4 Weak Links as Stabilizers of Complex Systems

4.1 An Emerging Synthesis: Weak Links Stabilize Complex Systems

In the previous chapters we learned how weak links stabilize complex systems. The classical study of Granovetter (1973) demonstrated that weak links help the cohesion of society (see Chap. 1). Weak links are necessary for small-worldness, emerging in parallel with topological scale-freeness, and making a key contribution to the formation of nestedness (see Chap. 2). Weak links buffer noise, help relaxation, form barriers against cascading failures, and stabilize the coupled oscillators of bottom networks (see Chap. 3). Table 4.1 summarizes the effects of weak links on network behavior.

Summarizing the previous chapters, Table 4.1 gives an initial synthesis and several hints to suggest that weak links may play a prominent role in defining network stability. The generality of network topology (see Chap. 2) and the imaginative power of the applications of this generalization prompt me to take up the challenge and form the main hypothesis of this book:

Weak links stabilize all complex systems (Csermely, 2004; 2005).

I cannot (yet) formally prove the general validity of weak-link-induced network stabilization but hope to show its generality and power to explain and regulate the world around us. However, a statement cannot be judged without definitions. When do I call a link weak? When do I call a system stable? Why do I speak of complex systems rather than networks and what is the definition of complexity? The rest of this chapter gives starting definitions for all these notions and discusses some of the weaknesses and strengths of the basic statement. Before attempting any definitions, a few comments are probably in order.

Table 4.1. Network behavior in the presence and absence of weak links

Network has many weak links	Network has few weak links
Long-range contacts give small-worldness, modules are well-connected	Average distance between elements is large, modules are sparsely connected
Behavior of bottom networks is optimally synchronized, giving small fluctuations	Bottom networks are either tightly coupled with large fluctuations or behave independently of each other
Communication is good in the network, relaxation goes smoothly	Communication is restricted in the network, relaxation is disturbed, relaxation avalanches may occur
Noise is easily dissipated or absorbed in the network	Network is noisy and noise stays in segments of the network
Network is integrated and behaves as a whole	Network is segregated and behaves as an assembly of its constituent modules and bottom networks
Changes are dissipated and occasional errors are isolated, so that the network is stable	Changes and noise persist, the network is error-prone and unstable

Misfortunes of the Statement: 1

Weak links are both elusive and overwhelming. Science has grown used to examining strong links. Strong links are always there. Strong links are reproducible. Strong links are few in number and hence comprehensible. Strong links are already known. Strong links are scientific. Strong links are exciting. In short, strong links are like friends to us. In contrast, weak links are transient. Weak links are undetectable. Weak links are overwhelmingly numerous. Weak links are unknown. Weak links are unscientific. Weak links are hopeless. In short, weak links are like foes to us.

Misfortunes of the Statement: 2

Stability can be defined at various levels (see Chap. 5) and may also behave as a rather elusive concept. To measure stability, we have to follow and quantify system dynamics. Non-equilibrium simulations are still too complex to be fully resolved in many cases. Moreover, stability is not easily measured. Fortunately, there is another way to approach it.

The level of system noise may give us valuable information on system stability. However, for the traditional mind, noise is a nuisance which is better avoided than measured. For the traditional way of thinking, we can offer yet another choice. As I showed in Sect. 3.1, increased noise is linked to increased diversity. However, monitoring diversity is not a usual feature of experimental documentation either. Odd findings are a matter of shame that should be hidden. Ignoring the advice of Bacon (1620): "Whoever knows her [Nature's] deviations will more accurately describe her ways", science deals with the average and ignores the exceptional. Exceptions are not mentioned in titles, abstracts or key words. I had to search for months for papers noting peculiarities. This book is not only about networks and weak links. It is also about the scientific method. We have to change our attitude. In writing this book, I would like to stress that irregularity is not an annoyance, but gives the true flavor of the world's richness. It gives us strength and stability to regulate and preserve all the complex systems inside and around us.

