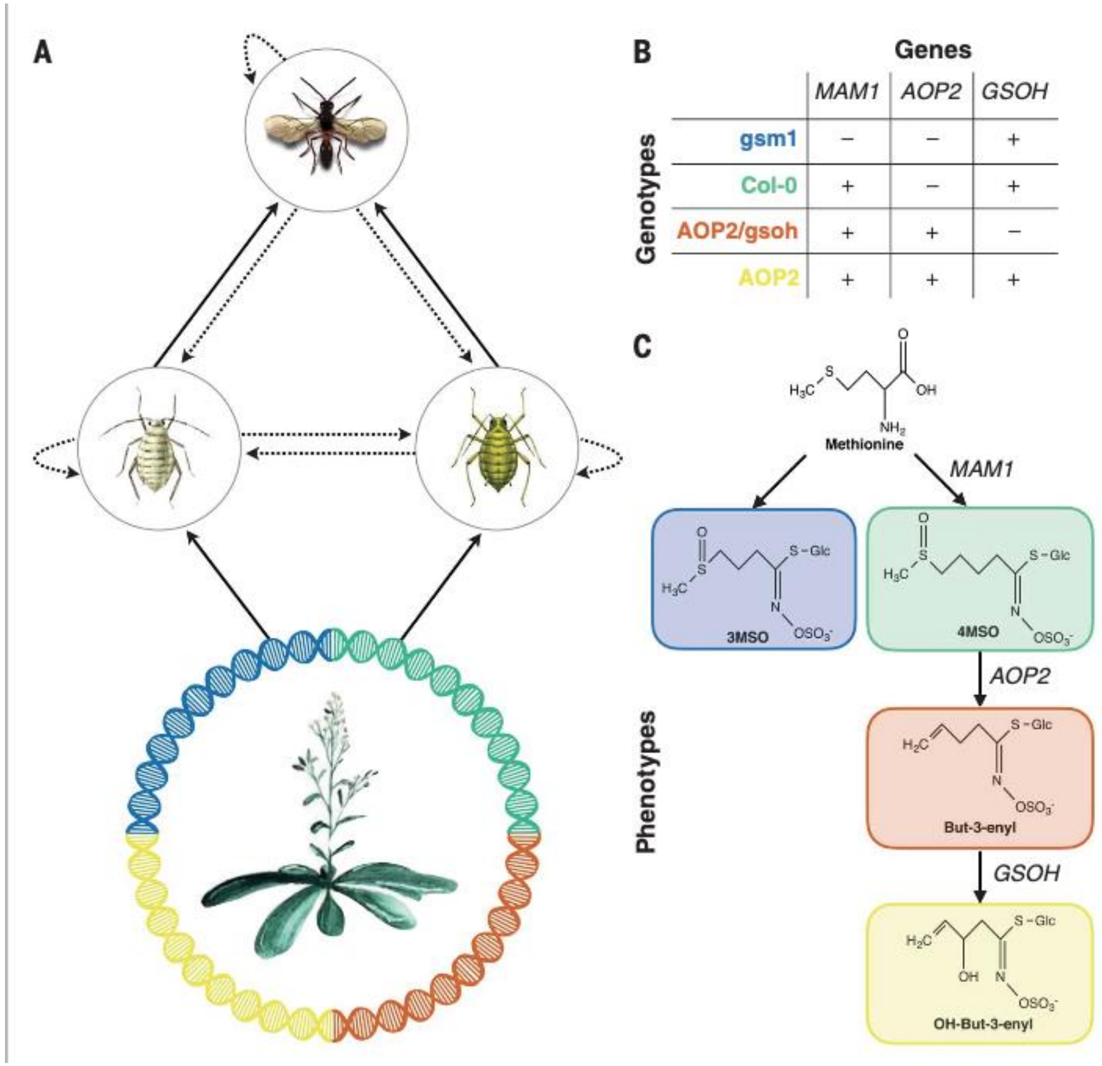
2.2. Increasing Heterogeneity

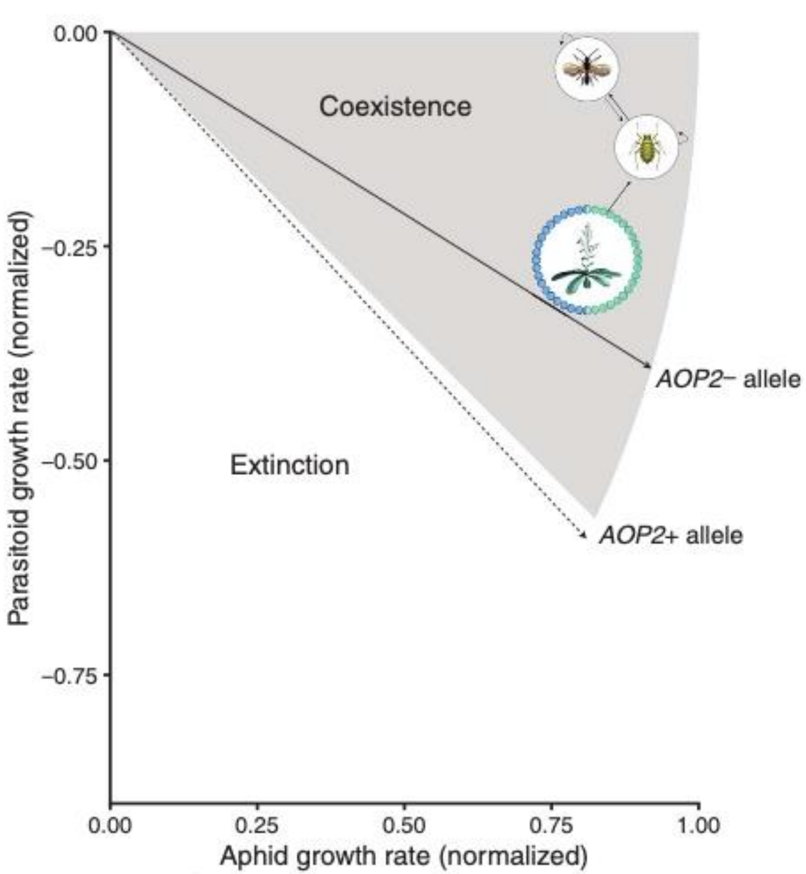
Consists of modifying the heterogeneity of the nodes



