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Complexity, system integration, and susceptibility to change: Biodiversity connection

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Abstract

Complexity of system organization involves hierarchy of structure. The hierarchy of structure emerges from the integration of components. Irrespective of the mode of system description, integration determines the hierarchy of the system and hence its effective complexity. Because hierarchy and integration are intrinsic features of ecological systems, they can serve to advance understanding of general properties of such systems. As hierarchical structure affects system assembly and repair, integration becomes a major determinant of such process. To demonstrate potential applications, I develop a quantitative model, grounded in the blind watchmaker analogy. This model shows that while hierarchical organization accords a substantial improvement in ability of a system to assemble or repair itself over a non-hierarchical assembly process, this improvement greatly depends on the interplay among three variables—the probability of perturbation, mean size of the subassembly, and the degree of integration. Specifically, high integration reduces time required to assemble (or repair) a system but it also demands higher levels of modularity (compartmentalization of interactions). In ecological terms, highly integrated systems should evolve towards increased specialization and compartmentalization (low direct connectivity), particularly in habitats where perturbation is locally infrequent.

Keywords: Ecological hierarchy; Integration; Complexity; Biodiversity; Perturbation

1. Introduction

Intuitively, ecologists recognize complexity as a challenging and critical factor with important repercussions for both research and, more importantly, the dynamics of ecological systems. Revived research into diversity-stability (e.g., McCann, 2000; Kolasa and Li, 2003) and ecosystem function-stability relationships (e.g., Loreau et al., 2001; Grime, 1997; Wardle et al., 2000) offer a case in point. Quantification of biodiversity, prediction of species interaction outcomes, and generalizations about the effects of spatial and temporal heterogeneity on a range of ecological phenomena intricately tie with the notion of complexity. A variety of definitions of complexity exist (see Rosen, 1991; Collot, 1995; Ahl and Allen, 1996; de Wailly, 1998; Ricard, 2003; Solé and Goodwin, 2000;

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Jørgensen, 2002 for some examples) but commonly comprise two aspects: complicatedness (the number of different elementary components), and hierarchical complexity (the number of hierarchical levels these components are arranged in) (see Allen et al., 1984; Allen and Hoekstra, 1992; Nehaniv and Rhodes, 2000; Van de Vijver et al., 2003 for more details).

Irrespective of the preferred definition of complexity, the concept contains an implicit, fundamental premise: whether functional or structural, the maintenance of a particular system topology (i.e. the maintenance of components in specific relationship to each other) involves hierarchy. Hierarchy arises whenever subsystems interact and form a system with new properties not additive from the properties of parts (see Li, 2000 for mathematic proof). Scientific literature recognizes hierarchical structure as the ubiquitous mode by which both natural and artificial systems are organized. In fact, the hierarchical nature of ecological systems is commonly taken for granted, as a perusal of current literature indicates, and gives the rise to the perception of their complexity. Thus, a germane question emerges: if hierarchical organization is inherent to complex systems, what makes complex systems hierarchical? Equivalently, we can ask: what are the general mechanisms leading to formation of higher level entities from individual components of the lower level? The answer leads to an examination of interaction between hierarchy, complexity, and perturbation—the main focus of the paper.

Integration as the crucial element of the answer appeared long time ago (Spencer, 1966). More recently, Kolasa and Pickett (1989) linked a gradient of integration to the hierarchical structure of biological systems but without further exploration of its consequences. They defined integration as an aggregate index reflecting both (i) the degree of coordination among components of a system and (ii) the rate of change those components undergo, with greater coordination indicating higher integration and greater degree of change of lower level components indicating lower integration.

Simply stated, integration captures the notion that components of a system must show some bond for the system to exist (see also Ricard, 2003) and the logical necessity that the absence of bond (=relations) implies absence of a system (cf. Mahner, 1998). We can represent such a bond as an additional boundary or envelope around the components (Fig. 1). Each new envelope then corresponds to a new hierarchical level. This basic arrangement is both common to ecological systems and potentially relevant to deeper understanding of their static and dynamic properties such as growth, maintenance, or recovery after perturbation.

Integrated ecological systems assume a wide range of material expressions. Tight symbiotic systems in

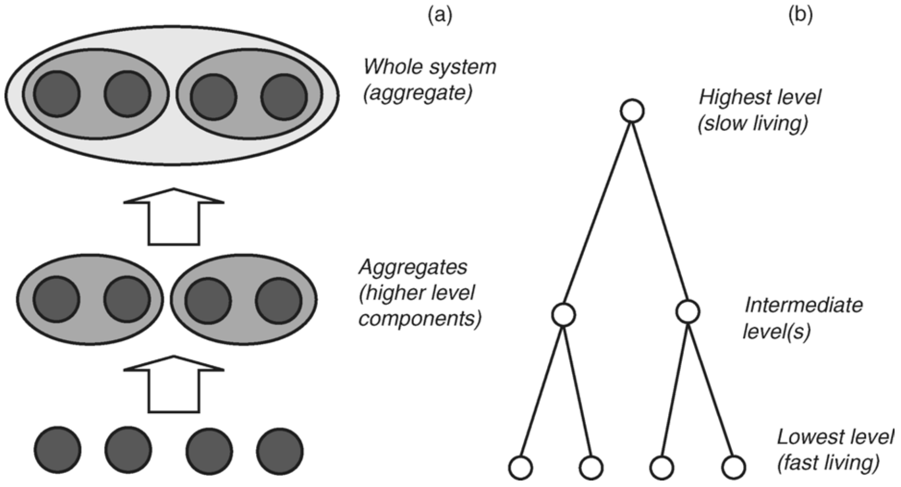

Fig. 1. Relationship between integration of components and system hierarchical structure. (a) Material systems (grey circles) can coalesce or integrate into higher level systems and form a corresponding hierarchical structure (b). Note that lower level components change at a faster rate than any component above them. The decreasing shading of successive envelopes corresponds to decreasing integration of higher level structures (cf. Kolasa and Pickett, 1989).

