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Viewpoint

Ecological complexity for unifying ecological theory across scales: A field ecologist's perspective

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ABSTRACT

The evening session in ecological complexity at the last Joint Meeting of the International Association for Ecology (INTECOL) and the Ecological Society of America (ESA) held in Montreal was an occasion to evaluate the pertinence and upcoming challenges of the complex systems approach (CSA) applied to ecology. Through concepts such as the interaction topology among biological objects, the phenotypic integration of individual traits, the meaning of biological objects and complexity measures in space and time, the management of human dominated ecosystems, and non-equilibrium thermodynamics as a paradigm for the development of ecosystems, the panel members covered some of the most active areas of research in ecological complexity. However, for many ecologists, and particularly field ecologists, a comprehensive framework clearly emphasizing how and why the CSA provides a unique corpus for studying ecosystem functions is missing. The purpose of this article is thus to provide an overview of the different themes visited during the evening session and to emphasize the distinctiveness of the CSA as an alternative to contemporary ecological issues. Examples from functional ecology and food webs are given to support the discussion.

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1. Introduction

The study of ecological complexity finds its day-to-day application through a multidisciplinary framework based on the complex systems approach (CSA). A complex system is generally described as a network of many components whose aggregate behavior is both due to, and gives rise to, multiple-scale structural and dynamical patterns which are not inferable from a system description that spans only a narrow window of resolution (Parrott, 2002). Popularized in statistical and non-linear physics, the CSA is relatively new to ecology where the dialectic cycle has recently exacerbated the tension between those who seek to explain nature by studying its parts

and those who seek to explain nature by studying whole-system behavior (Naeem, 2002). In this context, the CSA is neither holistic nor reductionist but asserts that ecological relationships between patterns and processes span multiple scales of organization. Many key concepts are often associated to the CSA: non-linearity, emergence, criticality, scaling, hierarchy and evolvability to list a few (Brown et al., 2002; Milne, 1998). Although the scientific community admits that ecosystems are indeed complex, for a majority of field ecologists it remains ambiguous how the CSA would facilitate their research. For instance, what can the CSA metaphor (cf., Keller, 2005; Levin, 2005) contribute to ecology that macro-ecology (e.g., species- and landscape-based scaling laws) and

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common garden approaches (e.g., in vivo and in silico experiments) do not already share?

2. Evening session on ecological complexity

The last Joint Meeting of the International Association for Ecology (INTECOL) and the Ecological Society of America (ESA) held in Montreal was an occasion to answer such questions. An evening session under the theme Ecological Complexity: unifying ecological theory across scales was organized by Dr. Bai-Lian (Larry) Li (University of California at Riverside) and Dr. Lael Parrott (Université de Montreal). The organizers invited seven panel members to briefly introduce their view on the topic and to answer questions from the audience (about 90 participants). The first portion of this article is a synthesis of the major points discussed during that session. The last section is my viewpoint on the contribution of the CSA to field ecology. This discussion is supported by examples borrowed from functional ecology and food webs.

The panel was composed of Simon Levin (Princeton University), Jurek Kolasa (McMaster University), Craig Loehle (NCASI), Madhur Anand (Laurentian University), Scott Slocombe (Wilfrid Laurier University), Felix Müller (University of Kiel), and Rusong Wang (Ecological Society of China). The panel members and organizers at first admitted that long standing ecological debates, particularly those regarding the stability and the predictability of ecosystem dynamics, could take new directions by adding spatial and temporal degrees of freedom to our models.

In this context, Dr. Levin exemplified the necessity to better understand how competitive exclusions are challenged in a system increasing its diversity of components. This understanding may be achieved through models describing the topology of interactions among species or individuals in the ecosystem. As such, the robustness of the system (i.e., its capacity to resist perturbations) should link with measures of the dynamic in the interaction topology. A weakening of the interaction topology, without necessarily losing species or individuals, is expected to initiate a decline of the overall system's robustness. Hence, ecosystems may develop a modular topology (i.e., compartmentalization of systems-within-systems) that prevents them against catastrophic regime shifts.