Misfortunes of the Statement: 3

Complexity is related to integrated behavior (see Sect. 4.4). To observe the stabilizing effects of network elements, one has to think about the whole network and its function. In some cases, the situation gets even worse. We cannot stay at the bottom network level, but have to go one level higher, to the level of the top network, to understand the emerging network function which is stabilized by the weak links. As an example, words neither stabilize themselves nor the sentences they form. Words may only stabilize the *meaning* of the whole textual network they belong to. With our deductive socialization in science,[1] it is not always easy to find the emerging, synthetic thought pointing towards the beneficiary of the stabilization.

Misfortunes of the Statement: 4

Since I am unable to prove the generality of the statement for the moment, it is rather wishful thinking to use the word 'all' here. Feel

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[1] Deduction became the main scientific method after the end of the 19th century, when scientists got enough experimental tools to analyze the smaller details and mechanisms of network properties. Although deduction is an incredibly useful tool to understand how nature works, for the analysis of large data sets and the understanding of nested networks, we need a better training in the reverse of deductive thinking, i.e., induction.

Fig. 4.1. Irregularity is not an annoyance, but gives the true flavor of the world's richness. It gives us strength and stability to regulate and preserve all the complex systems inside and around us

free to substitute 'many' in the place of 'all', if you prefer precise statements.

Misfortunes of the Statement: 5

You may have recognized that by now all parts of the original statement have been questioned. Only one is missing, namely the period at the end. To complete the job, I am not quite sure that a period is the most appropriate sign at the end of the sentence. Let me suggest that you imagine a light grey, vanishing period, at least for the time being. I hope that by Chap. 12, when I return to this sentence again, we will agree that the period should be replaced by an exclamation mark.

"Dear Peter, if your favorite statement is even weaker than the links it is about, why don't you leave this book and go for a swim?" Well, to begin my answer, I *will* go for a swim in a minute. But before doing so, I will end this section by listing some of the strengths of the same statement.

Strengths of the Statement: 1

Being weak is a relative category. When there is any difference between network elements, weak links emerge. In real networks, there are always differences between network elements. Consequently, we always have weak links. Moreover, real networks are not static. Links form,

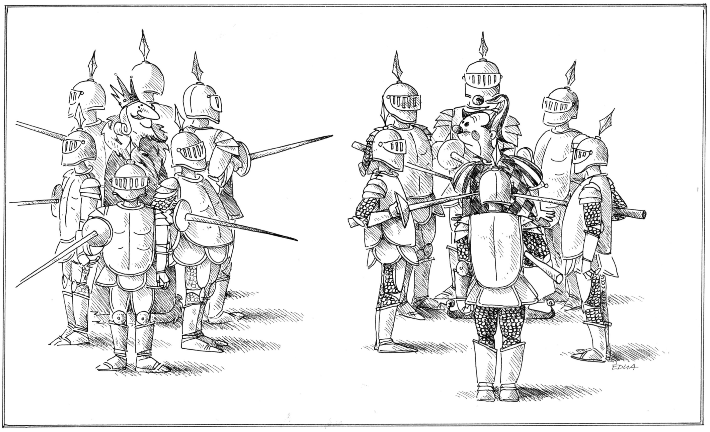

Fig. 4.2. If a system becomes too stable, it cannot change, cannot develop

then vanish. Weak links may also mean links with short duration or low probability. This gives another chance for weak links to emerge. Indirect, higher-order interactions are often perceived as weak links, especially in ecology. Lastly, both intermodular and long-range links are usually weak. These links are very important in network stabilization. Weak links emerge at critical points of the network. Weak links are not unique, they are general. Weak links are not just the leftovers when strong links have been taken into account. Weak links are important.

Strengths of the Statement: 2

All those networks we know about are more or less stable. Highly unstable networks cannot be studied. The time resolution of our methods defines the level of instability we are able to study and describe. Moreover, by definition, a network contains links between multiple elements. The simultaneous presence of multiple links also implies at least a minimal level of stability. Network stability is not just born from nowhere. Weak links do not need to establish it, but they do help to increase existing stability.