Zhu et al. 2025. *PNAS*

2.2. Increasing Heterogeneity

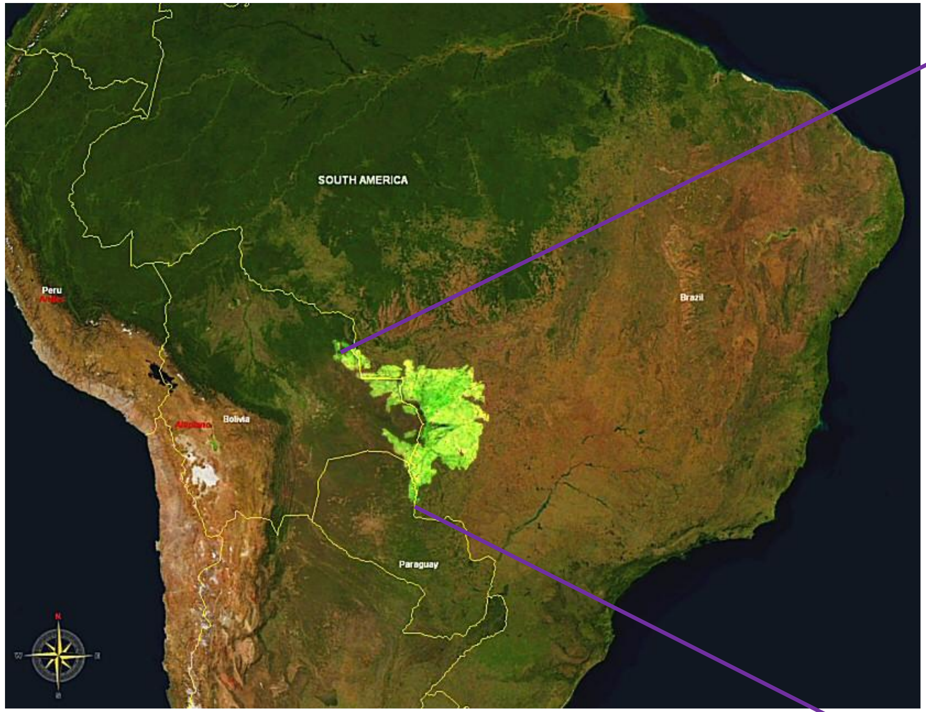


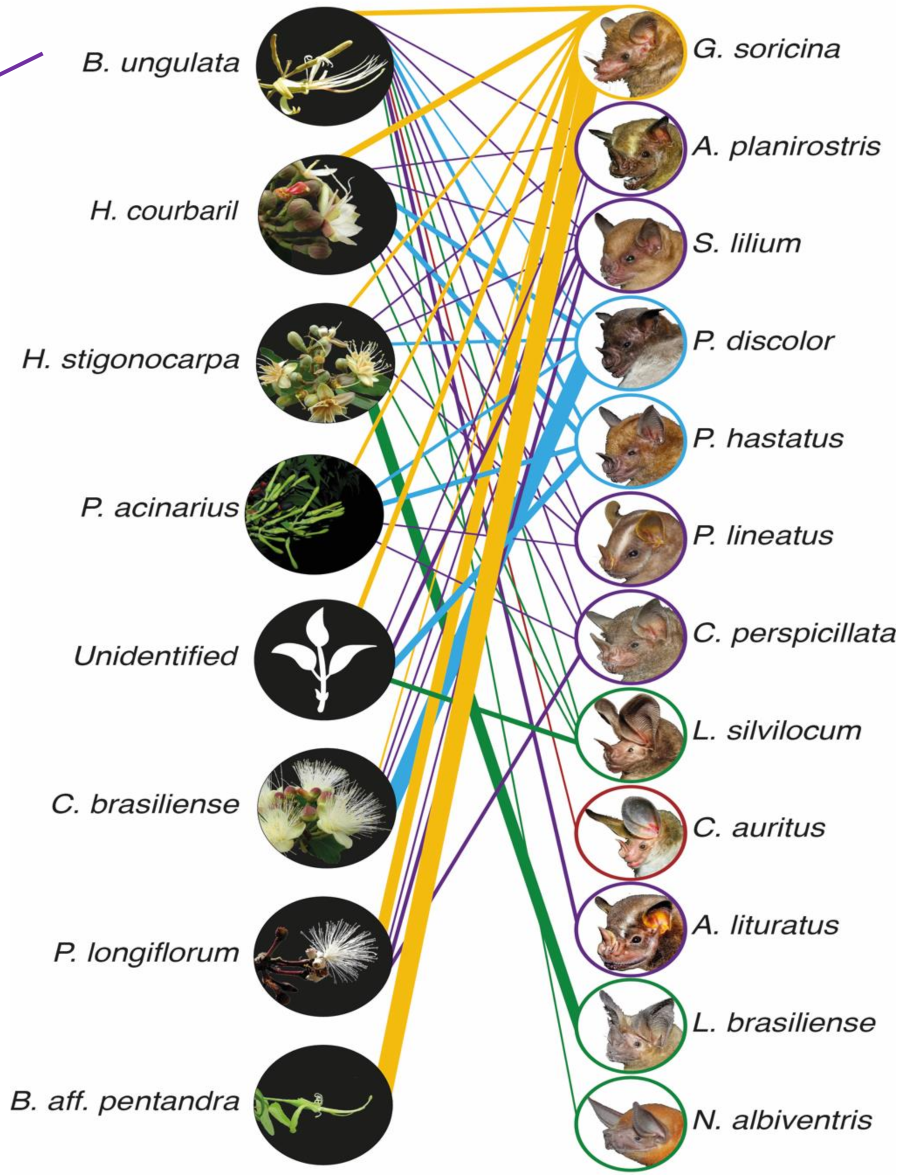


Barbour et al. 2022

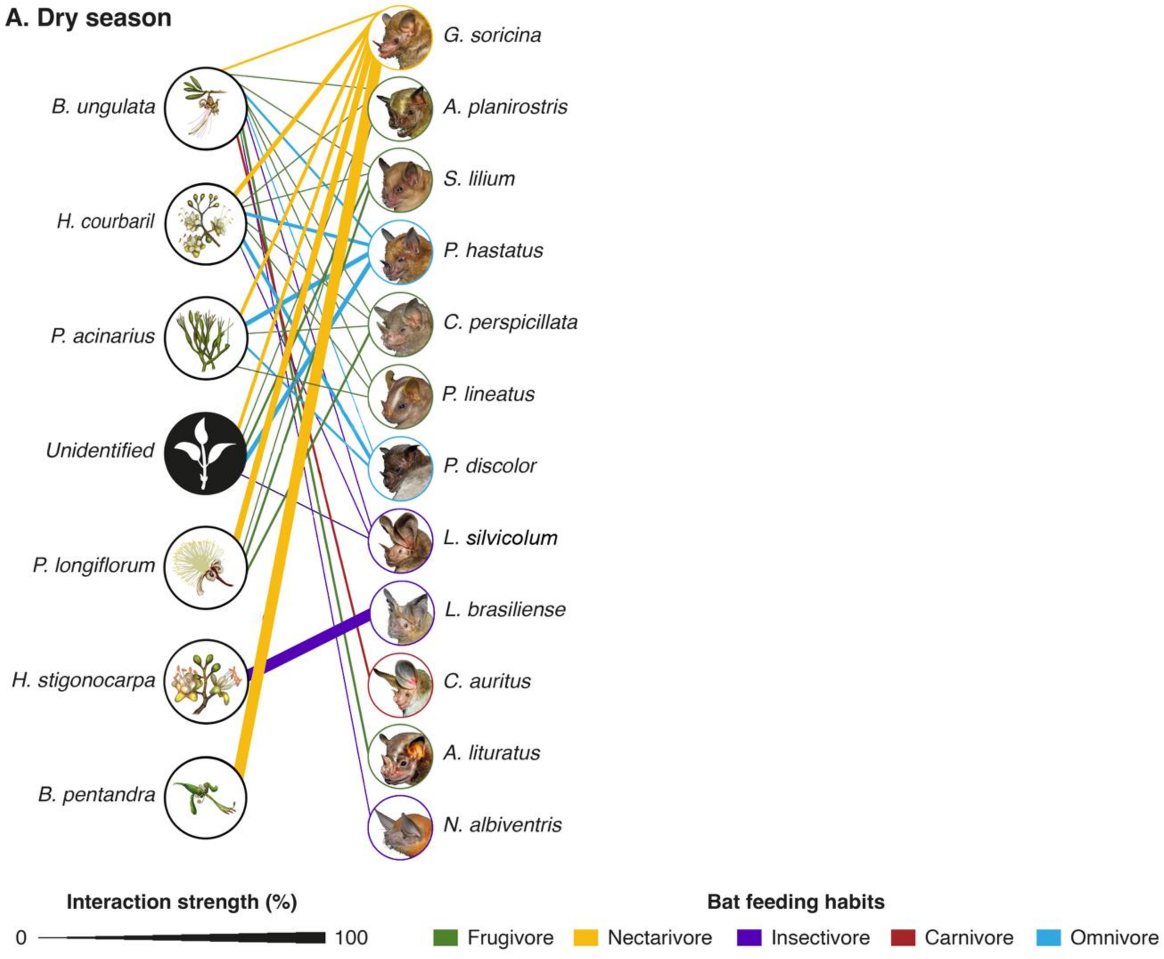
Allowing Variance

2.3. Allowing Variance



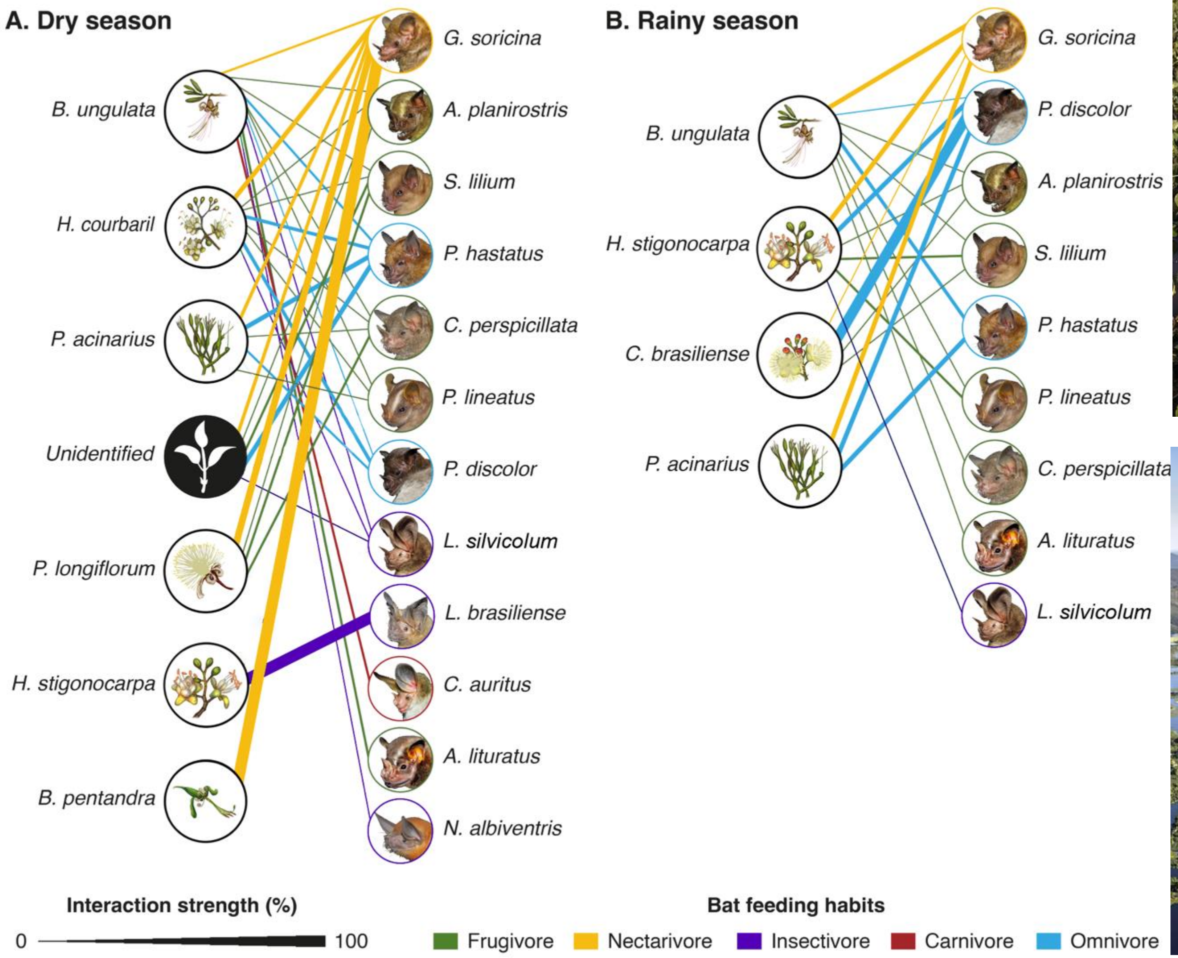


2.3. Allowing Variance



Gonçalves et al. 2025. *Funct. Ecol.*

2.3. Allowing Variance



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Allowing Coevolution

2.4. Allowing Coevolution

REPORT

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Coevolution increases robustness to extinctions in mutualistic but not exploitative communities