Dr. Kolasa used a chain-of-events analogy to argue that it is not only the pattern which is of interest in an ecosystem; it is also how the historical dynamic shapes the integration of a set of traits. The historical dynamic refers to the different choices each individual or group of individuals have to make in response to environmental constraints. How traits are coordinated with each other, to what extent this organization allows or constrains their behavior, and ultimately how traits may respond to selection is the focus of ecological integration. Proxy measures of integration should capture the degree of coordination among the system's components and the rate of change they undergo in time (Kolasa, 2005, 2006).

Dr. Loehle grounded his arguments on the foundation of scientific investigation, namely data collection. Is the object of my study itself scale-invariant such that hypotheses may be tested across multiple levels of organization? Is my sampling protocol clearly spatial, clearly temporal, neither or both? Is

the similarity criteria (e.g., taxonomic keys) used to classify biological objects sensitive to sampling resolution? These considerations should help us realize that the operationality of an object is defined by its measure not by its semantic. For example, the biodiversity concept suffers from this ambiguity (Ricotta, 2005) and is still widely utilized in scientific and public affairs.

Although humans possess the capacity to naturally experience complexity, what defines a complex process is still an open question. Dr. Anand argued that a step towards unifying ecological theory across scales entails the development of better quantitative tools for measuring complexity in space and time. Methods capable of discerning subtle internal changes in biological systems are expected to provide not only a measure of the system integrity but possibly a simplified version of its functioning. This view ties up once again the complexity notion to its measure.

Dr. Slocombe brought to our attention that humans interact heavily with ecosystems. Human activities generate a level of societal complexity governed by development, management and conservation practices. Societal and ecological levels can be described using typical complexity attributes (spatial, temporal, structural, process, behavioral, and geometric complexity; Loehle, 2004). Thus, future management practices promoting an ecosystem approach should consider both levels of organization in their planification scheme.

Non-equilibrium thermodynamics was introduced by Dr. Müller as a paradigm for the development and functioning of ecosystems. When moved away from a local equilibrium, or orientor, an ecosystem will behave in a way which opposes the applied gradients to move it back to its local orientor. Such dynamics can be tracked by quantifying the amount of path-flows of energy as a measure of the system's internal activity in response to gradients. A key achievement would be to correlate complexity measures to features of an undisturbed ecosystem. Then, an optimization process with respect to a management standard would provide a framework for decision makers.

Finally, Dr. Wang emphasized the fact that ecosystems are human dominated. Although apparently obvious, this statement has a large impact if we recognize that public and economical systems are at least as complex as ecosystems. Examples from traditional Chinese philosophy such as the five elements and opposing complementary forces were given to demonstrate how human societies behave like complex adaptive systems (Wang and Ye, 2004). In that context, the ecological engineer aims to integrate ways of constructing and maintaining a sustainable ecosystem by planning and enhancing technological, institutional and cultural issues, in order to benefit society while sustaining nature.

3. Concluding remarks on the evening session

Three common threads can be traced to link the different themes introduced by the panelists. First, all participants considered that more studies should incorporate humans as intrinsic parts of an ecosystem. Second, the functioning of ecosystems relies, somehow, on the interaction topology among biological objects, whereas measures of interaction

and biological objects must be precisely defined. Third, all declined the invitation to provide their definition of a complex system in the context of ecological complexity. While a technical definition is arguably unpractical, a comprehensive framework establishing how and why the CSA is beneficial to ecology was utterly missing.

As a matter of fact most of the evening's discussion revolved around the vocabulary of complexity theory. Why build complex models when simple ones are sufficiently difficult to handle? What is a Holon? What is hierarchy theory? If ecological complexity is content with a set of multi-disciplinary mathematical methods applied to ecological questions, then the CSA is likely to leave ecologists unsatisfied. For instance, many ecological studies published under the CSA cover did innovate on the analytical side, but failed to adapt field sampling protocols and scientific premises on the other side. If we clearly demonstrate the unique features pertaining to complexity theory, and succeed in showing how these challenge traditional ecological tenets, then the CSA will gain ground (Li, 2004; Proctor and Larson, 2005). The purpose of the following section is to better emphasize the distinctiveness of the CSA as an alternative to answer contemporary ecological questions.