Strong links are good too! After one of my lectures on weak links to high school students, a young student researcher approached me and asked: "Peter! You have have been talking all the time about the benefits of weak links. Does this mean that there is something wrong with strong links?" No! Not at all. A lot of weak links lead to over-stabilization. The system becomes too stable, too lazy, and cannot change or develop (for a more detailed description see Chap. 12). As with noise or synchrony, we need an optimal level of weak links. Moreover, if we have *only* weak links, we lose them. Weak can only be weak in the presence of strong. When I finished my answer, the young man sighed: "I am relieved. I thought perhaps you were suggesting that I should leave my best friend to get stability." Do not worry. Best friends can stay. Indeed, best friends *must* stay. Without best friends, simple acquaintances are useless (at least in the sense of network stability). However, acquaintances are *also* part of our stability. We should cherish both. I will return to this in Sect. 10.2 describing the need for *both* conservative and liberal thinking to build a stable society, as well as the advantage women obtain with regard to stability by building up more weak links in their contacts than men.

Are strong links stabilizing? To complete the rehabilitation of strong links, let us note that strong links are not only there to allow weak links to be weak. Strong links are the essence of all that makes a network a network. (I know, it is time to start my next book on strong links!) Strong links define the network. If I knock out a strong link, the network will generally behave differently. Strong links do contribute to network stability. The peculiarity of weak links is that, by removing any of them, the network does not necessarily change its main parameters (in contrast to the removal of strong links). However, there is still a change: after the removal of weak links (the more the better), the network will become unstable. This notion will be the core of the starting definition of weak links in the next section.

4.2 Weak Links: A Starting Definition

In Sect. 2.4, I showed that widely different natural networks develop a scale-free distribution not only in topology, space and time but also in the distribution of link strength (Almaas et al., 2004; Barrat et al., 2004a; Caldarelli et al., 2004; Garlaschelli et al., 2003; Ghim et al., 2004; Goh et al., 2001; Leland et al., 1994). If there is a continuous growth of link strength from vanishingly weak to extremely strong, it is rather difficult to define a discriminating value below which a link can be said to be weak. The examples in the following sections which illustrate weak-link-induced stabilization are not very helpful either. Most of these exciting examples are not detailed enough to use for a definition of the threshold link strength for network stabilization. I will nevertheless make an attempt and say, in analogy with the Pareto law, that all interactions falling below the strongest 20% will from now on be defined as weak. But my feeling is that this threshold is context-dependent, and cannot be generally defined.

Aware of the difficulties in marking a threshold value for weak links, I resort to a functional definition. I therefore begin with the definition due to Berlow (1999):

> **Definition of Weak Links.** A link is defined as weak when its addition or removal does not change the mean value of a target measure in a statistically discernible way.

I am aware that, like all functional definitions, this one is also highly context-dependent. For this definition, we have to set a target measure, we have to be able to add or remove the link, we have to be able to repeat the determination of the measure several times and, the most difficult condition, we have to maintain all conditions of the network intact (apart from the addition or removal of the link) between these measurements.

Ladies and Gentlemen! May I start my round with my empty hat for your generous contributions? The show is over: you have seen the sad life of the experimentalist, when asked for definitions.

Are all links weak? Remarks on a suspicious definition.

"Peter, if you delete a 'strong' link in a smaller network, like some of the ecological networks, you will obviously have a big change in the network parameters. What will be the behavior of large and highly redundant networks like those in cells and societies? Eric Berlow was certainly right to state his definition for small eco-webs, but your generalization is wrong. Large and redundant networks will not have a single strong link using this definition." I think I am safe here. Even large networks contain some links which are essential. 20% of yeast genes seem to be essential for viability. An additional 40% of yeast genes may become essential in various conditions (Papp et al., 2004). The number of unconditionally strong links is small (20%), but if you remember from Sect. 2.4, link strength has a scale-free distribution, and this means precisely that there are a small number of strong links. Actually, even the percentage is familiar. Indeed, the 80–20 rule of Pareto (1897), the archetype of scale-free distributions, also drew the line for strong contributions at 20%. The Berlow (1999) definition seems to behave quite well in general terms.

Indirect effects as weak links. Weak links need not always be direct. As an example of an indirect effect, the effect of a neighbor's neighbor can also be calculated. If all interactions are of equal strength, these second-neighbor effects will obviously be weaker than those due to direct neighbors. Indirect effects are often considered in ecology, where the effect of each participant of an ecosystem can be important to a given species (McCann, 2000).