Fernando Pedraza | Klementyna A. Gawecka | Jordi Bascompte

2.4. Allowing Coevolution

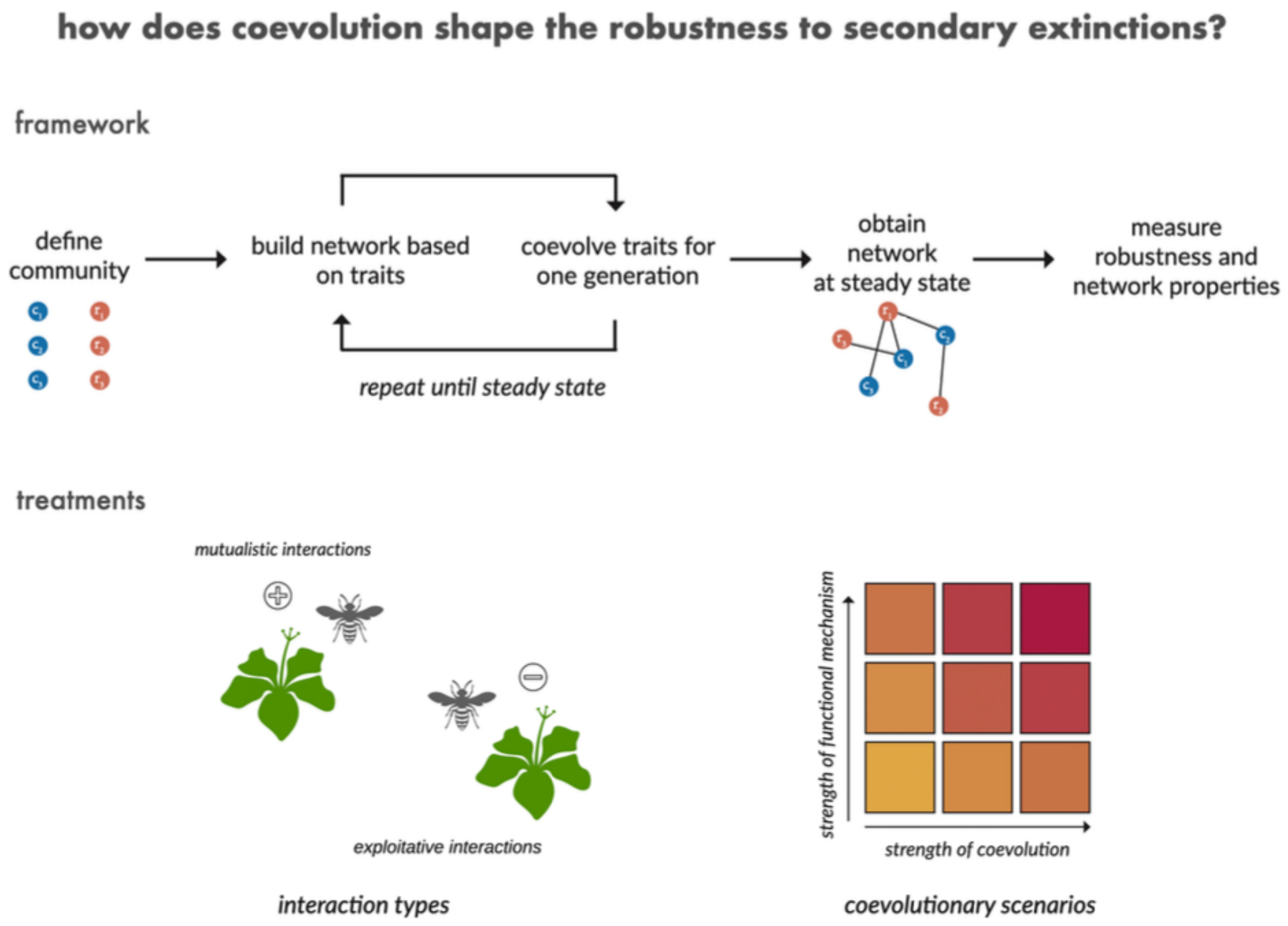


FIGURE 1 Outline of framework and experimental treatments. To test how coevolution shapes the robustness to secondary extinctions, we first define a community by: (i) specifying the number of consumer (c) and resource (r) species in each guild and (ii) assigning each species an initial trait value and environmental optimum. Then, we (iii) build a network of interactions based on species' similarity of traits and (iv) let species traits coevolve for one generation. We repeat steps (iii) and (iv) until we reach a steady state—when network structure no longer changes between time steps. Lastly, we (v) measure the robustness to secondary extinctions and the structure of the interaction networks obtained. We perform simulations for: Communities with antagonistic or mutualistic interactions and contrasting coevolutionary scenarios. Figure created by Fernando Pedraza using icons of the insect and plant from Apple Keynote Software.

Pedraza et al. 2025

2.4. Allowing Coevolution

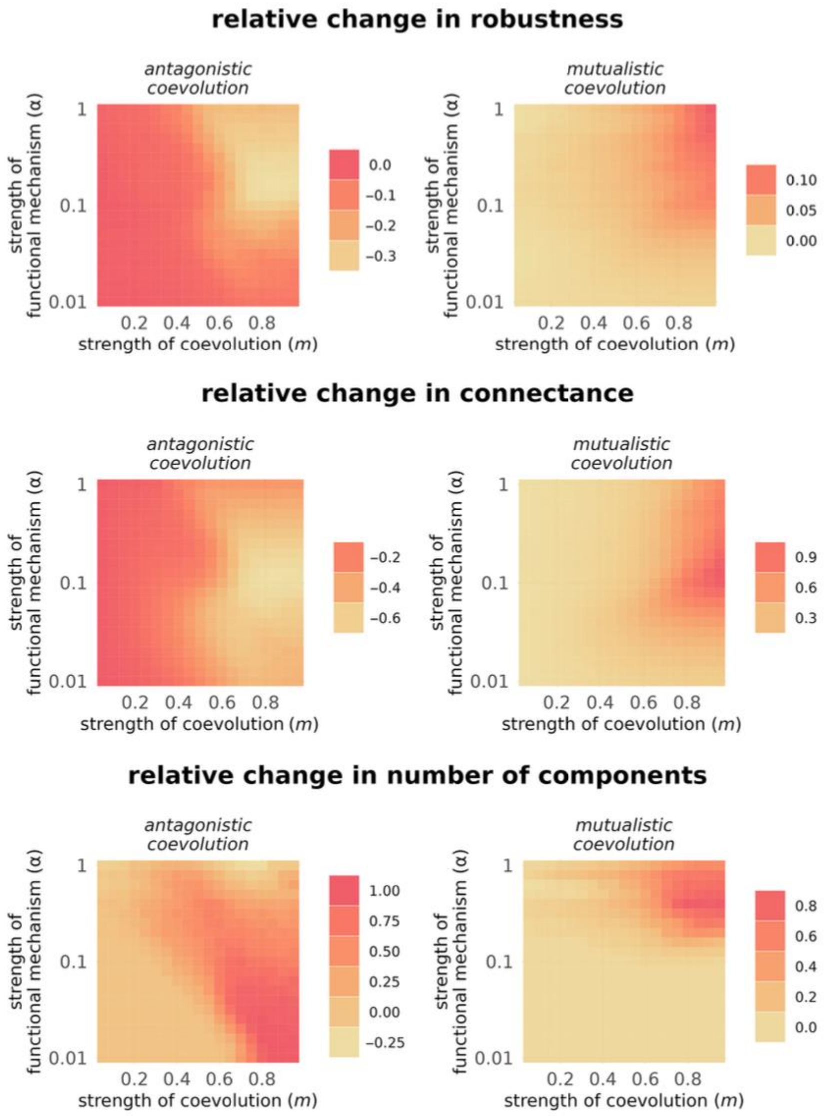
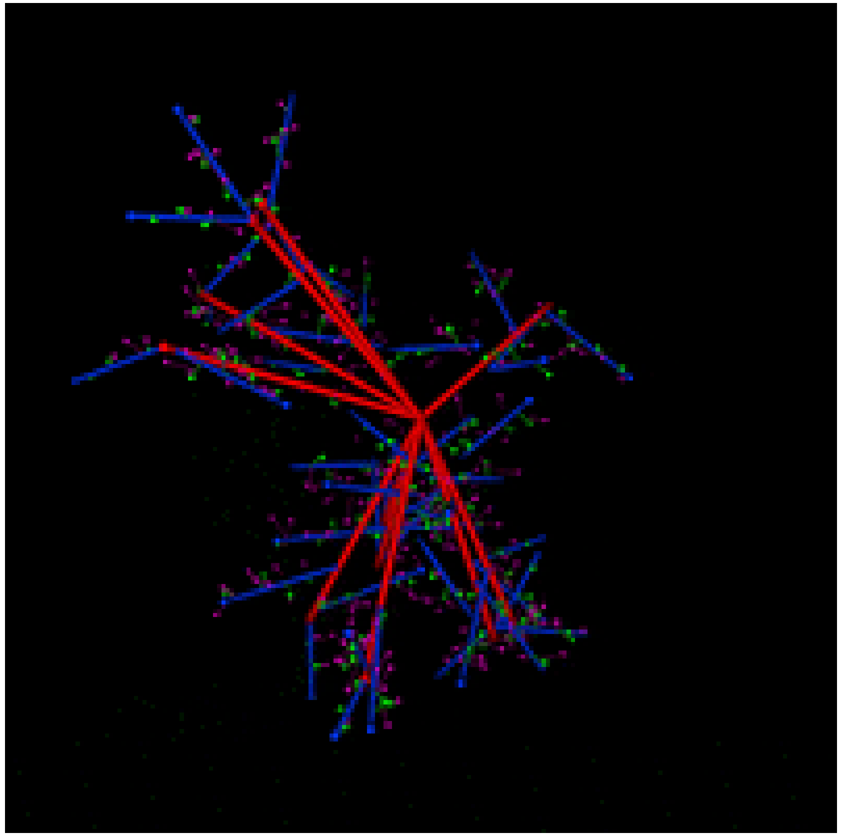


FIGURE 5 The strength of coevolution and functional mechanism controls the magnitude and direction of changes to robustness, connectance, and number of components. The grids summarize the relative change in robustness, connectance, or number of components due to coevolution, averaged across all communities for each coevolutionary scenario.