observed in corals and lichens resemble individual organisms while in fact consist of individuals of different species. Unrelated or related individuals such as social insects, a goby and a shrimp, a pack of wolves, or migrating lobsters form integrated groups at small spatial scales. At larger scales, more diffused entities, populations, show a recognizable degree of interactivity and cohesion. Food webs show a signature of integration as demonstrated by the presence of highly connected nodes, particularly at higher trophic levels, which resemble other complex network topologies (Solé and Montoya, 2001). In addition to the gradient of system integration correlated with spatial and temporal scales, integration emerges in connection with ecosystem properties like nutrient cycling and energy flow: as ecosystems develop, material cycles become increasingly internalized and closed.

In spite of the recognition that ecological systems are complex and that integration is an important aspect of that complexity, the interaction of complexity and integration and its ecological implications remains largely unexplored. Specifically, we know little about how integration affects the ability of a biological system to resist a disruptive external factor or to re-assemble itself in case of the structural disruption. This paper addresses these questions in two steps. In the first section, I present pertinent terminology and review several qualitative relations among concepts and variables used here. The aim of the first section is to facilitate the presentation of the second, quantitative section, where I explore the relationship between the level of integration of systems' hierarchical structure, and its effect on system response to perturbation.

2. Qualitative notes on integration

2.1. Integration and hierarchy

While Allen and Starr (1982) brought the concept of near-decomposability of structure to ecologists, it has not been used in ecological research or discourse to the same extent as scale and hierarchy have been. According to (Simon, 1973), if systems were completely decomposable, there would be no emergent whole (and thus no integration), because the parts would exist in isolation. Thus, the "near" in "near-decomposable" allows the upper level to emerge from the condition that the parts are not completely separate. The agent that makes parts near-decomposable or 'not completely separate' is integration: a dynamic combination of forces and mechanisms that bind parts together into a higher level system. One can portray integration as envelopes around elementary components of a lower level in the structure (Fig. 1) without, however, implying that such envelopes always have a material form. A pair of breeding birds is a higher level system composed of two individuals: while the individuals have skin that holds anatomical parts together, the pair itself has no such physical boundary, at this scale of observation. The bond they form emerges from their mutual response to each other's actions (Kolasa and Pickett, 1989). This reliance on the mutual response as a criterion has gained further support in the theoretical work by Langton (1992). He analyzed cooperation between cells in a computer model and emphasized the need for the two cells to recognize and respond to each others' states for complexity to arise (Langton, 1992). He further saw the gradational nature of this cooperation, which could range from low (the two cells remain virtually independent) to high values (the two cells becoming de facto one).

In brief, I start with the premise that hierarchy emerges through the integration of lower level components into higher level entities (Kolasa and Pickett, 1989). Although it is difficult to conceive a simple indicator or measure of integration, a number of its correlates can assist in gauging the magnitude of integration:

a. *Coordination*—coordination has a specific definition as a condition where one component responds to the action of another component at the same level such that the combined system persists (Kolasa and Pickett, 1989). There can be no integration without coordination, and, thus, coordination is of foundational importance in the emergence of hierarchical structures (Spencer, 1966). The breeding bird pair illustrates this point: coordination of behavior between the two birds leads an external observer to conclude that the pair is an integrated system.
b. *Exclusiveness of interactions*—components of the higher level system have specific interactions with

one another. This condition helps the system to maintain its individuality vis-à-vis other entities of the same level. A breeding pair of birds where two individuals recognize each other, a colony of social insects where individuals of one colony act cooperatively but attack intruders, and an obligatory pollinator–plant mutualism illustrate this point sufficiently.

c. '*Interaction density*'—the relative number of internal versus external interactions. Interaction density increases with integration and quantifies the observation that the mean number of interactions among components of a higher level entity is greater from the mean number of interactions all these components engage in with their equivalents outside the parent entity.
d. *Substitutability of parts*—refers to the potential for one lower level system component to be effectively replaced by something else. To some degree, this measure is related to exclusiveness of interactions, but emphasizes the uniqueness of the whole system in the context of other systems of the same kind. Substitutability of parts declines with integration.
e. *Proximity* in space and time—is a required but not a sufficient condition of integration. For systems of the same kind, one that has components in greater proximity is more integrated.
f. *Autonomy of parts*—declines with integration. When the autonomy of parts is at its maximum, no integrated material system exists (the system can be completely decomposed). When the autonomy of parts is at its minimum, the system is maximally integrated (see 'effective complexity' below).
g. *Coherence*—quasi-instant "non-local" correlation among parts of the observed systems (Laszlo, 2004). Coherence means that what happens in and to one of the system's parts, it also happens in all its other parts and hence indicates the wholeness of the system. Low coherence implies low integration.