Weak links are cheap. Both the formation and maintenance of weak links come much more cheaply than they do for strong links. Weak links are formed easily and do not constitute a great loss when they are thrown away.[2]

Weak links are undirected. Strong links are formed between stable network elements. If an interaction has been refined to the point where the participating elements are reproducibly and often engaged in it, than this strong interaction has a greater chance of being directed than a weaker interaction. Strong links are predictable, whereas weak links are transient, meaning here that the direction of the interaction may just reverse from time to time.[3]

Weak links are remnants of our past. Were 'the first weak links' developed after strong links to maintain the stability of the networks determined by the strong links? This sounds rather unlikely, if not impossible. A strong link, a high affinity binding, requires a developed and mutually adjusted structure of the two partners. At the very beginning of life, these conditions were not present on Earth. Life started from weak links.[4] Strong links were only added later. This also means that originally we had no networks on Earth, in the current sense of the term. Networks were not solid, stable assemblies, but were continuously formed and reformed. The proposed widespread lateral gene transfer (Rivera and Lake, 2004; Woese, 1998), implying that at the very beginning no living creature on Earth possessed stable genetic information and that all life could be regarded as one single organism from the genetic point of view, is one of the many suggestions pointing towards this view. In other words, early networks had links of

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[2] I am grateful to István Molnár for this suggestion.

[3] I am grateful to Attila Steták for this suggestion.

[4] I am grateful to György Buzsáki for this suggestion.

equal (weak) strength. They were much closer to a random network than our networks today. During the preparation of this book, this hypothesis was also formulated by Shenhav et al. (2005), as already mentioned in the context of network phase transitions in Sect. 3.4.[5]

4.3 Stability: A Starting Definition

Stability of networks can be assessed minimally at two levels. These two levels of stability are defined here to help discriminate between them in later chapters of the book:

Definition of Network Stability (or Parameter Stability). A network is stable if it shows a tendency to return to its original parameter values after a perturbation.[6]

This definition resembles the Le Chatelier principle[7] with the important difference that complex systems are almost never in a traditional equilibrium. It would thus be better to talk about robust behavior gravitating towards certain parameter sets, or attractors of the network, after perturbations.

Definition of Netsistance (or Network Persistence). A network has netsistance if it can preserve its giant component and percolation by keeping most of its elements connected to each other.[8]

At this level of stability, the network may leave the original attractors and shift to new ones, or even undergo a topological phase transition,

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[5] Random networks are stable when resources are plentiful. At the very beginning, there were quite a few self-organized systems on Earth, so they probably enjoyed a relative abundance of resources in their environment.

[6] The network parameters in this definition are often emergent properties of the network, which do not exist without the formation of the network and cannot be measured by knowing only the constituents of the network.

[7] The Le Chatelier–Brown principle describes the behavior of systems after their equilibrium has been perturbed. When a system in equilibrium suffers an effect which changes its conditions, the system will adjust itself to minimize this change.

[8] Some readers may feel uncomfortable about seeing the clause 'most of its elements' in this definition. The undefined ratio of connected elements might make the definition of the giant component and netsistance useless. Do we need to connect 5% or 95% of the elements to get the giant component? The necessity of percolation for the existence of the giant component saves the definition. Percolation develops as a phase transition in most networks. With a little approximation

e.g., change its scale-free degree distribution to a star, or random degree distribution as the outside conditions become harder or easier, respectively (see Sect. 3.4). At netsistance, the stability criterion is to keep the network functional, i.e., to preserve its giant component, percolation and emergent properties. In the case of cells or organisms, this means that the network stays alive. In the case of supra-individual networks, netsistance is often called resilience, to discriminate it from the ‘simpler’ chemical type of stability (Holling, 1973).

Relaxation as a measure of stability. Stability is preserved by efficient relaxation. If relaxation is fast, e.g., exponential, the network most probably has quite good stability.

Noise as a measure of stability. From the network point of view, noise can be regarded as a perturbation. If stability is high, the observed fast relaxation helps noise dissipation or noise damping. A high average level of noise in the network is a good indicator of low stability.

