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Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks

Elisa Thébault[1,2]* and Colin Fontaine[1,3]*

Research on the relationship between the architecture of ecological networks and community stability has mainly focused on one type of interaction at a time, making difficult any comparison between different network types. We used a theoretical approach to show that the network architecture favoring stability fundamentally differs between trophic and mutualistic networks. A highly connected and nested architecture promotes community stability in mutualistic networks, whereas the stability of trophic networks is enhanced in compartmented and weakly connected architectures. These theoretical predictions are supported by a meta-analysis on the architecture of a large series of real pollination (mutualistic) and herbivory (trophic) networks. We conclude that strong variations in the stability of architectural patterns constrain ecological networks toward different architectures, depending on the type of interaction.

Robert May (*1*) showed that ecological complexity (defined in terms of the number of interacting species and the frequency of their interactions) constraints the stability of randomly assembled interaction networks. Although May's model included different types of interactions, most theoretical studies since then have focused mainly on trophic interactions. These studies have revealed that many architectural patterns found in real food webs, such as patterns of interaction strength in omnivory loops (*2, 3*) and allometric degree distributions (*4*), tend to enhance community stability and species coexistence (*5*). During the past decade, studies have also investigated with success the particular architecture of mutualistic interactions (*6, 7*). For those mutualistic networks, asymmetry in interaction strength (*8*) and nestedness (*9, 10*) appear to stabilize the community. The variety of approaches used, as well as the focus on a single interaction type at a time, make the differences between trophic and mutu-

alistic networks still unclear and very speculative, especially because food webs are traditionally represented as unipartite networks, whereas mutualistic networks are bipartite (*7*). We made a systematic comparison between trophic and mutualistic bipartite networks, at different levels of complexity, to test whether the type of interaction affects the relationship between network architecture and stability. First, we followed a model approach in which we analyzed the relations between community stability and a wide range of major network architectural patterns in mutualistic and trophic networks. Then we compared the model prediction with observed network architectures in a large collection of real pollination (mutualistic) and herbivory (trophic) networks.

We built a population dynamics model that can simulate the changes in species densities over time in either mutualistic or trophic networks (*11*). We used it to simulate the dynamic of 7.2×10^3 mutualistic and trophic networks, which varied in architecture regarding four main architectural patterns: diversity, connectance, nestedness, and modularity. The values of these indices respectively describe the number of species, the relative number of interactions, the level of sharing of interaction partners among species, and the degree of compartmentalization of the networks. These architectural patterns have been historically

described in ecological networks (*7, 12*), and despite the relationships between them, they can provide complementary information on how interactions are organized in communities (*13*). During the simulations, some species could become extinct before equilibrium was reached, thus altering the initial architecture of the networks. These extinctions led mutualistic networks to become more connected, more nested, and less modular. In contrast, species extinctions led to trophic networks that were less connected, less nested, and more modular (Fig. 1, A to D, F, and G). Because nestedness and modularity values are related to network diversity and connectance, we also calculated the relative nestedness and the relative modularity. These indices measure how nested and modular a network is as compared with the mean expected nestedness and modularity under a given null model. Following the approach developed for the study of nestedness in mutualistic networks, we used a null model that assumes that the probability of interaction between a plant and an animal depends on the observed number of interactions of both species (*7, 11*). Changes in relative nestedness and relative modularity follow qualitatively the same trend as changes in nestedness and modularity. Mutualistic networks increase in relative nestedness whereas trophic networks increase in relative modularity and decrease in relative nestedness. These results indicate that the alterations in network architecture are linked not only with modifications of diversity and connectance but also with complex arrangements of interactions (Fig. 1, E and H). The dynamic and stability of the networks thus constrain the existing structure of mutualistic and trophic networks toward opposite network patterns.