4. Getting started

To keep things clear, I hereafter define concepts which are recurrent throughout the following discussion. An object is the fundamental unit from which observations are drawn. Biological objects are generally defined according to physical (e.g., individuals), ecological (e.g., species), or statistical (e.g., clusters and patches) similarity criteria. An observation is represented by qualitative or quantitative measures which serve to describe one particular object among others. The grain is the size of the smallest resolvable unit of observation, while the extent represents the breadth of a set of observations. Both grain and extent amount to what is generally called the resolution. The resolution applies equally to the taxonomic, the spatial and the temporal dimensions of a sampling protocol. Nevertheless, the number of biological objects, the sample size and the sampling frequency are, respectively, affected by taxonomic, spatial and temporal dimensions, such that for logistical reasons a trade-off exists when designing a field protocol. The level of organization usually refers to the taxonomic resolution, while the term scale is preferred to designate the spatial or temporal resolution.

Thus, the expression scale-invariant is employed hereafter to describe measures transferable across a wide range of taxonomic, spatial, and temporal resolutions. The term scale-invariant is used in reference to fractals which possess self-similar properties, but no further comparisons should be drawn here between fractal objects and scale-invariant measures.

5. First principle: general indeterminacy from specific predictability

The first CSA principle applied to ecology is more philosophical than truly pragmatic. It accounts for our inherent lack

of knowledge about the variables maintaining ecosystem integrity, mainly because of the complexity of natural systems (De Leo and Levin, 1997; Slocumbe, 1998). Otherwise stated, there are just too many biological objects (ranging from small individuals to large communities) and variables (including the almost infinite number of potentially relevant measures) for hope of ecosystem generalization from specific investigations. Specific predictability refers to our ability to calibrate models with low residual error (unexplained variation) on a specific subset of biological objects (e.g., individuals of a single population) and variables (e.g., matrix of environmental descriptors). Consequently, general indeterminacy refers to the difficulty of extrapolating these specific models to other ecological contexts, or ecosystem levels. Thus, the first principle somehow accounts for problems encountered with validation and prediction assessment in distribution models of natural populations (e.g., presence-absence models of species occurrence). Considering the increasing number of competing statistical models produced, researchers now urge field ecologists to use proper cross-validation methods involving independent data sets for the assessment of prediction errors (Fielding and Bell, 1997; Guisan and Zimmermann, 2000; Olden et al., 2002). General indeterminacy can be interpreted as the result of either one or a mixture of interrelated mechanisms such as: ecological integration, large number of local interactions, multiple stable-states, chaotic attractors, open dissipative networks, hierarchy, etc.

Acknowledging not the causes but the consequences of general indeterminacy should find many ramifications in experimental field ecology. Although it may at first sound irrational to think of consequences without necessarily engaging causes, ecosystem theory is nonetheless full of macroecological patterns for which causal relationships are still vigorously debated (Gaston, 2000; Marquet et al., 2005). The species-area and diversity-stability relationships provide contemporary examples of ecological patterns whose mechanisms are not well understood. Accordingly, attempts to infer patterns or processes at a specific level of organization are likely to yield conclusions interpretable within narrow bounds. A more extensive discussion on the subject can be found in Maurer (1999, pp. 112–141).

In ecological words, field models focusing only on narrow taxonomic ranges will likely yield general indeterminacy from specific predictability. Stability of one population in one site by no means entails that other populations are stable at that site and vice versa. Worse, populations may even stabilize because of the collapse of a few others at a given time and place. Similar counterintuitive results are observed in meta-community models (Leibold et al., 2004; for a recent overview). General indeterminacy, however, does not proclaim that biological systems are without predictable dynamics; instead it dictates that such dynamics cannot be untangled from a narrow window of taxonomic resolution (Blackburn and Gaston, 2002).