Pedraza et al. 2025

The collapse of mutualistic networks

The rate and shape of network collapse once the boundaries of such a space are crossed



3.1. Tipping points

REVIEW

doi:10.1038/nature11018

Approaching a state shift in Earth's biosphere

Anthony D. Barnosky[1,2,3], Elizabeth A. Hadly[4], Jordi Bascompte[5], Eric L. Berlow[6], James H. Brown[7], Mikael Fortelius[8], Wayne M. Getz[9], John Harte[9,10], Alan Hastings[11], Pablo A. Marquet[12,13,14,15], Neo D. Martinez[16], Arne Mooers[17], Peter Roopnarine[18], Geerat Vermeij[19], John W. Williams[20], Rosemary Gillespie[9], Justin Kitzes[9], Charles Marshall[1,2], Nicholas Matzke[1], David P. Mindell[21], Eloy Revilla[22] & Adam B. Smith[23]

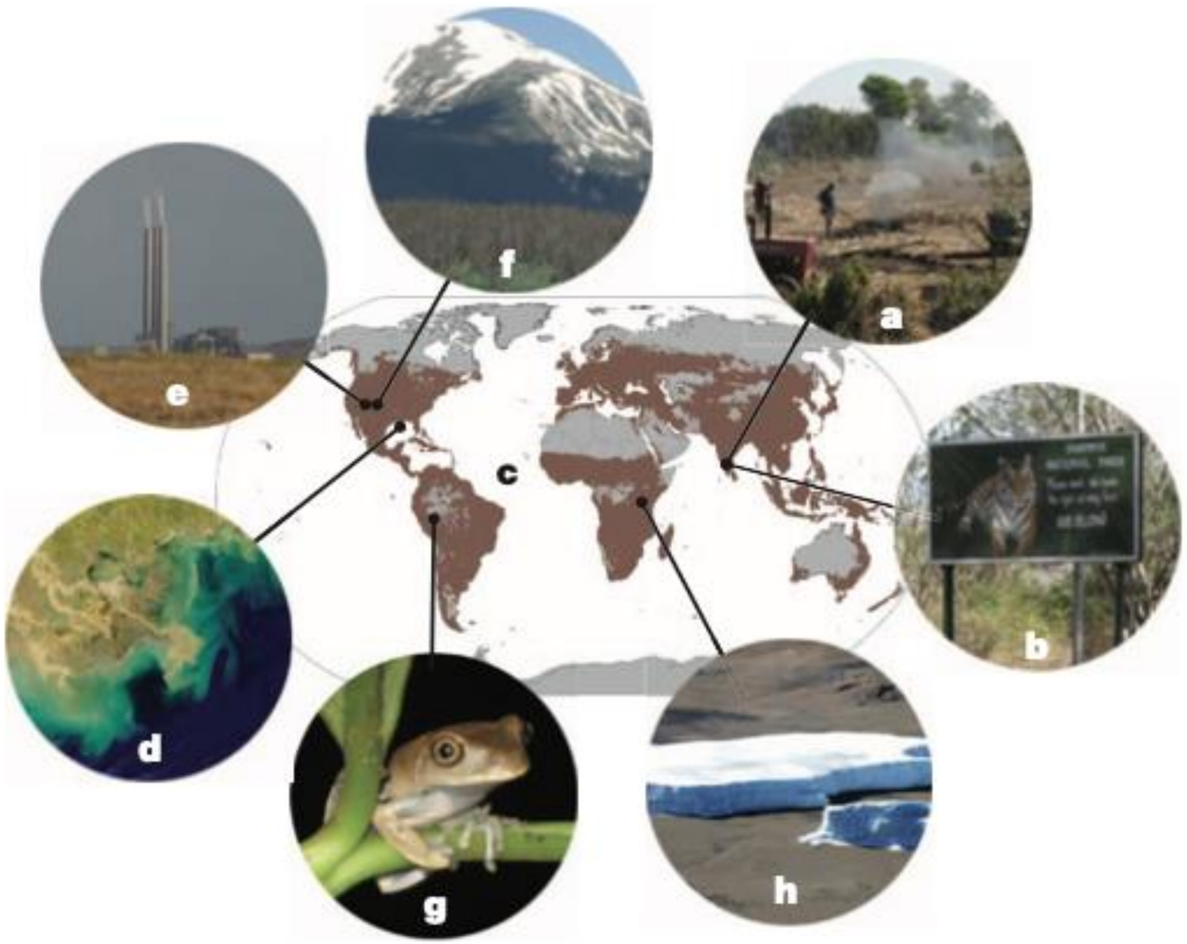


Figure 1 | **Drivers of a potential planetary-scale critical transition.**

3.1. Tipping points

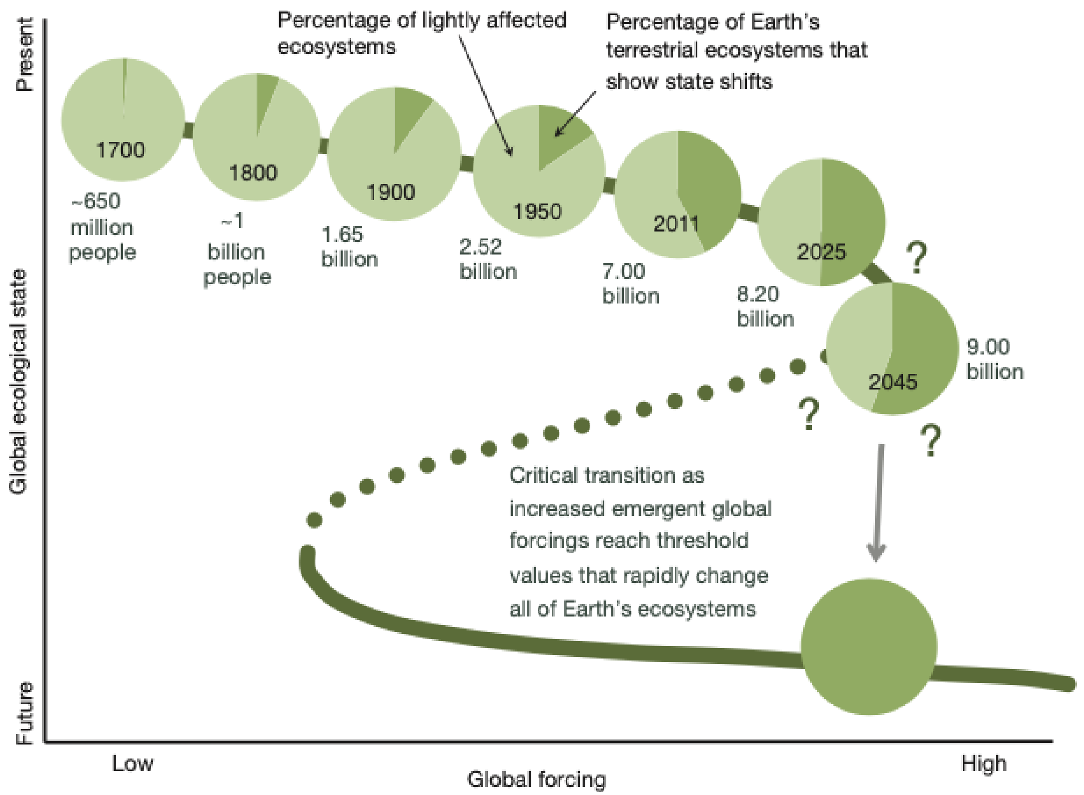


Figure 2 | Quantifying land use as one method of anticipating a planetary state shift. The trajectory of the green line represents a fold bifurcation with hysteresis[12]. At each time point, light green represents the fraction of Earth's land that probably has dynamics within the limits characteristic of the past 11,000 yr. Dark green indicates the fraction of terrestrial ecosystems that have unarguably undergone drastic state changes; these are minimum values because they count only agricultural and urban lands. The percentages of such transformed lands in 2011 come from refs 1, 34, 35, and when divided by 7,000,000,000 (the present global human population) yield a value of approximately 2.27 acres (0.92 ha) of transformed land for each person. That value was used to estimate the amount of transformed land that probably existed in the years 1800, 1900 and 1950, and which would exist in 2025 and 2045 assuming conservative population growth and that resource use does not become any more efficient. Population estimates are from refs 31–33. An estimate of 0.68 transformed acres (0.28 ha) per capita (approximately that for India today) was used for the year 1700, assuming a lesser effect on the global landscape before the industrial revolution. Question marks emphasize that at present we still do not know how much land would have to be directly transformed by humans before a planetary state shift was imminent, but landscape-scale studies and theory suggest that the critical threshold may lie between 50 and 90% (although it could be even lower owing to synergies between emergent global forcings). See the main text for further explanation. Billion, 10^9.

Barnosky et al., 2012

3.1. Tipping points

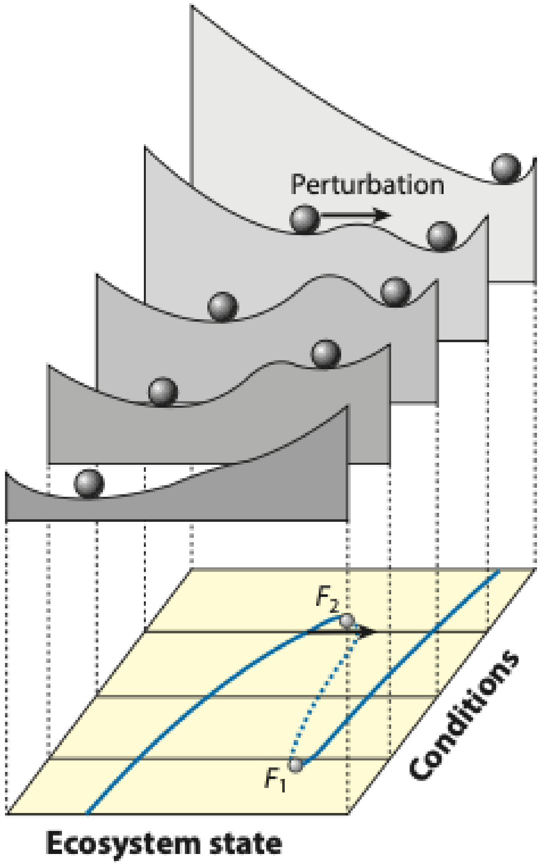


Figure 4

Tipping points and system resilience. The map at the bottom represents the response of a nonlinear system as conditions are changed. The system remains in its original state (*upper branch*) until it reaches a tipping point where it jumps to an alternative steady state (*lower branch*). The graph above illustrates how resilience—represented by the tendency of the ball to return to the valley after being pushed—decreases as the system approaches the tipping point. Figure adapted with permission from Reference 85.