Ecologists use most of these criteria either directly or in guise of other terms. For example, coordination at the community level may be quantified, depending on specific research goals: at the level of the individual by covariance or partial correlation matrices; at the population level by gene flow, reproductive synchrony, or cohesion (e.g., Earn et al., 2000); at the ecosystem level by metrics of nutrient cycles. Exclusiveness of interactions is estimated via measurements of niche breadth or specialization/tolerances in community ecology, mate selection at the population level, or network information in ecosystem science (cf. Ulanowicz, 1997). Similarly, the loss of autonomy may take many forms: the loss of freedom for independent movement as in migrating individual caribou; the loss of reproductive 'rights' as in wild dogs, mole rats, or social wasps; the loss of independent reproductive ability in plants involved in mutualism with obligatory pollinators. Thus, ecologists examine effects of integration on their study system across all levels of organization and scale. Later on I represent integration as an arbitrary parameter I that assumes values between 0 and 1 and affects the strength of hierarchy, or distinctness of its components (cf. decomposability), as a useful albeit the simplest substitute for the above indicators of integration.

Specific aspects of integration could potentially be quantified by mutual information (cf. Langton, 1992; Ulanowicz, 1997). Mutual information is a measure of dependence between two variables akin to correlation, with correlation limited to measuring linear dependence only (Li, 1990). Mutual information can measure the amount of constraint exerted on an arbitrary quantum of currency flowing from one compartment to another (Ulanowicz, 1997). In ecosystem models this will often be carbon but in other ecological systems it could be one of many other currencies; for example, for a pair of breeding birds one might prefer fitness. In brief, mutual information could serve as a measure of integration for some aspects of organization.

2.2. Interaction strength

I have omitted interaction strength from the list of integration correlates because it can cause some confusion. Interaction strength may be a good measure of integration when it is evaluated within a specific system but not among systems. In the former case, evaluation of interaction strength would involve quantification of mutual impact among components using some suitable index variable(s) such as element flows, fitness, survival, and many others. This impact could result in coordination (another correlate), loss or gain of autonomy, change in substitutability, or change in a number of other system attributes. Interactions between different systems may be destructive and thus, irrespective of their strength, do not contribute to integration. In other words, interaction strength between separate systems contributes directly nothing to understanding of the relationship between hierarchy, integration, and complexity and becomes a caveat.

2.3. Effective complexity

The conceptual and material importance of integration reveals itself through its impact on complexity. Fully decomposable (non-integrated) systems are simple, as are fully integrated higher level systems (in fact, it could be argued that they are one and the same thing): between the two extremes lie degrees of integration of components and, thus, complexity. If one considers the individual components of a prospective system (the lowest elements in Fig. 1a), the magnitude of complexity (whether algorithmic, hierarchical, or informational) they present is limited. As a hierarchy of integrated entities emerges from lower level components (Fig. 2), the effective complexity increases because the relations between new higher level components resulting from integration must now be considered in addition to the relations among components of a single level. Thus, the effective complexity of relations among levels, with the attendant increase in the number of possible interactions and effects, increases as the system model includes components beyond the first level in the hierarchy. This process can be thought of as involving an increase in the degrees of freedom (or more entropy) and thus, according to Ricard (2003) defining a complex system. With progressive increases in integration, the autonomy of subcomponents (components at lower hierarchical levels) diminishes and their behavior and attributes cease being relevant to understanding or predicting system behavior (Fig. 2). Consequently, the system's complexity disappears (cf. Ricard, 2003) and the observer experiences it as a single opaque object (cf. Allen et al., 1984; who employ the concept of surface to convey the degree of opaqueness).

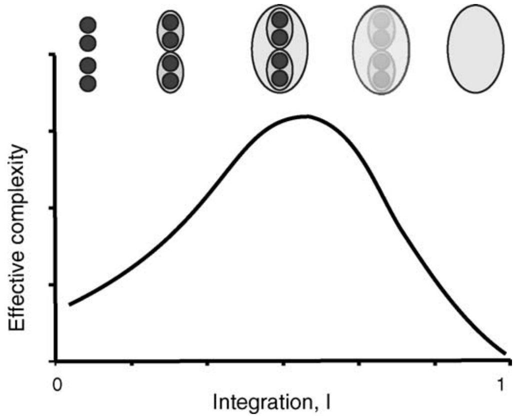

Fig. 2. Changes in effective complexity as a function of integration. The diagrams above the curve illustrate progressive integration of four components (round dark circles). Increasing opacity stands for progressive loss of autonomy of lower level components resulting from integration. Note that the effective complexity of an arbitrary collection of four independent components is higher than that of a fully integrated system.

For example, for many applications, theoretical or practical, we are able to ignore the internal structure of atoms. Similarly, in community ecology studies, lichens and corals lose their taxonomic composition, while angler fish lose their gender aspect (males are reduced to an appendage in females) and are treated as sexually unstructured populations.