Diversity as a sign of instability at the bottom network level. Low relaxation usually accompanies parameter instability. If relaxation is low, perturbing energy may stay at a network segment, helping the whole network to reach a novel local energy minimum which could not have been reached before due to the prohibitively high activation energy. Once the network has jumped to the new local energy minimum, it stays there and becomes different from the original network. Now let us imagine

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we may say: percolation is either there or it is not. Whatever segment of the full network exhibits percolation will be what constitutes ‘most of its elements’ in our definition. *“This definition is still not good enough for me. What if 95% of the network is left as a lonely element and the residual 5% forms a VIP club and starts to percolate?”* In principle, you are right, Spite. This may happen and may be rather disturbing. But in practice, if 95% remains as a lonely element, why do you want to include it in the definition of the network? *“Okay, you win. But I have another objection: what if you have 5 fully connected happy elements, which percolate, and the residual 5 000 elements have not joined the network yet?”* In principle, you are right again, but your 5-clique is too small to produce a phase transition. Moreover, when percolation is born, the network usually starts to show most of its emergent properties. As a possible example, if your 5 fully connected happy elements can reproduce the network, show a large number of adaptive responses and save this information from the dissipative changes, then I will be happy to call them a network without a phase transition.

several clones of the original network. Since both the site and magnitude of perturbations differ from each other in the various network copies, changes of these networks will also differ. Therefore, the different copies will develop and explore entirely different new local energy minima which did not exist previously or had prohibitively high activation energies. After a while many of the clones will end up in different states and will all differ from the original network and from each other. Parameter instability develops diversity. Diversity reveals the instability of the diverse (bottom) networks. However, the same diversity will stabilize the network of these networks, the top network, as I will show later.

Nestedness: stability from top to bottom. In Sect. 2.3, I showed that elements of the top network are themselves networks, i.e., networks show nestedness. If the bottom networks constituting the elements of the top network are not stable, they cannot make strong links, and therefore many of them cannot be used for building the top network. The top network has to figure out mechanisms to (a) stabilize, (b) segregate, or (c) disassemble unstable bottom networks. Chaperones perform precisely this task in the cell, as will be described in Sect. 6.2. As another example, in societies (a) stabilization is provided by psychologists, physicians, teachers, laws, rules, norms, gossips or closed communities; (b) segregation is achieved by prisons, madhouses, hospitals, quarantines, and last but not least, research institutes. Fortunately, the methods of purposeful disintegration (c) have been mostly outlawed in civilized societies by the 21st century, with the exception of some third world countries and a few states of the USA.

Nestedness: stability from bottom to top. Networks try to stabilize not only their bottom networks, but also their environment.[9] Stabilization of any environmental parameter (think about your house, heating and air conditioning systems) gives an advantage for survival. Symbiotic relationships (Margulis, 1998), the formation of top networks, species diversification, and the whole process of self-organization are also signs of environment stabilization efforts.

When does the top network kill its bottom networks? When are the top network and the bottom networks combined to such an

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[9] I am grateful to Péter Száraz for this suggestion.

extent that the disintegration of the top network automatically leads to the disintegration of its bottom networks?[10]

Network stability as a source of the scientific method. As already mentioned in Sect. 4.1, without network stability, science would not have developed as a form of human cognition. Without network stability we would have had no reproducible experimental results and no chance of generalizing any of our constantly changing observations.

4.4 Complex Systems

Complexity has been the focal point of extremely powerful thought and concepts. However, complexity is often poorly defined (Tononi et al., 1998): "While we think that we recognize complexity when we see it, complexity is an attribute that is often employed generically without any attempt at conceptual clarity or, even less, quantification." Trying to avoid these problems, I will give a very brief overview of the most important concepts concerned with the numerical definition of complexity, as well as the most important properties of complexity.

Definition of Complexity as a Measure. I begin the references to numerical definitions of complexity with the definition due to Kolmogorov (1965), which says that the *algorithmic information complexity* of a string of characters computing x equals the length of the shortest program that computes x and then stops. The erroneously high complexity value attributed to random processes by this definition led Murray Gell-Mann (1994; 1995) to formulate the concept of *effective complexity*, which is the length of a highly compressed description of the regularities of the entity. A similar definition concerns *statistical complexity*, which is related to the amount of information required to produce optimal forecasts of the system (Crutchfield, 1994).