Bascompte & Scheffer 2023

3.1. Tipping points

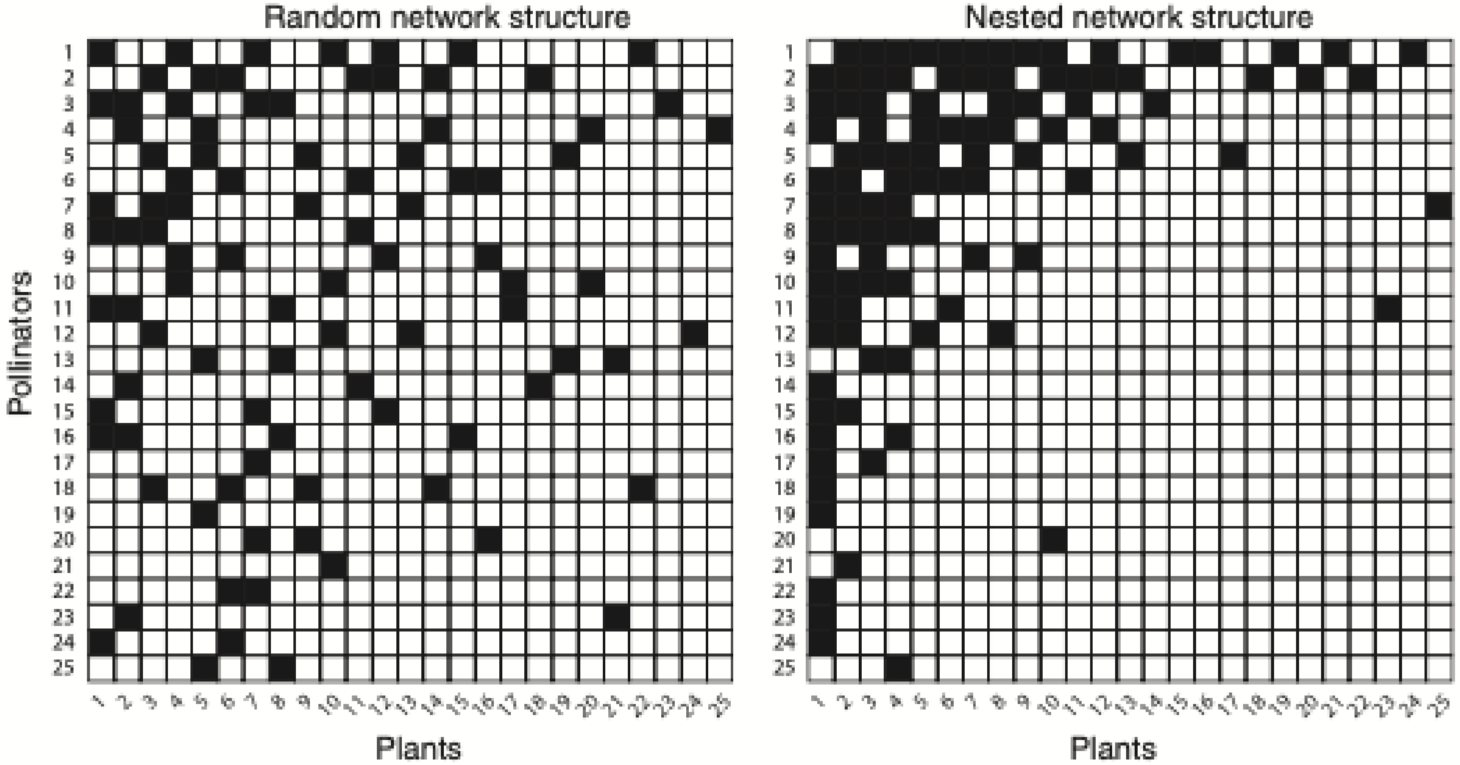


Figure 1 Matrix representations of a randomly structured network (left) and a nested network (right, N = 0.6). Filled squares indicate interactions between species. Column and row numbers correspond to individual plant and pollinator species. Species are ordered based upon their number of interactions.

Bascompte & Scheffer 2023

3.1. Tipping points

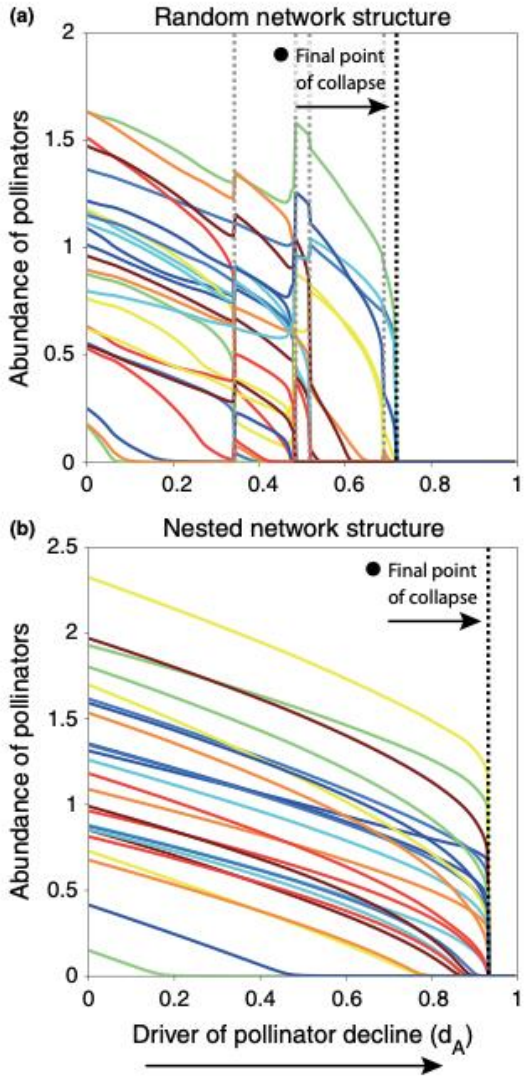


Figure 2 The collapse of pollinator populations when the driver of pollinator decline, d_A, affecting growth and/or mortality of pollinators, is gradually increased from zero to one. Results are shown for a random (a) and a nested (b, N = 0.6) network. Connectance of both networks is equal (D = 0.15). Several extinction events precede the final collapse of the randomly structured plant-pollinator community, while the nested community exhibits only one point of community-wide collapse.

Lever et al., 2014

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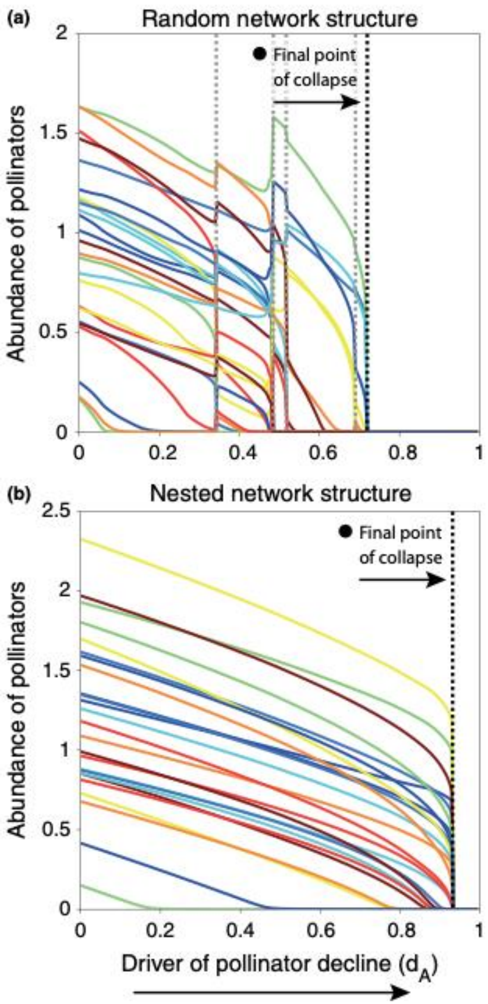

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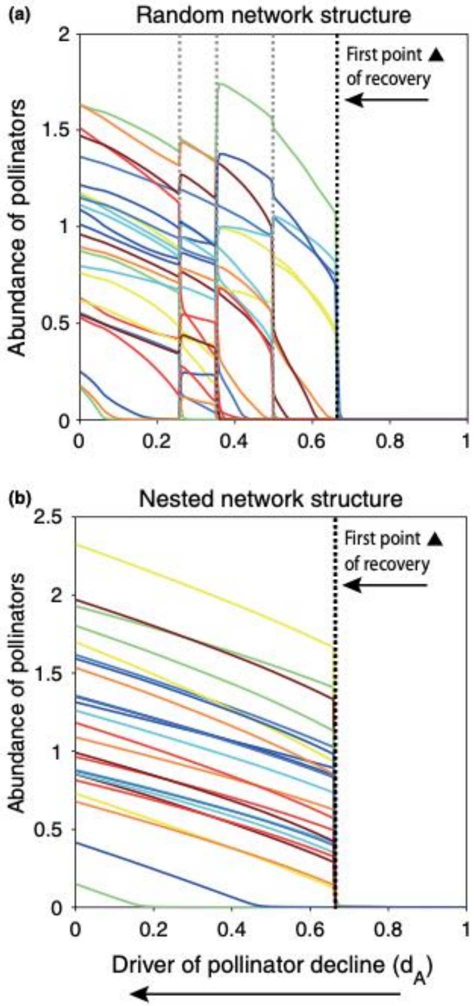


Figure 3 The recovery of pollinator populations when the driver of pollinator decline, d_A, is gradually decreased from one to zero. The points of recovery are not necessarily equal to the points of collapse (see Fig. 2). Especially in the nested community a large difference is observed between the final point of collapse and the first point of recovery. A substantial reduction of the driver of pollinator decline might thus be necessary for pollinator populations to recover from a collapse.