This phenomenon appears to be general and can be formulated as a rule: 'Complexity is highest at intermediate degrees of integration'. This rule applies irrespective of the language used to represent a class of systems, as long as the integration gradient associated with the model spans the full range of parameter values observed or expected in that class. Others (Langton, 1992; Solé and Goodwin, 2000) have obtained similar results along the axis defined by mutual information, i.e., random versus ordered (mutually predictive) states. However, from the argument presented above it appears that effective complexity does arise in all situations where the mutual dependence of parts varies, with randomness—order axis being one of the of specific cases.

Furthermore, the rule linking integration and complexity intuitively agrees with the concept and properties of middle number systems (cf. Allen and Starr, 1982). Because hierarchical systems are middle number systems and, because integration appears to generate hierarchical structure, middle number systems and complexity may be different reflections of this shared underlying attribute.

One undesirable consequence of intermediate integration, wherever it is encountered, is a need to construct complex explanatory models (cf. Pickett et al., 2004). The only obvious way around this problem is to redefine the system (cf. Allen et al., 2005) in such a way so as to reduce or enhance its integration and thus reduce the effective complexity of the system representation.

3. Quantitative effects of integration and hierarchy on system assembly, persistence, and resistance to perturbation

Simon (1962) considered consequences of hierarchy by calculating time required to assemble a watch out of a given number of parts in two ways: a watch maker may attempt to add all the parts in one continuous effort (direct assembly), or may chose to first assemble groups of parts into several subassemblies and then combine subassemblies into the final product (hierarchical assembly). Simon (1962) further assumed that each assembly process involves errors and that an error would result in the loss of all the work completed prior to it. Under these assumptions, Simon (1962) showed that the hierarchical assembly process will be completed much sooner than the direct process that involves no subassemblies.

While Simon aimed at demonstrating that hierarchical systems can evolve much faster than directly assembled systems—fast enough to counter arguments made by opponents of evolution—I suggest that his explorations have also broad applicability to ecology. This applicability becomes more obvious when the watch assembly represents the development or recovery of an ecological system, and the watchmaker's error is taken as a metaphor for a stochastic perturbation to that system. In this paper, I intend to show that this line of exploration offers insights and a general explanatory value when applied to highly complex and diverse multispecies systems.

3.1. Approach and methods

Calculations of the effects of hierarchical structure on system persistence or susceptibility to perturbation employ a generalized version of the model proposed by Simon [(1962); Eq. (1)]. In addition, modifying assumptions were added to examine the effect of integration strength on system properties. First, consider a system composed of n components in subassembly, with n_{tot}, the total number of components to assemble, in k subassemblies (Fig. 3).

Further, the time required to complete a system assembly, T_{a} is given by

$$T_{\text{a}} = kE\left(\frac{1}{1-p}\right)^{n} \tag{1}$$

where p is the probability of perturbation while adding a component and E is the mean number of components assembled before a collapse, and where T_{a} is evaluated by the number of assembly steps (which equals the number of components involved in the process of assembly; see Appendix 1). E obtains from the following (see Appendix 1 for details):

$$E = \frac{(1-p)[1-(1-p)^{n}]}{p} \tag{2}$$

Effects of integration were obtained via its effect on n and k such that partial integration produces partial subassemblies. Such partial subassemblies have intermediate values of n and k that are subsequently used in Eq. (1) and (2). For example, a system of four components integrated at 0.5 level can be seen as a mean ($k = 2$, $n = 3$) of a fully integrated hierarchical system ($k = 3$, $n = 2$) and a non-hierarchical assembly ($k = 1$, $n = 4$). Thus, in the model, full integration occurs and is defined by the state such that n can be unambiguously evaluated at any single level of hierarchy (does not involve two levels).

Finally, disturbance was assumed to propagate between subassemblies at a constant rate and thus in

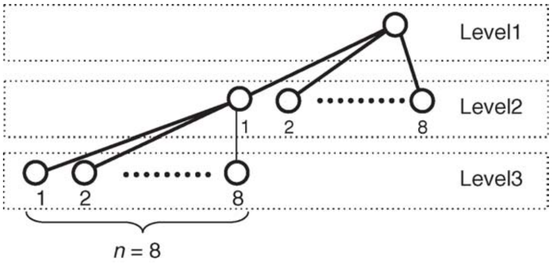

Fig. 3. An example of a hierarchical system composed of $k = 9$ subassemblies (8 at level 2 and 1 at level 1); each comprising $n = 8$ components. In this configuration $n_{\text{tot}} = 64 + 8 = 72$. Dotted boxes identify hierarchical levels.

inverse proportion to the number of compartments or subassemblies, k. Using the previous example, in a non-hierarchical system ($k = 1$) disturbance will propagate without hindrance and will result in a complete disruption of the singular assembly process. This process will have to restart anew.

4. Results

As proposed by Simon (1962), a hierarchical system assembles orders of magnitude faster than a system without nested compartments (Fig. 4a; line 0 versus other lines). Furthermore, the size of compartment measured in terms of the number of elementary components, n, makes a substantial difference (compare lines 2, …, 32 in Fig. 4a; noting the log scale of the y-axis). However, the most interesting observation resulting from this analysis is that the effect of subassembly size depends on the probability of perturbation, p, and that it reverses at some specific and small value of p (Fig. 4b). In general, small subassembly sizes lead to faster assembly or repair of a system when the perturbation probability is low. This advantage disappears and switches to larger compartment sizes when p increases.