For a system with random behavior, the regularity is zero and the characterization of future states may also require only one parameter.

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[10] This is certainly true for a living organism, like ourselves: our cells die with us. However, individual power plants will not necessarily die if the power lines are cut.

Random systems are simple in this sense. Similarly, periodic (lattice-type) systems are also simple. If I know the frequency, amplitude and phase of a periodic signal, I can both describe its regularities and predict any of its future states. Complex systems lie in-between these two extremes, mixing random behavior and periodic structure (Gell-Mann, 1994; Tononi et al., 1998). Complexity can arise in the topology, link strength, dynamics and numerous other features of the network. In this book, complexity is not used in the strict, numerical sense, since the stabilizing role of weak links has never been systematically tested as a function of numerical complexity. This exciting task awaits future work.

Do weak links increase complexity? The use of complexity in a strict numerical sense as a system property to study weak-link-induced stabilization may lead to an even more complicated task, since the system complexity itself may be changed by changing weak links. As summarized in Table 4.1, weak links make networks integrated. If the system is an irregular, but not random network (and not a regular lattice, for example, where integration of two parts will not increase the complexity at all) the integrity and complexity of the network are strongly related. Deletion of weak links will most probably induce a decrease in system complexity. A formal proof for this assumption represents another nice challenge.

Definition of Complexity as a Property. If we do not require a numerical definition of complexity, what can be said about the 'signature properties' of complexity? Gerald Edelman gave the following brief definition (Wilkins, 2004): "A complex system is a system which has heterogeneous smaller parts, each carrying out some specialized function, not necessarily exclusively, which then interact in such a way as to give integrated responses." 'Complex' is not synonymous with 'complicated'. In contrast with complicated systems, the function of the whole in a complex system cannot always be guessed from the function of the parts, and the reassembly of the parts does not always give back this function (Ottino, 2004).

Weak links stabilize complex systems. Weak-link-induced stabilization refers to complex systems. I purposefully did not write: weak links stabilize networks. Weak-link-induced stabilization is not a network property in the sense that it would be true of all networks. Networks with very low complexity do not have weak links. The parallel presence of weak and strong links excludes both fully random and fully regular networks. Weak links can only help the stability of complex systems, since the presence of weak links already attributes an element of complexity to the system.

How does weak link-induced stabilization depend on system complexity? Is there a complexity threshold below which weak links do not stabilize appreciably? Does weak-link-induced stabilization level off as complexity exceeds another threshold?

4.5 Weak Links and System Degeneracy

Degeneracy is a property of most complex systems, in which a system function is performed by two different system components. "Degeneracy is not a property simply selected by evolution, but rather is a prerequisite and an inescapable product of the process of natural selection itself" (Edelman and Gally, 2001). In this section, I show that degeneracy is linked to the emergence of scale-free networks, co-occurring with the emergence of weak links and helping to stabilize complex systems. Occurrence of degeneracy will provide a tool for demonstrating the generality of the stabilization induced by weak links at all levels of development.

Degeneracy gives rise to weak links. Degeneracy is caused by network elements, motifs, or modules performing a similar function. Elements, motifs or modules displaying a similar function will all be linked to the same set of other network elements, but will certainly have a different affinity towards them. Equal strengths of these interactions will be the exception rather than the norm. With each pair of degenerate elements, motifs or modules, new weak links are born. Degeneracy also gives rise to modular structure. Intermodular contacts are yet another source of weak links.

Degeneracy leads to the stabilization of the network. As a typical starting point in the development of degeneracy, gene duplication has been shown to induce developmental stability (Wilkins, 1997). Degeneracy is also a stabilizer of complex systems (Edelman and Gally,