What should we learn from this principle? The quantification of the whole-system behavior should be favored over the local (specific) behavior. Field ecologists should seek the consequences of a given perturbation or gradient, not necessarily their causal relationships. This obviously begs the question of what variable one should use to quantify the

whole-system behavior. At this point, our personal field experience of the system becomes crucial in the choice of an appropriate variable. Importantly, this variable must be transferable over a large breadth of taxonomic, spatial and temporal scales (i.e., be scale-invariant). The shape geometry (surface roughness, fractal dimension), the spectral characteristics (heat, colors, sounds) and the biochemical composition (stable isotopes, carbon, water content, total biomass) of the biotic–abiotic material are ad hoc examples of scale-invariant measures.

6. Second principle: complex dynamics in space and time

From the standpoint that increasing dimensionality increases the degrees of freedom in a system, the second principle of the CSA applied to ecology requires both space and time to be explicitly considered (Chen et al., 2005; Weins and Milne, 1989). While the first principle dictates that ecologists should attempt to track the whole-system behavior, the second principle specifies that field experiments should be planned in the context of a clear spatio-temporal design. Cellular automata, percolation theory, coupled map lattices, and other modeling tools have served to show, at least in theory, how adding spatial dimensions can generate complex dynamics from local deterministic rules (Bascompte and Solé, 1998; Dieckmann et al., 2000).

Moreover, according to non-equilibrium thermodynamics, more developed and diversified ecosystems are more efficient energy degraders than depauperate ones (Bass et al., 1998; Müller, 1997; Schneider and Kay, 1994). Thus, dynamics of more diversified ecosystems maximize the utilization of the spatio-temporal volume for entrapping exergy (i.e., the energy capable of creating and supporting ecological structures in an open system; Jorgensen and Fath, 2004; Ulanowicz, 2004). The spatio-temporal volume encloses the whole set of opportunities for creating ecological structures through a dissipative process. More opportunities are exploited in an ecosystem when its dynamics are forming a complex interleaving of trajectories with an intricate pattern in space and time. Both high-dimensional models and non-equilibrium thermodynamics, although essentially supported by theoretical examples (see Li, 2002, for an application), illustrate the importance of using a spatio-temporal framework in ecosystem studies.

Ecologically speaking, without a clear spatio-temporal sampling design the modular and hierarchical topology of ecological systems is likely to be missed. Conventional ecological set-ups involving snapshot sampling, small spatial resolution, and relative rather than absolute comparisons of biological objects should be reconsidered in that respect. It is, however, common practice in field ecology to calibrate statistical models on snapshot data, often providing specific models with little predictive power outside their local ecological context. The second principle further suggests that long-term monitoring programs like LTER and sensor networks such as FLUXNET should be encouraged (Green et al., 2005). An automated sensor network for monitoring diversity in real-time would serve to educate the public and governments about ecological issues (e.g., National Ecological

Observatory Network; Automated Radio Telemetry System). Finally, the large body of knowledge accumulated in the different branches of ecology, far from being dismissed would help in pointing out what consequences typically emerge under a given perturbation, in a given ecosystem. The application of the CSA in ecology is now possible because of the scientific advances made by illuminating black boxes of ecosystem functions through studies of local mechanisms.

7. Concluding remarks on the CSA's principles

Researchers are conditioned to understand their systems in terms of causes underlying expected and observed consequences. Anyhow, when dealing with complex ecosystems it may be too hard to redraw engineering plans without knowing what they were devised for. What about pinpointing scale-invariant measures which best describe the overall behavior of the system? These variables should represent the body temperature and pressure, the heartbeat, the spleen swelling, and the skin's color that a physician examines when you feel sick. They convey the notion of system integrity, and if measured across multiple scales in an ecosystem may further indicate where and when the illness has started. A set of ecological orientors (sensu Müller and Leupelt, 1998) could be determined for a given ecosystem type, whereas an ecological orientor is defined as the quantity a living system tends to optimize, from a nonteleological view, in the course of its development. The CSA provides ecology with this unique corpus for studying ecological questions from a general and multiscale viewpoint. Examples from functional ecology and food webs are given next to illustrate the major differences between CSA and more traditional approaches.