In a system with no damage propagation, the magnitude of damage measured in this case by the loss of parts (out of 64 components) strongly depends on system integration (see Section 3.1). Two limiting cases describe the response phase space of interest (Fig. 5). Here, a system containing no intervening structure of subassemblies, suffers the highest damage when perturbation probability, p, is low. This is largely due to the fact that low p permits considerable advancement of the assembly process before a

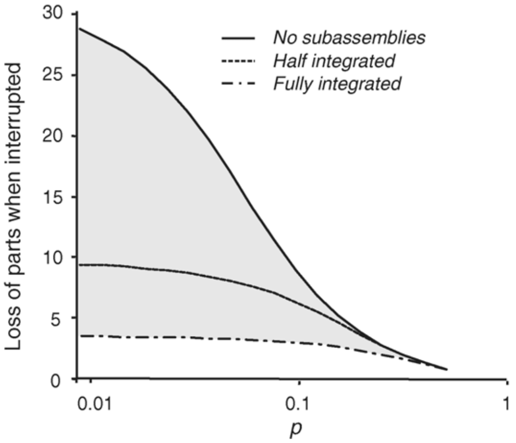

Fig. 5. The extent of structural damage to a perturbed system as a function of probability of perturbation, p, and degree of integration, I. For any system, the response space must lie between the curves describing $I = 0$ (continuous line) and $I = 1$ (dash and dot line). Consequently, all organized ecological structures must lie within the shaded area and all structures or patterns outside this area remain collections of independent particles best treated by simple statistics.

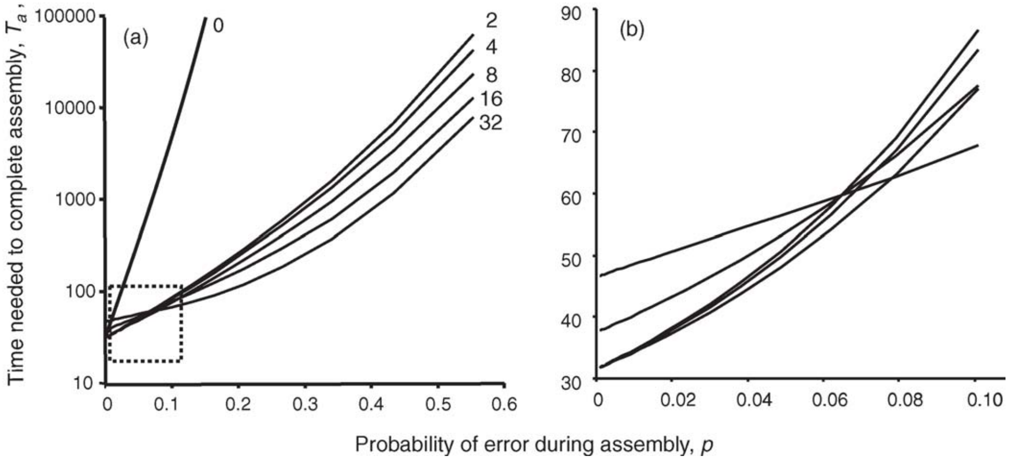

Fig. 4. Time needed to complete the assembly as a function of probability of error during the assembly and of the subassembly size (n). (a) Numerals to the right of curves are n values, with 0 indicating direct assembly of 64 components into a complete system, 2 indicating the subassembly size of 2, and so on. The dotted rectangle identifies the area enlarged in (b).

collapse takes place. The opposite limiting case of fully modular assembly process exhibits very limited amount of damage at low *p*. The significance of the difference between these two limiting cases becomes obvious when viewed in combination with the high rate of successful assembly process in compartmentalized system (system with small values of *n*). To sum the results up to this point, a system with a hierarchical structure assembles much faster and this can be attributed to the minimization of setbacks incurred from perturbation.

So far, the analyses have related perturbation probability to the structural attributes of the system at the level of elementary components. Specifically, they explored whole system consequences of a perturbation to a single elementary component. These consequences appear to depend strongly on the size of a subassembly, *n*, and the probability of perturbation, *p*, with the two interacting in complex ways.

The results become much more relevant to ecology when we add realism to the general picture using supplementary assumptions. This additional realism reflects the intuitive expectation that, following a perturbation event, damage spreads (a) in proportion to integration and (b) inversely to the degree of compartmentalization (by way of sub-assemblies). The first assumption states that the destruction of one subassembly may induce (propagate to) failure of other subassemblies and that this propagation of perturbation will increase with the degree of integration of the whole system. The second assumption reflects the fact that this propagation is easier within a subassembly than between subassemblies (compartments) of the system. Thus, a system with a higher degree of compartmentalization, that is higher value of *k* (and, correspondingly, lower value of *n*), should show higher resistance to the spread of perturbation.

A calculated example (Fig. 6) illustrates that damage (in terms of parts lost) is most severe in highly integrated systems and in systems with larger subassembly sizes. Furthermore, it shows that the greatest increase in the magnitude of damage occurs during the transition from the smallest (low *n*) subassemblies to intermediate size subassemblies. Read from a different perspective, the graph reveals a phenomenon of great importance to ecology: a highly integrated system should also be highly modular (compartmentalized) if it is to reduce the extent of damage resulting from a perturbation. Alternatively, a highly integrated multispecies system will be most vulnerable to perturbation unless it is also highly compartmentalized.