Because the links between community architecture and stability can depend on the stability metric used (*14*), we measured two distinct indices of stability: persistence (the proportion of persisting species once equilibrium is reached) and resilience (the speed at which the community returns to the equilibrium after a perturbation). We analyzed the results of our simulations by using structural equation modeling (path analysis) to disentangle the direct effects of network diversity and connectance on community stability, as well as their indirect effects mediated through changes in nestedness and modularity. As illustrated in Fig. 2

[1]Division of Biology, Natural Environment Research Council Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK. [2]Biometris, Wageningen University, Droevendaalsesteeg 1, 6708 PB Wageningen, Netherlands. [3]Laboratoire de Conservation des Espèces, Restauration et Suivi des Populations, UMR 7204 CNRS-MNHN, Muséum National d'Histoire Naturelle, 61 rue Buffon, 75005 Paris, France.

*Both authors contributed equally to this work.

Fig. 1. Final architecture of mutualistic (gray) and trophic (red) networks once equilibrium was reached, against their initial structure, regarding connectance (**A** and **B**), nestedness (**C** and **D**), and modularity (**F** and **G**). (**E**) and (**H**) represent box plots of the difference between final and initial architectures in relative nestedness and relative modularity, respectively, for mutualistic (red) and trophic (gray) networks. The bottom and top limits of each box are the lower and upper quartiles, respectively; the horizontal black band within each box is the median; and error bars equal ±1.5 times the interquartile range.
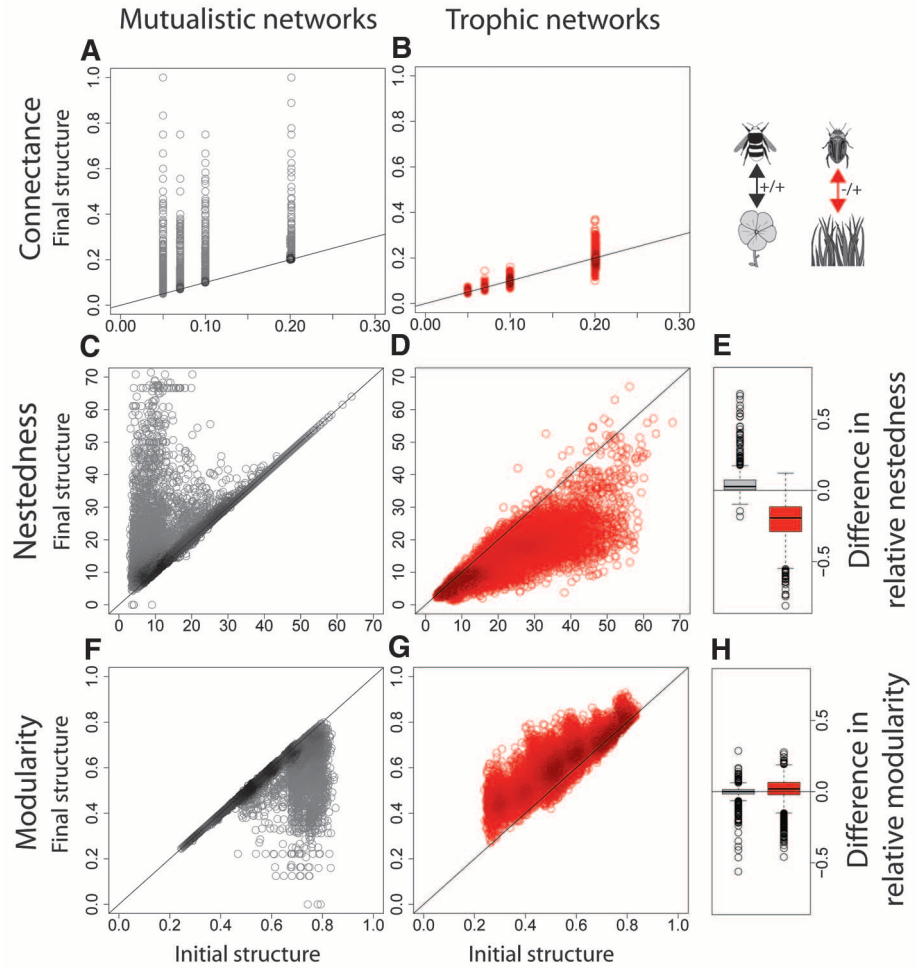