8. Functional ecology

Functional ecology aims to establish links between phenotypic traits and their relative function in the environment for which they appear to be adapted. Phenotypic traits are defined as the whole set of variables that one could measure from an individual. Links between phenotypes and their function are generally sought through the use of deductive methods that address the following objectives (Wainwright and Reilly, 1994): (1) to evaluate inter-individual relationships through the analysis of phenotypic distances, (2) to measure the correlation between the hypothetical and the realized niche of different phenotypes, (3) to investigate the adaptive value of functional phenotypes, and indirectly their potential for divergent selection, through the comparison of their reaction norms (i.e., the rate of phenotypic change along an environmental gradient), and (4) to assess the generality of causal models from an evolutionary perspective. The complex dynamics giving rise to phenotypic integration at the level of the individual organism make these objectives extremely difficult to achieve using a mechanistic approach. The distinction of phenotype (or community) and environment (or resource) is intimately linked to the niche concept and, therefore, to functional ecology (Leibold, 1995).

Thus, rather than seeking causal or historical explanations for particular phenotypes, we may seek to identify phenotypic patterns (i.e., collections of integrated traits) that are characteristic of a particular environment. If such patterns exist, we may argue that the associated traits have emerged together as a consequence of a coupling between the developmental and selective forces specific to a given environment. This coupling serves to restrict the number of patterns that can be created from a wide range of possibilities to a limited subset of emergent phenotypes (Goodwin et al., 1993; Goodwin, 1994). In other words, traits would emerge as the result of physical forces of organization at the individual level and are not necessarily selected for their function. So, rather than viewing particular traits as being strictly adapted for an environment, we may place them in the broader context of an emergent pattern that is the product of a feedback process between an individual and its environment.

According to Goodwin's theory (1994), I introduce an emergent phenotype as a stable attractor shaped by present and past strategies experienced by the organism. Accordingly, I consider the basin of attraction of an emergent phenotype as its realized niche (i.e., the range of conditions, biological and physical, under which an organism can exist as a result of pressure from, and interactions with, other organisms).

Have we learned anything new so far? The novelty arises if one assumes that emergent phenotypes are spatio-temporal integrators of their environment, in which biological objects of both environmental and phenotypic nature are better understood as parts of a single matrix (Ahl and Allen, 1996, pp. 21–27). Put otherwise, the emergent phenotype should resemble its environment according to a set of relevant scale-invariant measures and vice versa, i.e., there is no distinction between the phenotype and its environment. For instance, from arthropods to whales one can theoretically measure the biomass, the color pattern, or the shape geometry of individuals, at any given time and place. The biomass is expected to approximate the spatio-temporal scale at which an individual experiences the habitat (Haskell et al., 2002; Holling, 1992; Morse et al., 1985; Peters, 1983). Color pattern and shape geometry otherwise reflect the individual's feedback processes with the habitat. Technically, this can be done by repeatedly sampling individuals across sites, tracking how the shape geometry and color patterns change according to a broad biomass spectrum, and verifying if fluctuations follow predictable patterns in time and space. The complementary approach would consist in quantifying the habitat spatio-temporal heterogeneity through structural (physical) complexity measures (assuming here a greater diversity of emergent phenotypes in a more structurally complex environment; Kolasa, 2006; Tews et al., 2004). The latter approach is certainly not new and can be traced back to pioneer works of MacArthur and MacArthur (1961) on bird communities. Interestingly, the emergent phenotype view has recently attracted evolutionary ecologists through theories such as the sensory drive hypothesis (Boughman, 2001; Endler and Basolo, 1998).