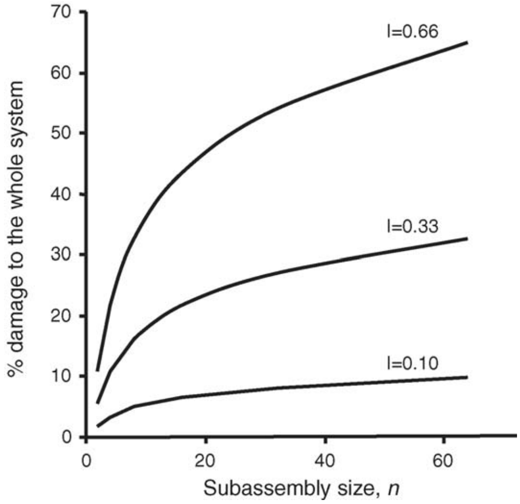

Fig. 6. Effect of integration on the magnitude of damage to the whole systems (in percentage of elementary components lost) and as a function of subassembly size, *n*, for $p = 0.1$. The damage propagation is highest when integration and subassembly size are large.

5. Discussion

In the qualitative section of the paper I proposed the notion of effective complexity. Its name is identical to a concept proposed by Gell-Mann and Lloyd (1996) but its substance differs. In this paper, I emphasize the dependence of the perception of complexity on component integration while Gell-Mann and Lloyd (1996) effective complexity evaluates complexity of a system against the background of randomness in the arrangement of elementary components in that system.

The quantitative exploration confirms Simon (1962) postulate of the positive effect of hierarchy on the system to assemble or repair itself. However, the new finding is that this general effect is strongly modulated by the structural properties of hierarchy. Specifically, I find that subassembly size and discreteness (compartmentalization) are important. The probability of perturbation and the compartmentalization of the system structure do interact in such a way that different combinations of their values may lead to opposite effects. Small perturbation probabilities give advantage to assembly process using small components while, counter intuitively, large perturbation probabilities favor assembly using large components (large *n*). Furthermore, the analysis indicates that the positive effect of hierarchy is enhanced by integration but only when accompanied by increasing compartmentalization of structure. The latter result appears to parallel the classical complexity-stability debate (cf. May, 1973) by pointing out that diverse systems must not be unstable as long as the increase in integration (∼connectance and ∼interaction strength) is compensated by compartmentalization (∼1/connectance). Unlike food web analyses, the approach presented here does not imply any internal system instability, deals with ecological systems ranging from groups of individuals such as fish schools to complete ecosystems and metacommunities, and goes beyond trophic interactions among species. Trophic connections may constitute, if applicable, just one of many mechanisms producing interdependence among components at different hierarchical levels. Many other interactions may also affect the membership in a system. In the domain of community ecology, such interactions may include competition for space among plants or other sedentary organisms, symbiotic relationships (pollination, commensalism, security), facilitation via mutual or asymmetric habitat modification), nutrient recycling and others. Each of these interactions may involve a group of species of some size (subassembly) that are isolated to varying degrees (compartmentalization) from other groups of species in the system.

Solé and Goodwin (2000) proposed a measure of complexity that is directly linked to integration outlined above. Specifically, they evaluate the 'distance to independence' which is the difference between the probability of observing independent states of non-interacting components and the probability of observing states of components mutually influencing their states. This idea maps well to the concept of coordination (Kolasa and Pickett, 1989). When the component's state is predicated by the other component's state, coordination is high. When these states are entirely random, coordination does not exist and hence there is no integration. Intermediate states have both the elements of predictability and randomness—a configuration that Solé and Goodwin (2000) consider as signature of complexity (but see Jørgensen (2002) for a diametrically opposite view, or Ulanowicz (1997) who associates complexity with a number of unique although not necessarily random events). While in this paper I draw on the view that integration and complexity interact, I emphasize that they are not the same. The need to discriminate between these concepts arises because states of two components can be predictable from but not causally linked to one another if both respond predictably to an external force. In such a situation, complexity would be a function of the arbitrary observation window (inclusion of objects or states that do not interact) as opposed to intrinsically generated complexity of an integrated system. Importantly, it is the latter that is of interest to ecologists who want to know how differently constructed systems function and respond to external agents.

5.1. Predictions/hypotheses

Given the interplay between compartmentalization and integration (Fig. 6), it is possible to suggest that for any environmental template there will be an equilibrium organization described by these two variables such that any system will have maximum integration and minimum compartmentalization for a given probability of perturbation (size or frequency, or their combination). Thus, physically stable habitats, stable communities, or stable ecosystems will attain high integration but support small compartments (high modularity of interactions) and physically variable habitats, communities, or ecosystems will support larger compartments and lower specificity of component interactions. Ecological communities offer a contrasting example: two species that engage in obligatory mutualism form a smaller and more discrete compartment (or interactive module) than two facultative mutualists, with orchids and their pollinators or ants and plants showing a broad range of transitions. I believe that these conditions are generally scalable without losing their qualitative relations. If this is so, then ecologists should determine a degree of compartmentalization for the more complex and less understood systems in order to guide the management and conservation strategies.