Lever et al., 2014

Early-Warning Indicators of Network Collapse

Lever et al., 2014

3.2. Early-warning signals

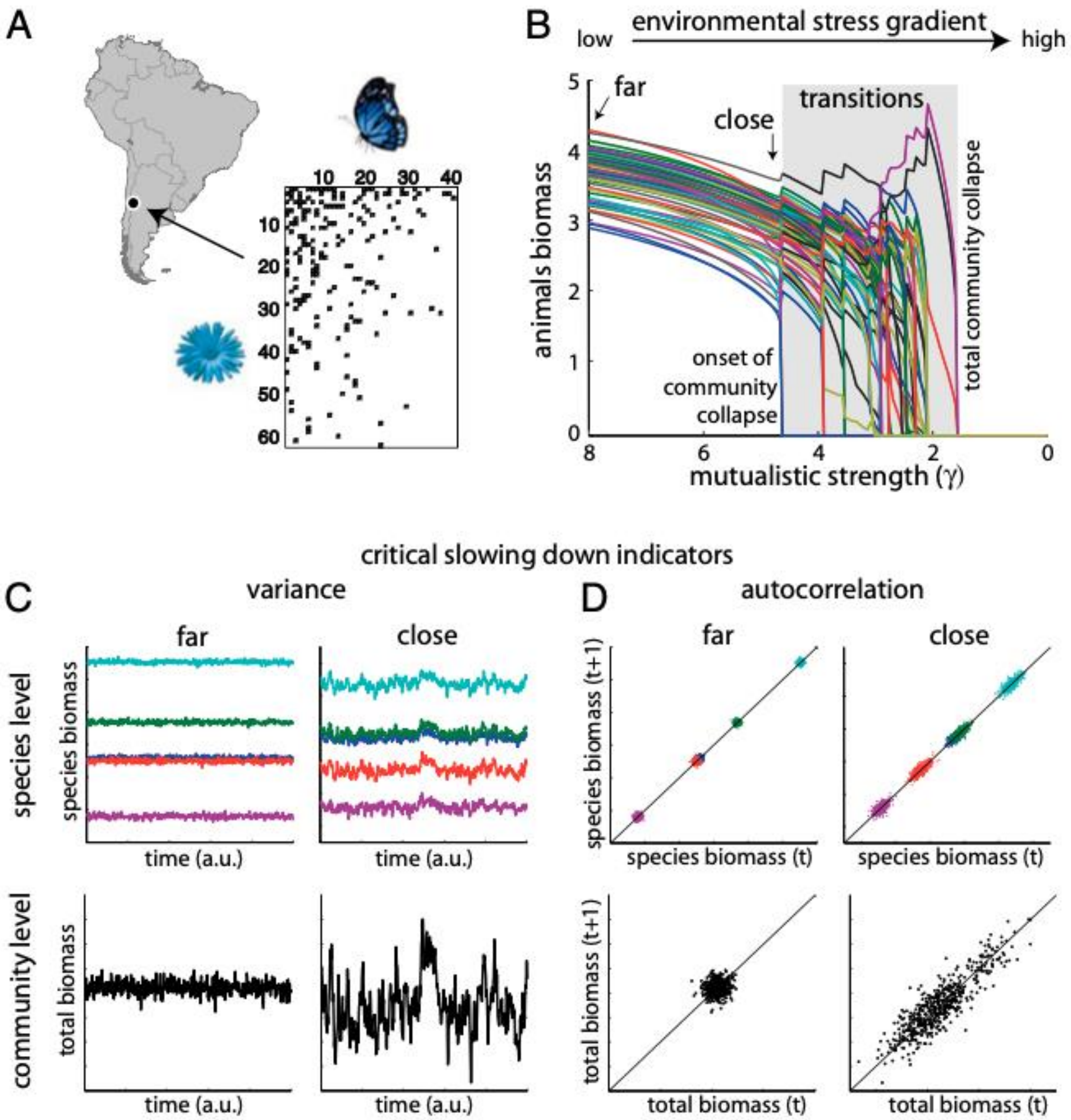


Fig. 1. Detection of the abrupt onset of collapse using critical slowing-down (CSD) indicators in mutualistic communities. (*A*) A plant–pollinator community from Cordon del Cepo, Chile. The black boxes represent mutualistic links between plants and animals. We used the structure of 79 empirical mutualistic networks to simulate their dynamics and potential collapse under gradual environmental change. (*B*) Decreasing mutualistic strength γ stresses species biomasses until unexpectedly an abrupt transition is induced. This first transition marks the onset of a sequence of extinctions until the collapse of the complete community. (*C* and *D*) Identifying critical slowing down at the species and community level. Close to the onset of community collapse, variance and correlation tend to increase. This increase is evident measured both from species biomasses and from the aggregated total community biomass.

Dakos & Bascompte 2014

3.2. Early-warning signals

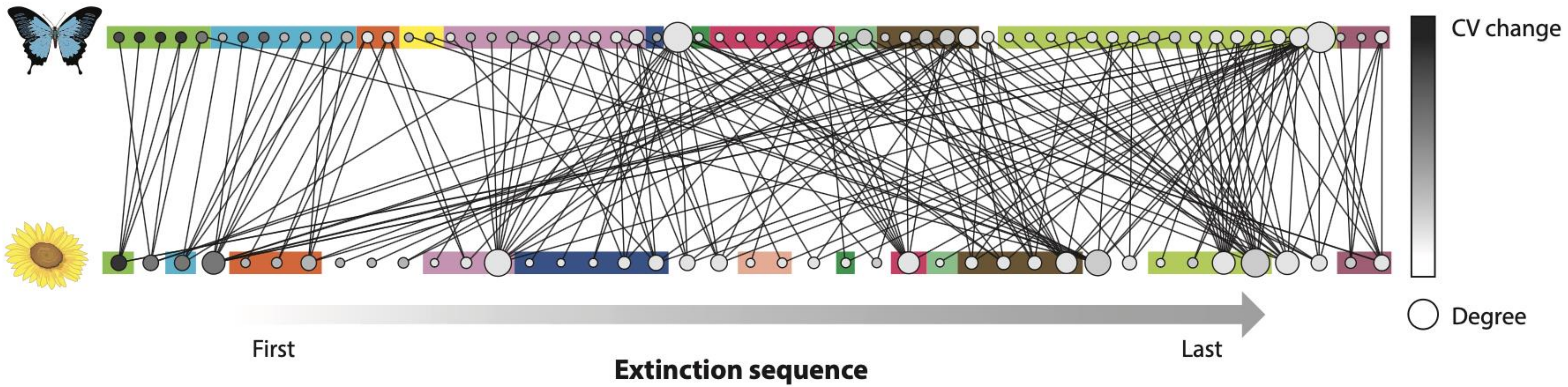


Figure 7

Mapping species resilience based on critical slowing down indicators. The figure represents the pollination network of Cordón del Cepo, Chilean Andes (6; network *M_PL_002* available at **https://www.web-of-life.es**). From left to right, the different species are ranked according to their order of extinction in the numerical simulations. The size and color of each species indicate their number of interactions and change in their coefficient of variability (CV) before the onset of community collapse, respectively. Black colors indicate strong increases in CV. Color boxes group species that went coextinct. There is a positive correlation between the magnitude of the CV change and the order of species extinctions, which can be used to rank species risk of extinction. Figure adapted with permission from Reference 25.