correspond to objects and edges illustrate the presence of a relationship. The nature of the relationship between objects can be uni- (trophic interactions) or bi-directional (competitive interactions), and binary (presence-absence of interactions) or quantitative (weighted interactions often associated to the relative biomass or abundance). Biological objects are sometimes allowed to interact with themselves (edge forming a back loop). Food web studies are primarily concerned with the description of the interaction topology after building mass-balance models (Christensen and Pauly, 1992; Yodzis, 1998) or network architectures (Dunne et al., 2002; Polis and Strong, 1996) under equilibrium assumptions. Sensitivity analyses then serve to evaluate the robustness of these models by removing interactions or modifying weights between species. Food webs can be constructed by collecting field and literature data, or artificially created from oriented computer procedures.

In mass-balance models, the pattern is quantified by evaluating changes of species biomass under perturbation scenarios (e.g., fishing pressure, epidemics, temperature increase, etc.). Network architectures are quantified through parametric measures of the graph, such as the connectance, the characteristic path length, the clustering coefficient (Dunne et al., 2002) and many others. Invariant patterns are sought across natural ecosystems as a general mechanism for explaining species assemblages in ecological communities. The robustness of the community is commonly verified through step-wise removal of species that initiate critical modifications cascading down the network. For practical applications, concepts such as keystone or indicator species have been introduced to designate species whose impact on the ecosystem is disproportionately large relative to its biomass or abundance. Keystone and indicator species are, respectively, expected to increase robustness and to respond predictably (either positively or negatively) when an ecosystem is perturbed.

The food web approach has enjoined ecologists to focus on the interaction topology among biological objects. Moreover, food web studies employ scale-invariant measures derived from network properties to quantify the whole-system behavior (see the previous paragraph for some examples). However, in practice food webs also suffer from several drawbacks: (1) keystone and indicator species are very difficult to identify in nature and are likely to vary in space and time (Hilty and Merenlender, 2000); (2) weak interactions among biological objects are probably of great importance in maintaining the ecosystem integrity (McCann et al., 1998) but are usually overlooked in field surveys. For instance, weak interactions include omnivory and the large array of competitive exclusions between individuals; (3) to use species as biological objects can also lead to pitfalls at the stage of data collection. A fuzzy taxonomic status, an irregular detection probability across scales, and the absence of clear spatial boundaries associated to species distributions may render the conclusions tricky. This last point is one of the reasons why species richness may not constitute an appropriate scale-invariant measure in the field.

A food web is regarded as a succession of organisms that forms path-flows for food energy in an ecosystem. The more structured is the food web, the more efficient is the ecosystem

9. Food webs

Food webs depict interactions between biological objects (usually species) in the form of a graph where vertices

for processing, entrapping, recycling and degrading the solar energy (Odum, 1969 and later works). Ways of quantifying these processes vary considerably but usually rely on the estimation of energy transfer rates among biological objects (Christensen, 1995; Costanza and Mageau, 1999; Jorgensen and Fath, 2004). Proxies for energy transfer rates can take different forms: the net CO₂ exchange and the Bowen ratio (Baldocchi et al., 2001), respiration and evapotranspiration (Quattrochi and Luvall, 1999) or estimates of Normalized Difference Vegetation Index (NDVI; Stöckli and Vidale, 2004) from thermal infrared remote sensing, as well as trophic tracers such as stable isotopes (Cabana and Rasmussen, 1996; Post, 2002).

Thus, an alternative to the species-oriented approach of food webs would be to redefine biological objects in the context of a scale-oriented approach. In the latter, the idea is to examine energy transfer rates among spatio-temporal nodes rather than among species nodes by means of proximate scale-invariant measures such as those stated above. This distinction is not trivial since it clearly focuses on where rather than how the energy flows in an ecosystem; again as an epiphenomenon of setting the consequences (where) before the causes (how). Phenology in particular, which concerns the timing of natural events in space, has benefited from novel metrics for monitoring vegetation dynamics at high resolution, such as freeze–thaw cycles determined from radar scatterometer (Kimball et al., 2004), and NDVI estimates from satellite radiometer (Stöckli and Vidale, 2004). The understanding of food web dynamics in space and time is among research areas in ecology where empirical studies lag behind theoretical works.