These ideas have clear affinity to the concept of poised systems (Kauffman, 1993; Perry, 1995), systems that have reached self-critically and remain robust through being adapted to specific conditions but become subject to threshold changes when their bounds of adaptation are exceeded. For such systems, greater integration might imply greater resistance to perturbation when the bounds of adaptation are not exceeded but greater magnitude of damage when they are. Recent refinements of the notion of alternative stable states (Beisner et al., 2003) suggest empirical approaches to testing these connections.

5.2. *Areas of promising exploration*

The model I used ignores one fundamental property of hierarchical organization—the rate differences among nested components or components occurring at different levels. Normally, higher level components operate at slower rates (O'Neill et al., 1986). In the model, the probability of perturbation was calculated in relation to the number of assembly steps without, however, differentiation among levels. A more general and realistic model should account for the fact that the assembly steps at higher levels are slower. Consequently, mean effect of perturbation will depend not only on mean n but also on the distribution frequency of subassemblies within the hierarchical structure.

A number of traditional areas of research might also benefit from the new perspective. For example, analysis of integration and its consequences could help identify additional general trends in system organization during succession. The results presented earlier suggest that one should expect a gradual development of more specific, modular interactions as species accumulate and integrate into a community during succession. The limits to the development of modularity will be set by antagonistic, exogenous processes (cf. Li, 2000), modeled here as size of perturbation. In addition, an increase in modularity, or splitting of higher level states into new, complementary states, can be seen as an increase in order (Li, 2000).

Lessons from metapopulation and metacommunity studies (e.g., Hastings, 2003) suggest that barriers to dispersal due to distance or unsuitable habitat matrix can disrupt spatial cohesion of populations and multispecies assemblages. Since the increase in spatial scale of the system is negatively correlated with its integration (see Section 2), metacommunity models may offer a valuable tool for examination of integration in multispecies systems, particularly as far as their vulnerability to fragmentation, perturbation frequency and amplification, asymmetry of interactions, and the degree of compartmentalization are concerned. The latter has not been examined by the existing models (cf. Leibold et al., 2004).

Integration of communities and ecosystems in stable and variable environments could provide further insights into the interdependence of species and the best modes for their conservation. For example, as a widely distributed population becomes restricted to small habitat fragments, it undergoes transition from a poorly integrated large scale system that can be managed as ''averages'' to a collection of much more integrated systems that each requires specific and different management. In addition, invasion and vulnerability to invasion represent ecological situations of great interest that may depend on system integration in general. Finally, integration is likely to play a major role in determining boundaries on the number of species in a community, a problem of both practical and theoretical importance.

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Appendix A. Derivation of equations

Equation 1
Define

T_a—time required to complete system assembly. T_a is evaluated by the number of assembly steps counted as the total number of components that

must enter the assembly process. Hence, T_a is expressed in terms of the number of components.
p—probability of perturbation while adding a component. This perturbation results in resetting the assembly process for a given subassembly.
n—number of components in subassembly (=subassembly size).
k—the number of subassemblies (k is a function of system size and n). For example, a system of 1000 components assembled in groups of $n = 10$ will require 111 assemblies to construct (100 groups of 10, which are then assembled in 10 more groups, and which in turn will require one final assembly). Consequently, k is a dimensionless quantity describing 'packaging' of components, or the amount of work that must be accomplished once the mean subassembly size is given.

The total assembly steps needed too construct the system will be proportional to a product of the mean number of components assembled before a collapse within a subassembly, E, the number of subassemblies, and the time required to complete one subassembly. The time required to complete one subassembly is given by (Simon, 1996, p. 190) as

$$\left(\frac{1}{1-p}\right)^n$$

For the whole system we can write

$$T_a = kE\left(\frac{1}{1-p}\right)^n$$

Thus, T_a is expressed in terms of the total number of components that will be involved in the system construction until its completion. This number will be much larger that the total number of system components because many of the components will have to be reused many times before the construction is completed.

Equation 2

For a system made up of n components, the expected number of successfully assembled components until a perturbation occurs can be calculated as follows. Denote by z the number of successfully assembled components. This value indicates that before a perturbation occurs, z components were successfully assembled, the probability of this happening is

$$(1-p)^z p, \quad z = 0, 1, 2, \ldots, n-1,$$

where p is the probability of experiencing a perturbation in assembling (i.e., adding) any single component. The probability of successfully assembling all the components in the system is $(1 - p)n$. Hence the expected number of components successfully assembled, called E, is the average of the z values weighed by their probabilities (see e.g., Devore, 2004, p. 112), that is

$$E = \sum_{z=0}^{n-1} z(1-p)^z p + n(1-p)^n.$$

This can be written as

$$E = p(1-p)\sum_{z=0}^{n-1} z(1-p)^{z-1} + n(1-p)^n$$

To work out the sum involved, take derivatives with respect to p on both sides of the well-known geometric identity

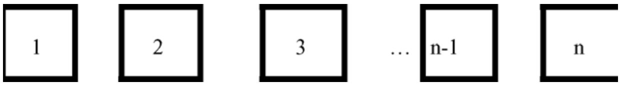
$$1 + (1-p) + (1-p)^2 + \cdots + (1-p)^{n-1} = \frac{1-(1-p)^n}{p}$$

to obtain

$$\sum_{z=0}^{n-1} z(1-p)^{z-1} = \frac{1-(1-p)^n - np(1-p)^{n-1}}{p^2}.$$

Replacing this expression for the sum in the above form for E gives

$$E = \frac{(1-p)[1-(1-p)^n]}{p}.$$



References

Ahl, V., Allen, T.F.H., 1996. Hierarchy Theory: A Vision, Vocabulary, and Epistemology. Columbia University Press, New York, NY, 206 pp.