Fig. 2. Summary diagrams of the effects of the different network architectural patterns on the persistence (**A** and **B**) and resilience (**C** and **D**) of mutualistic [(A) and (C)] and trophic [(B) and (D)] networks. The thickness of the arrows is scaled to standardized coefficients from path analysis and illustrates the relative effect strength. Negative effects are represented in red and positive effects in black. The effects of connectance and diversity are split between direct effects and indirect effects through changes in modularity and nestedness. The strength of the indirect effects is calculated by the product of the coefficients along the path. For example, in (A), connectance has a direct effect of strength 0.07, an indirect effect through modularity of strength 0.43 (-0.81×-0.53), and an indirect effect through nestedness of strength -0.026 (0.87×-0.03), which lead to an overall connectance effect of 0.47.
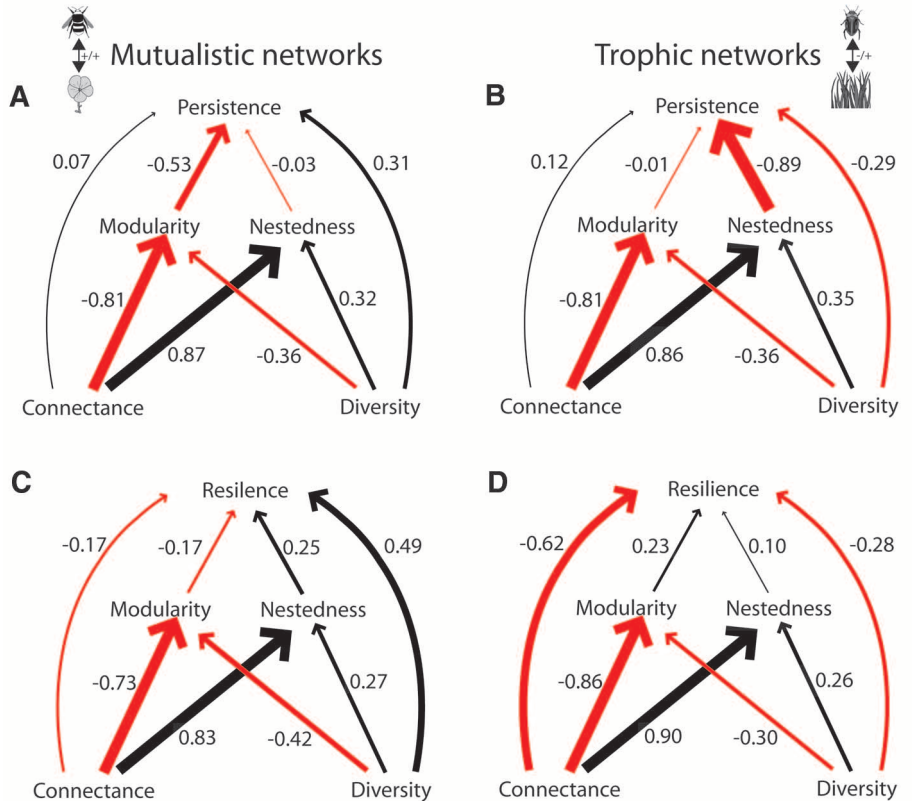
and fig. S1, network architecture has an opposite effect on the stability of mutualistic networks as compared to trophic ones, a result that is consistent along diversity, connectance, nestedness, and modularity gradients and for both the persistence and resilience of the community (*15*). Higher diversity and connectance promote the persistence and resilience of mutualistic networks, but they destabilize trophic networks. For mutualistic networks, modularity decreases the persistence of the network, and nestedness increases its resilience. In contrast, for trophic networks, nestedness decreases the persistence of the network, and modularity enhances its resilience. The results of the structural equation models further reveal that a large part of the effects of connectance and diversity on persistence is mediated through changes in network modularity and nestedness (Fig. 2). On the contrary, connectance and diversity directly affect community resilience, whereas the indirect effects mediated through changes in nestedness and modularity are weaker. These results also show that nestedness and modularity have singular effects on

stability, especially on persistence, and despite their strong negative correlation, these two indices thus capture different aspects of network architecture. This highlights the importance of moving beyond traditional measures of topology (such as connectance) and using more integrative indices (such as nestedness and modularity) to improve our understanding of the determinants of community stability.