Dakos & Bascompte 2014

3.2. Early-warning signals

Predicting the Alternative State

3.3. Predicting the alternative state


ECOLOGY LETTERS

Ecology Letters, (2020) 23: 2–15 doi: 10.1111/ele.13401

IDEA AND PERSPECTIVE

Foreseeing the future of mutualistic communities beyond collapse

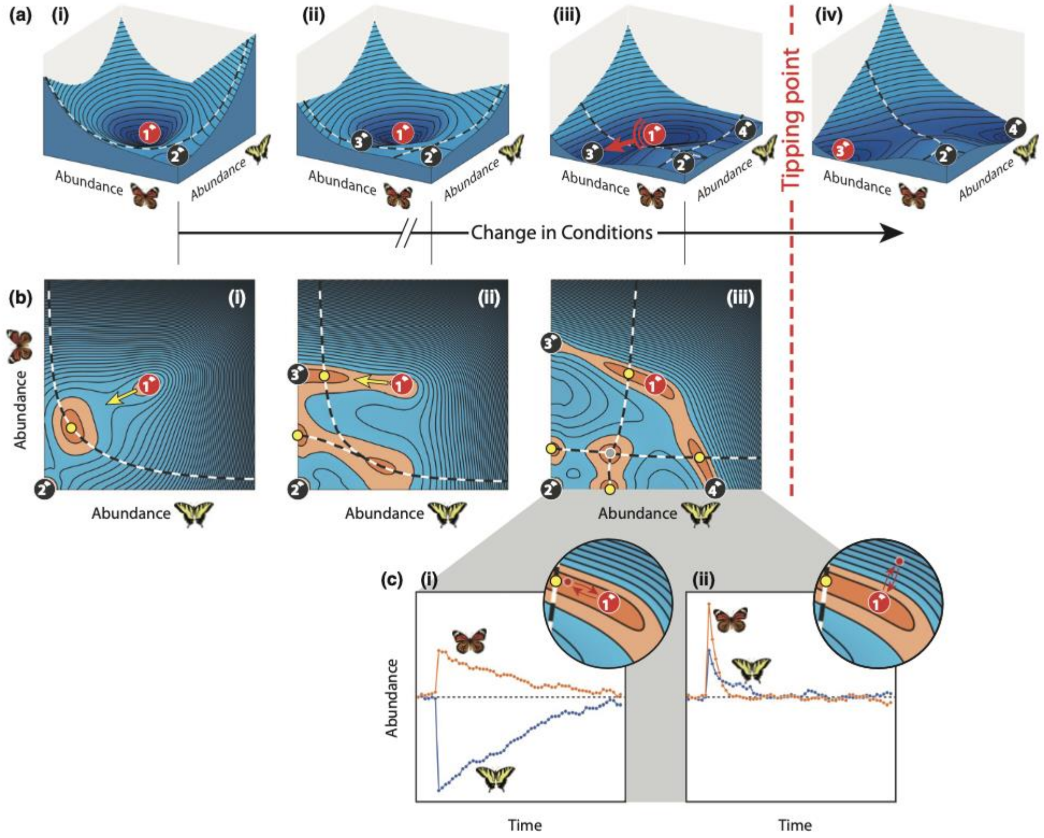


Figure 1 Stability properties for a small network of two pollinators (shown) and two plants (not shown). (a) Attraction basins (valleys) of alternative stable states (balls) are separated by thresholds (dashed curves). Initially, the only alternative to pristine state 1 is fully collapsed state 2 (a.I). When conditions change, two additional, partially collapsed states appear (states 3 and 4). The initial, pristine state loses resilience after state 3 appears (a.II and a.III). Eventually, the threshold towards state 3 approaches the pristine state so closely that a critical transition towards this state becomes inevitable (a.III and a.IV). (b) Alternative stable states, saddle points (yellow dots) and hilltops (grey dots) are surrounded by areas in which the landscape's slope, and thus the rate at which abundances change, is nearly zero (indicated in orange). Higher speeds are found further away from these points. The direction of slowest recovery changes substantially before future state 3 appears (yellow arrow, b.I and b.II). After state 3 appears, the system slows down in the direction of the saddle point on the approaching threshold (b.II and b.III). (c) Slow recovery from a perturbation towards the saddle point (c.I) as opposed to the much faster recovery from an equally large perturbation in another direction (c.II).

Lever et al. 2020

3.3. Predicting the alternative state

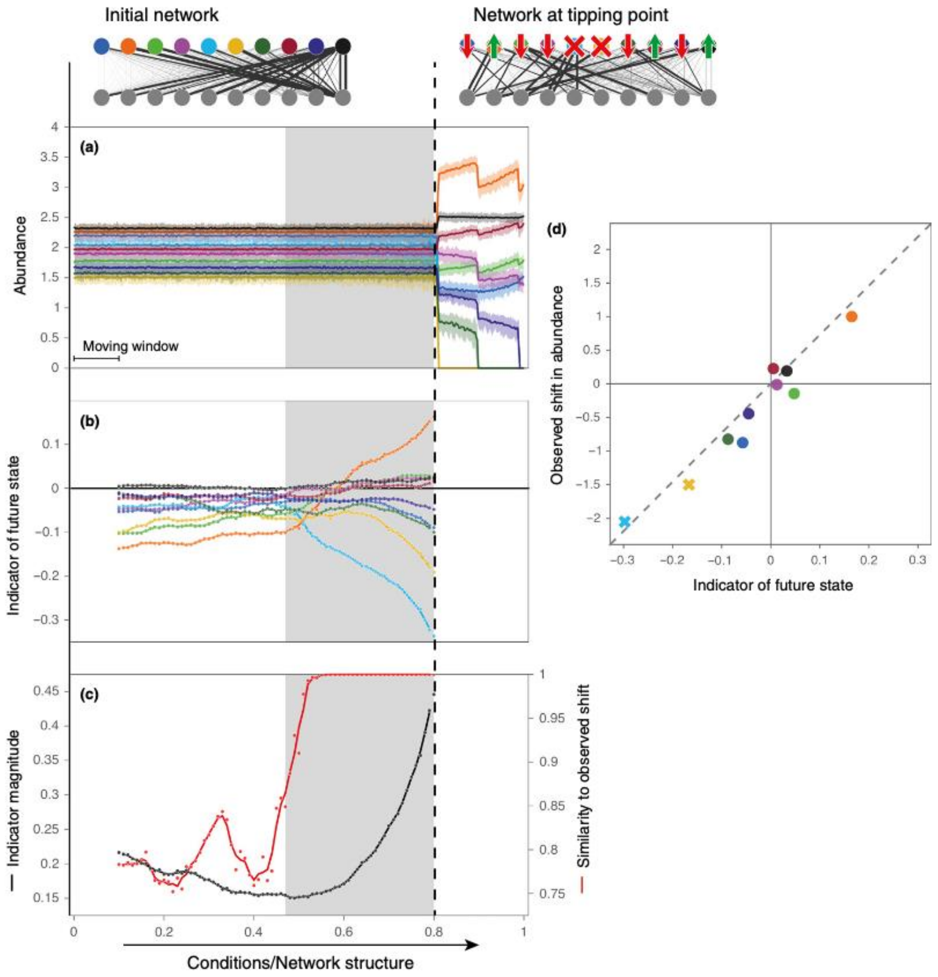


Figure 2 Directional slowing down in a mutualistic network as detected by our indicator. (a) Time series of species belonging to one part of a bipartite mutualistic network (i.e. the pollinators). At the tipping point two species collapse to extinction (light blue and yellow). (b) The indicator of the future state measuring the direction in which fluctuations are distributed asymmetrically. Scores on the indicator indicate the relative predicted gain or loss of each node. (c) The magnitude of the indicator, reflecting the extent to which fluctuations are distributed asymmetrically, plotted together with the accuracy measured as the similarity between its direction and the observed shift in abundance. Grey bands indicate the period in which the indicator's magnitude increases significantly. This period likely corresponds to the period in which the network rapidly loses resilience (as in Fig. 1a.II and 1a.III). The accuracy increases rapidly at the beginning of this period. (d) The observed changes in abundance versus the scores on the indicator just before the tipping point. Extinct species are indicated with crosses. The observed shift is nearly proportional to the scores on the indicator as points are close to a straight line through the origin.

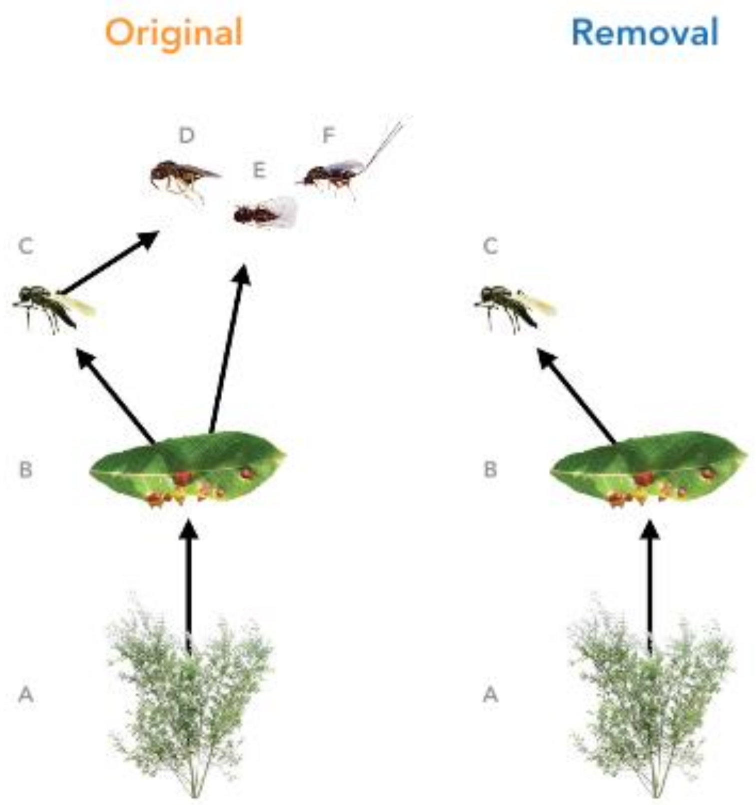
Lever et al. 2020

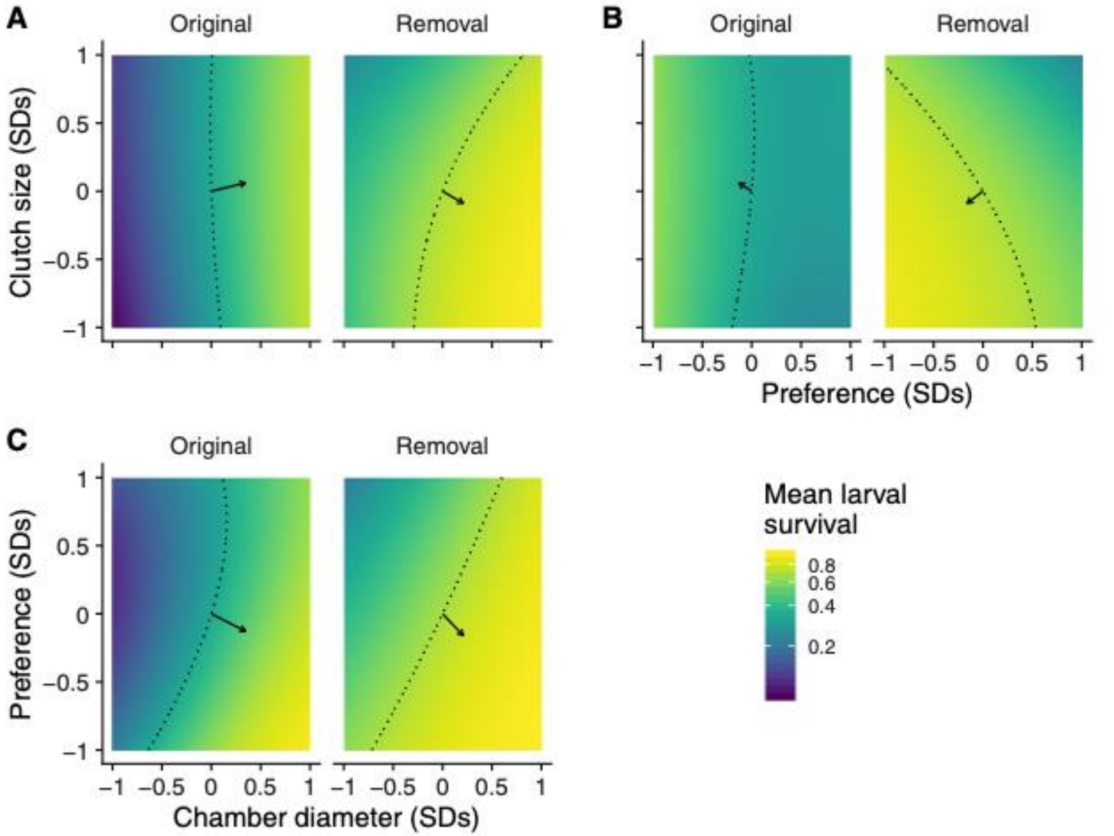
Consequences of Network Collapse for Selection and Evolution of Species