10. Concluding remarks on the case studies

The above prototypical case studies incorporate notions of: interaction topology, ecological integration, biological object, spatio-temporal patterns, ecosystem management, and non-equilibrium thermodynamics, initially introduced at the evening session on ecological complexity. To test hypotheses regarding functional ecology one may rely on the emergent phenotype and select scale-invariant measures across a range of individual biomasses. To tackle path-flows of food energy one may use a scale-oriented approach which frees us of the complicated task of constructing species networks. Notice that both solutions permit the elaboration of a multiscale sampling protocol in space and time. It is only by selecting few relevant scale-invariant measures that this colossal task happens to be possible, because the logistical (often financial) trade-off between the number of variables, the sample size and the sampling frequency is deflated. Tools such as remote sensing, digital imagery, telemetry, and bioacoustics' records should enhance our capacity to survey large areas without losing spatio-temporal resolution.

Ecological consequences happen all the time without us fully grasping their causes. Some may consider this a weak scientific position glorifying our ignorance. I do not think so. If the process of modeling ecosystems by constructing an oversimplification of their functioning is easily perceived as ecological engineering (Parrott, 2002), then the CSA applied

to field ecology is a sort of reverse engineering. The scientific literature publishes each week a myriad of new iterated computer models which all attempt to recreate complex ecological patterns from simple deterministic rules. These models are worth all the effort we put into them especially if reliable field data are available for comparison. Therefore, from both sides of engineering processes we might be able to assemble ecosystem theories upon solid foundations.

11. General conclusion

I have discussed the importance of monitoring ecosystems in space and time but provided little information on the methods. Details about the different mathematical approaches available for exploring spatio-temporal series are well beyond the scope of this article (see Dale et al., 2002; Li, 2000, 2002; Rand and Wilson, 1995). Finding robust methods for quantifying spatio-temporal signals in the presence of noise, non-stationarity, and short data series is an active area of research in many disciplines. For ecosystem applications, we would expect these methods to detect pattern transitions (i.e., sequences of stable, periodic, quasi-periodic, chaotic, or random trends) as well as where and when they occur. Different perturbation types may show different spatio-temporal signatures in a given ecosystem and if rapidly detected should complement guidelines for ecosystem management. On theoretical grounds, quantifying spatio-temporal dynamics should provide novel solutions to old and new ecological debates such as the diversity–stability, self-organization and multiple-stable-states hypotheses.

Custom ecological approaches for quantifying spatial and temporal patterns are often risky, mostly because of inadequate choices of taxonomic, spatial and temporal resolution made at the stage of data collection (Blackburn and Gaston, 2002; Gotelli and Colwell, 2001; Jelinski and Wu, 1996; Rahbek, 2005). Consequently, ecosystem studies should clearly specify their spatio-temporal grain and extent, and the levels of taxonomic organization spanned by their sampling protocol. From two principles, general indeterminacy from specific predictability and complex dynamics in space and time, I aimed to show how the CSA modifies our view of functional ecology and food webs. At the end of the introduction was asked: What can the CSA contribute to ecology that macroecology and common garden approaches do not already share? Clearly, it is the notion that ecosystem dynamics should be explicitly monitored through space and time. To accomplish that one needs to study the whole-system behavior from scale-invariant measures obtained across multiple taxonomic, spatial and temporal resolutions.

If ecology is the science of interactions among living things and their environment, then ecosystems are what we get out of these ecological processes, and there is a world of difference between the two. Ecological principles will continue to operate despite gaps in our knowledge of the underlying mechanisms. Field ecologists may learn a great deal from real-time spatio-temporal dynamics.

Emergent variables quantifying the whole-system behavior integrate for us all specific processes in a very elegant and

intricate way into few nontheological ecological orientors. Then, any functional model capable of reproducing patterns we observe in nature, and under a variety of ecological scenarios, will naturally come out as the front-runner.

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