To test our theoretical predictions, we compiled a large data set of published networks describing either mutualistic or trophic interactions, and we analyzed their architecture (*16*). These networks represent 34 pollination networks and 23 herbivory networks (table S5). Pollination and herbivory network architectures differ in the relationship between diversity and connectance, as well as in their values of nestedness and modularity. Connectance is negatively related to diversity ($F_{1,53} = 67.59$, $P < 0.0001$), but it decreases faster with increasing diversity in herbivory networks than in pollination networks ($F_{1,53} = 5.01$, $P = 0.0295$; Fig. 3), indicating that highly diverse

herbivory webs tend to be less connected than pollination webs of similar diversity. Even after accounting for these differences in connectance, pollination networks are more nested than herbivory networks ($F_{1,51} = 25.12$, $P < 0.0001$; Fig. 3, table S2, and fig. S2), whereas the opposite pattern is found for modularity ($F_{1,51} = 77.93$, $P < 0.0001$; Fig. 3, table S2, and fig. S2). Two herbivory networks, however, exhibit a very high level of nestedness. Although both involve leaf-chewing insects (grasshoppers), these outliers do not seem to be related to this particular type of feeding (see table S5). We also calculated the relative nestedness of these empirical data sets to test whether the observed values are different from what is expected from a null model. Relative nestedness is significantly higher in pollination networks than in herbivory networks (Welch *t* test, $t = -4.75$, df = 25.85, $P = 6 \times 10^{-6}$), thus strengthening our previous results. Although herbivory networks tend to have a higher relative modularity than pollination networks, the difference is not significant (Welch *t* test, $t = 1.47$, df = 52.74, $P =$
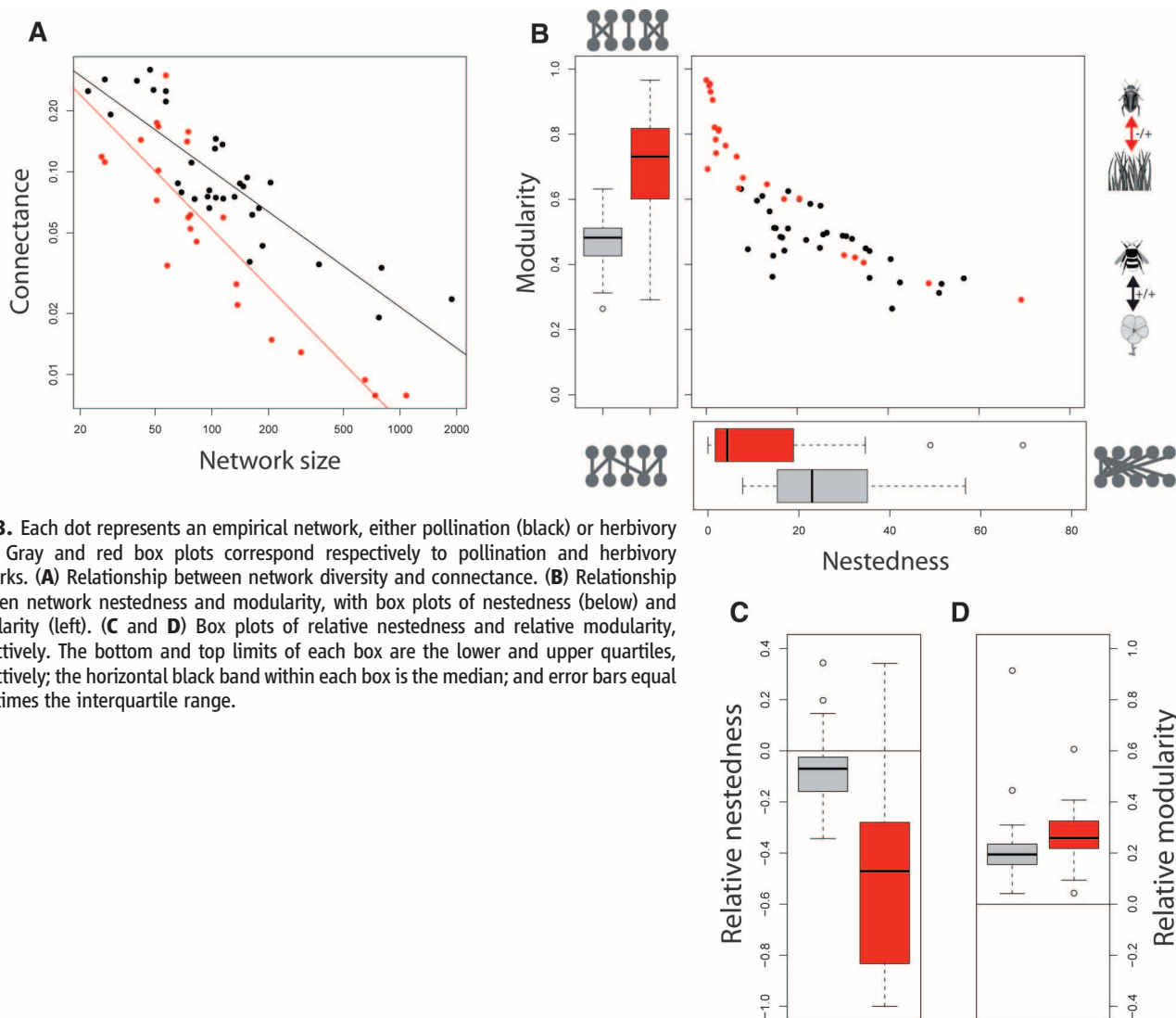
Fig. 3. Each dot represents an empirical network, either pollination (black) or herbivory (red). Gray and red box plots correspond respectively to pollination and herbivory networks. (**A**) Relationship between network diversity and connectance. (**B**) Relationship between network nestedness and modularity, with box plots of nestedness (below) and modularity (left). (**C** and **D**) Box plots of relative nestedness and relative modularity, respectively. The bottom and top limits of each box are the lower and upper quartiles, respectively; the horizontal black band within each box is the median; and error bars equal ±1.5 times the interquartile range.