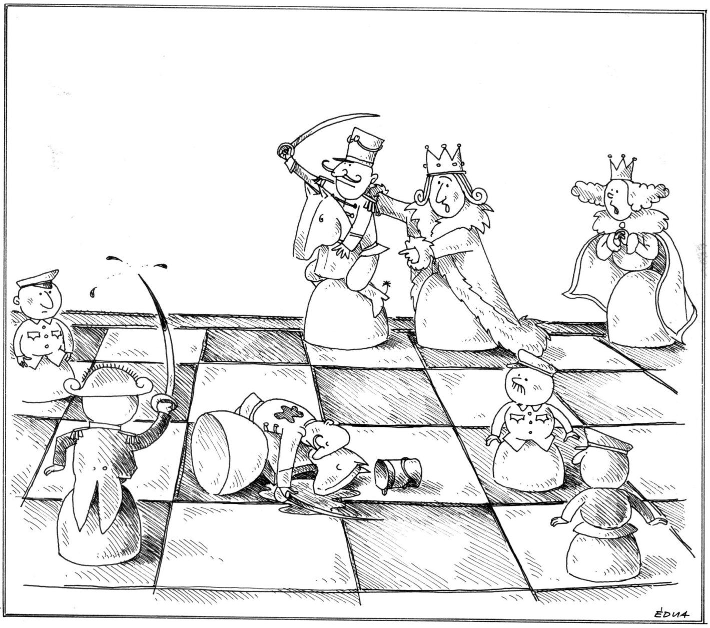

Fig. 4.3. With each pair of degenerate elements, motifs or modules, new weak links are born

2001; Sole et al., 2003a). In fact, degeneracy stabilizes genetic networks more than simple gene duplication (Wagner, 2000; Kitami and Nadeau, 2002). Table 4.2 lists some examples of degeneracy-linked weak links and the functions which may become stabilized by both.

I am happy to inform you that half of our job is completed. I have now summarized many important properties of networks, listing the relevant effects of weak links. The central hypothesis of the book has been formulated and an initial definition has been provided for all its elements. Lastly, using system degeneracy, I have introduced the astonishing variety of networks which may be stabilized by weak links. In the second part of the book, let me invite you on a great journey through Netland. We shall use weak links as a thread (do not worry, I hope to convince you that this thread is even stronger than its proverbial Cretaean ancestor helping Theseus out of the Labyrinth) to visit a number of networks at different levels of complexity. Weak links will give me a good excuse for introducing these networks and exposing their wonderful unity.

Table 4.2. Degeneracy in various networks as a source of weak links and network stability. Partner A denotes the degenerate component which has multiple forms performing a highly similar function. Partner B denotes the component which is the common partner of the multiple degenerate components. Since both partners A and B are members of networks, their 'binding' is often not physical

Source of degeneracy[a]	Emergence of weak links between:		Stabilized function[b]
	Partner A	Partner B	
Multiple nucleotide triplets coding the same amino acid	t-RNA	Ribosome	Translation
Multiple transcription factors inducing the same gene	Transcription factors	Promoter region	Gene transcription
Multiple protein sequences with the same folds	Similar proteins	Binding partner	Cellular responses
Multiple iso-enzymes catalyzing the same reaction	Iso-enzymes	Metabolic pathway	Metabolic networks
Multiple structural proteins with similar binding properties	Structural proteins	Cyto-architecture	Cellular structure
Proteins with multiple subcellular localization	Organelle-specific docking sites	Protein stabilization	Subcellular organelle
Non-identical subcellular organelles	Organelles	Organelle function	Cellular responses
Multiple mechanisms of synaptic plasticity	Protein complexes	Plasticity	Memory
Non-identical cells in tissues	Cells	Cellular function	Tissue function
Parallel signaling pathways	Pathways	Response	Signaling networks
Multiple immune cells against the same antigen	Immune cells	Effect	Immune response
Parallel neural networks performing the same function	Neurons	Function	Neural response
Parallel non-identical muscle fibers with similar functions	Motor units	Contraction	Body movement
Multiple bone trabecules stabilizing against the same pressure	Bone trabecules	Pressure	Bone stability
Multiple stimuli provoking a similar sensory response	Stimuli	Sensory output	Sensation
Multiple behavioral elements with the same final effect	Behavioral elements	Environment, stimulus	Full behavioral response
Multiple words with similar meaning, ambiguity	Words	Meaning	Message

[a] Most examples are from the seminal paper by Edelman and Gally (2001). Bone asymmetry was included after Fox and Keaveny (2001) and da Fontoura Costa and Palhares Viana (2005).
[b] Most of these examples are hypothetical.