3.4. Consequences of network collapse

Loss of consumers constrains phenotypic evolution in the resulting food web

Matthew A. Barbour,[1,2,3] Christopher J. Greyson-Gaito,[2,4] Arezoo Sotoodeh,[2] Brendan Locke,[5] and Jordi Bascompte[1]





Concluding remarks

The boundaries of the safe operational space preserving all species

(i) rewiring the network of interactions

(ii) increasing species heterogeneity

(iii) allowing variability

(iv) enhancing coevolution

→

(i) increasing nestedness to a level that maximizes feasibility without compromising stability

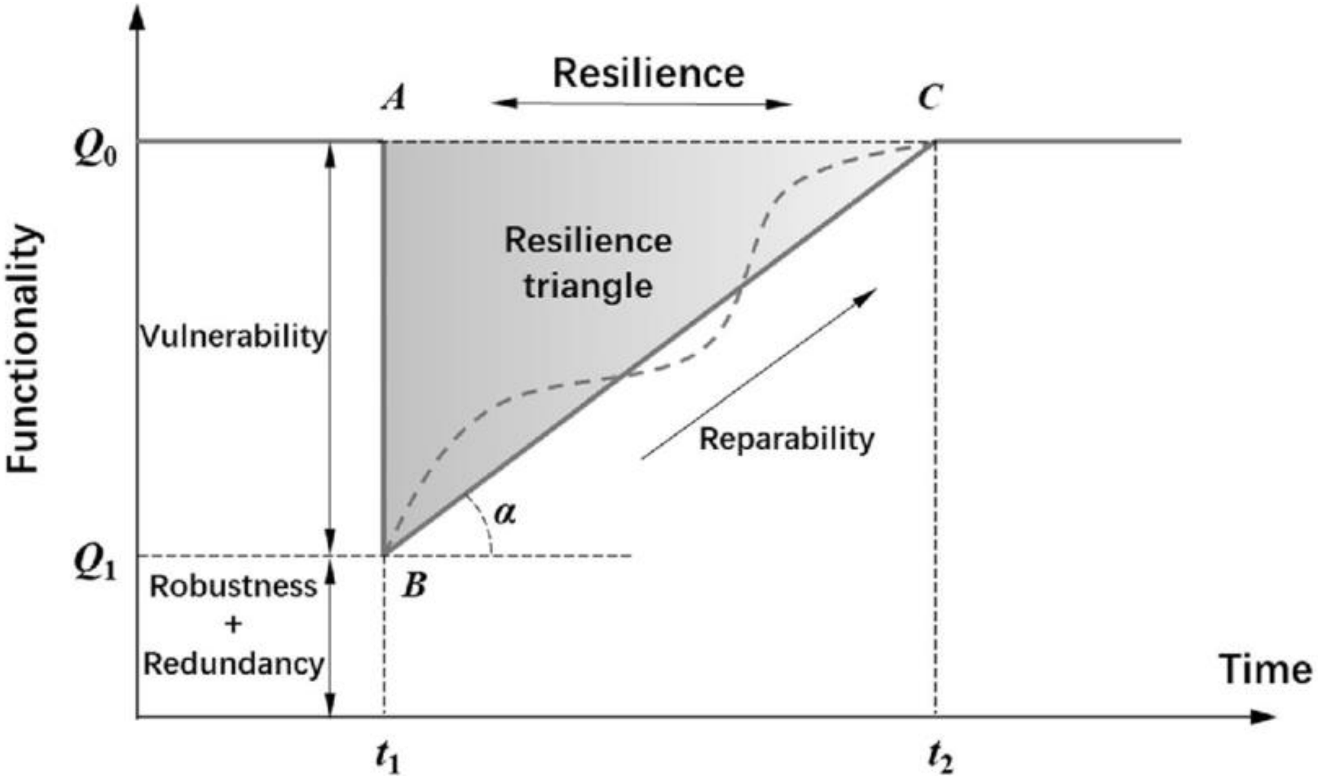
(ii) promoting genetic diversity among species

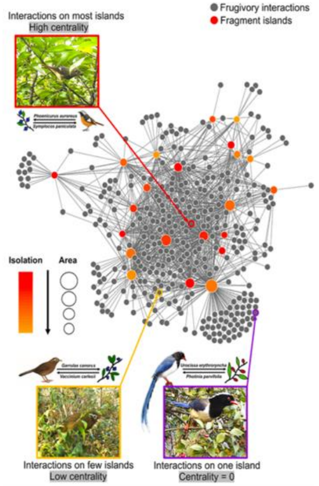
(iii) allowing population fluctuations

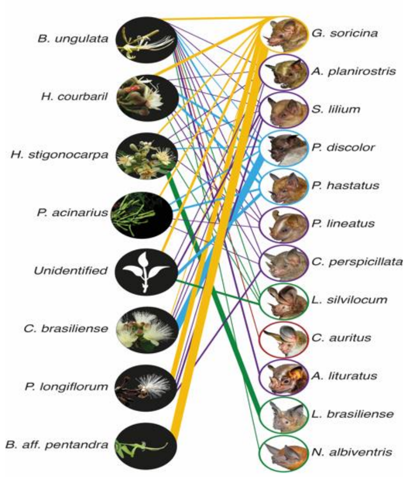
(iv) fostering the coevolution of local populations.

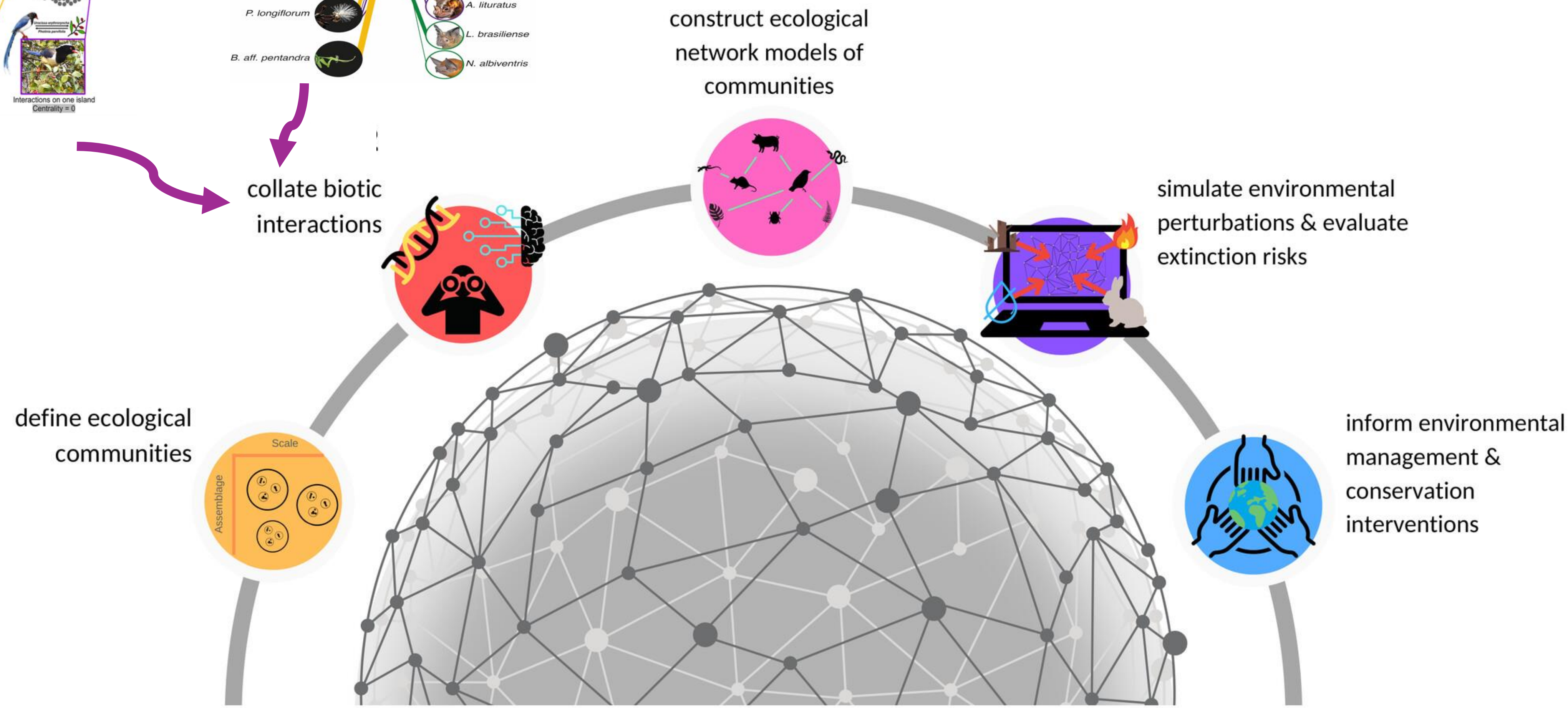
The rate and shape of network collapse once the boundaries of such a space are crossed

Fundamental trade-off in which enhancing resilience comes at the cost of making a possible future collapse more dramatic









oherty et al. 2023

Danke!

Thanks!

Obrigado!

University of Zurich[UZH]

Swiss National Science Foundation

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The red-necked amazon (*Amazona arausiaca*)

Photo: Faraaz Abdool