0.15). This last result indicates that the higher modularity of herbivory networks might be partly linked with their lower connectance. Although recent studies found both nested and modular patterns in a same mutualistic or trophic network (*17*), our results show that nestedness is stronger in mutualistic networks than in trophic ones; in contrast, trophic networks tend to have a higher modularity, in relation with a lower connectance. The network characteristics that are observed in each type of empirical network are thus the ones predicted to promote biodiversity persistence and stability by our model.

This work is a step toward a better understanding of the impact of the type of interaction on the architecture of ecological networks, an issue that has begun to be investigated only recently (*18–21*). Previous studies have focused on one type of interaction at a time [but see (*10*)] and usually investigated the effects of one particular architectural pattern (*2, 3, 9, 10*). Here we show that the combination of different architectural patterns is essential to understand the mechanisms behind the stability of communities, and we further predict emerging network architectures that differ strikingly between interaction types. The congruence between these theoretical predictions and the empirical observations in our study strongly suggests that community dynamic and stability constrain mutualistic and trophic networks toward different architectural patterns. The mechanism behind these different architectures might be linked to indirect interactions, maybe even more so than direct interactions. For example, the negative indirect effects of apparent competition should pre-vail in trophic networks (*22*), restricting the sharing of interacting partners among species and thereby the propagation of negative effects across the network, and thus promoting a low connectance and a high modularity. In contrast, positive indirect effects of apparent facilitation occur in mutualistic networks (*23*) and should favor a highly connected and nested architecture characterized by the sharing of interaction partners in the network (*10*).