Allen, T.F.H., Hoekstra, T.W., 1992. Toward a Unified Ecology. Columbia University Press, New York, NY, 384 pp.

Allen, T.F.H., O'Neill, R.V., Hoekstra, T.W., 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110:1–11.

Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspectives for Ecological Complexity. The University of Chicago Press, Chicago, 310 pp.

Allen, T.F.H., Zellmer, A.J., Wuennenberg., C., 2005. The loss of narrative. In: Cuddington, K., Beisner, B.E. (Eds.), Ecological Paradigms Lost: Routes to Theory Change. Theoretical Ecology Series [Series Ed., A. Hastings]. Academic Press, New York.

Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. Frontiers Ecol. Environ. 1, 376–382.

Collot, F., 1995. Correlations entre complexification et instabilité dans une formalisation de concept de complexité. Acta Biotheoretica 43, 195–204.

Devore, J.L., 2004. Probability and Statistics for Engineering and the Sciences. Thomson Books/Cole, Pacific Grove, California, USA, 816 pp.

de Wailly, A., 1998. The ambiguity of the word "complexity". A proposal for clarification. Acta Biotheoretica 46, 177–183.

Earn, D.J.D., Levin, S.A., Rohani, P., 2000. Coherence and conservation. Science 290, 1360–1364.

Gell-Mann, M., Lloyd, S., 1996. Information measures, effective complexity, and total information. Complexity 2 44-42.

Grime, J.P., 1997. Biodiversity and ecosystem function: the debate deepens. Science 277, 1260–1261.

Hastings, A., 2003. Metapopulation persistence with age-dependent disturbance or succession. Science 301, 1525–1526.

Jørgensen, S.E., 2002. Integration of Ecosystem Theories: A Pattern. Kluwer Academic Publishers, Dortrecht, 420 pp.

Kauffman, S., 1993. The Origins of Order. Oxford University Press, Oxford.

Kolasa, J., Li, B.-L., 2003. Removing the confounding effect of habitat specialization reveals stabilizing contribution of diversity to species variability. Proc. R. Soc. Lond. B (Suppl.) 270, 198–201.

Kolasa, J., Pickett, S.T.A., 1989. Ecological systems and the concept of biological organization. Proc. Natl. Acad. Sci. U.S.A. 86, 8837–8841.

Langton, C.G., 1992. Life at the edge of chaos. In: Langton, C.G., Taylor, C., Farmer, J.D., Rasmussen, S. (Eds.), Artificial Life II. Addison-Wesley Publishing Company, Redwood City, California, pp. 41–91.

Laszlo, E., 2004. Nonlocal coherence in the living world. Ecol. Complexity 1, 7–15.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzales, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613.

Li, W., 1990. Mutual information functions versus correlation functions. J. Stat. Phys. 60, 823–837.

Li, B.-L., 2000. Why is the holistic approach becoming so important in landscape ecology? Landscape Urban Plann. 50, 27–41.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.

Mahner, M., 1998. Operationalist fallacies in biology. Sci. Educ. 7, 403–421.

May, R.M., 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ, 235 pp.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228–233.

Nehaniv, C.L., Rhodes, J.L., 2000. The evolution and understanding of hierarchical complexity in biology from an algebraic perspective. Artif. Life 6, 45–67.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B., Allen, T.F.H., 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, NJ, 253 pp.

Perry, D.A., 1995. Self-organizing systems across scales. TREE 10, 241–244.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., 2004. Resilient cities: meaning, models, and metaphor for integrating the ecological, socio-economic, and planning realms. Landscape Urban Plann. 69, 369–384.

Ricard, J., 2003. What do we mean by biological complexity? Comptes Rendus Biologies 326, 133–140.

Rosen, R., 1991. Life Itself. Columbia University Press, New York, NY, 285 pp.

Simon, H.A., 1962. The architecture of complexity. Proc. Am. Phil. Soc. 106, 467–482.

Simon, H.A., 1973. The organization of complex systems. In: Pattee, H.H. (Ed.), The Challenge of Complex Systems. Braziller, New York, NY, pp. 1–28.

Simon, H.A., 1996. The sciences of the artificial. In: The Architecture of Complexity: Hierarchic Systems, 3rd edition. MIT Press.

Solé, R., Goodwin, B., 2000. Signs of Life. Basic Books, New York, 322 pp.

Solé, R.V., Montoya, J.M., 2001. Complexity and fragility in ecological networks. Proc. R. Soc. Lond. B 268, 1–7.

Spencer, H., 1898. Principles of Biology (Appendix A). In: Zeller, O. (Ed.), Reprinted 1966. Proff, Osnabrück.

Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective. Columbia University, New York, NY, 201 pp.

Van de Vijver, G., Van Speybroeck, L., Vandevyvere, W., 2003. Reflecting on complexity of biological systems: Kant and beyond. Acta Biotheoretica 51, 101–140.

Wardle, D.A., Bonner, K.I., Barker, G.M., 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. Oikos 89, 11–23.