Next steps of research will need to tackle two fascinating challenges. First, how these dynamical constraints interact with other determinants of network architecture, such as trait matching, phylogenetic constraints, and coevolutionary dynamics (*24–26*). Second, how various interaction networks with different architecture combine themselves to shape the broader network that links all the species within an ecosystem, and how this relates to the functioning and stability of ecosystems.

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Rational Design of Envelope Identifies Broadly Neutralizing Human Monoclonal Antibodies to HIV-1

Xueling Wu,[1]* Zhi-Yong Yang,[1]* Yuxing Li,[1]* Carl-Magnus Hogerkorp,[1]† William R. Schief,[4] Michael S. Seaman,[5] Tongqing Zhou,[1] Stephen D. Schmidt,[1] Lan Wu,[1] Ling Xu,[1] Nancy S. Longo,[1] Krisha McKee,[1] Sijy O'Dell,[1] Mark K. Louder,[1] Diane L. Wycuff,[1] Yu Feng,[1]‡ Martha Nason,[2] Nicole Doria-Rose,[3] Mark Connors,[3] Peter D. Kwong,[1] Mario Roederer,[1] Richard T. Wyatt,[1]‡ Gary J. Nabel,[1]§ John R. Mascola[1]§

Cross-reactive neutralizing antibodies (NAbs) are found in the sera of many HIV-1–infected individuals, but the virologic basis of their neutralization remains poorly understood. We used knowledge of HIV-1 envelope structure to develop antigenically resurfaced glycoproteins specific for the structurally conserved site of initial CD4 receptor binding. These probes were used to identify sera with NAbs to the CD4-binding site (CD4bs) and to isolate individual B cells from such an HIV-1–infected donor. By expressing immunoglobulin genes from individual cells, we identified three monoclonal antibodies, including a pair of somatic variants that neutralized over 90% of circulating HIV-1 isolates. Exceptionally broad HIV-1 neutralization can be achieved with individual antibodies targeted to the functionally conserved CD4bs of glycoprotein 120, an important insight for future HIV-1 vaccine design.

Having crossed from chimpanzees to humans in only the past century, HIV-1 has rapidly evolved a daunting degree of diversity, posing a considerable challenge for vaccine development. The definition of naturally occurring broadly neutralizing antibodies (NAbs) has proven elusive, and the ability to target conserved determinants of the viral envelope (Env) has proven difficult (*1, 2*). During HIV-1 infection, almost all individuals produce antibodies to Env, but only a small fraction can neutralize the virus (*1, 2*). Recently, several groups have shown that the sera of 10 to 25% of infected participants contain broadly reactive NAbs (*3–6*), including some sera that neutralize the majority of viruses from diverse genetic subtypes (*5–7*). NAbs react with the HIV-1 Env spike, which is composed of three heavily glycosylated glycoprotein (gp)120 molecules, each noncovalently associated with a

[1]Vaccine Research Center, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, MD 20892, USA. [2]Biostatistics Research Branch, Division of Clinical Research, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, MD 20892, USA. [3]Laboratory of Immunoregulation, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, MD 20892, USA. [4]Department of Biochemistry, University of Washington, Seattle, WA 98195, USA. [5]Beth Israel Deaconess Medical Center, Harvard Medical School, Boston, MA 02115, USA.

*These authors contributed equally to this work.
†Present address: Department of Molecular Genetics, Novo Nordisk A/S, Novo Nordisk Park, 2760 Måløv, Denmark.
‡Present address: Department of Immunology and Microbial Science, and IAVI Center for Neutralizing Antibody at TSRI, Scripps Research Institute, La Jolla, CA 92037, USA.
§To whom correspondence should be addressed. E-mail: gnabel@nih.gov (G.J.N.); jmascola@nih.gov (J.R.M.)