ANNALS OF THE NEW YORK ACADEMY OF SCIENCES Issue: Ecological Complexity and Sustainability

Complexity, collective effects, and modeling of ecosystems: formation, function, and stability

Henrik Jeldtoft Jensen^{1,2} and Elsa Arcaute³

¹Institute for Mathematical Sciences, Imperial College London, 53 Prince's Gate, South Kensington Campus, London, UK ²Department of Mathematics, Imperial College London, South Kensington Campus, London, UK. ³Department of Physics, Imperial College London, South Kensington Campus, London, UK

Address for correspondence: Henrik Jeldtoft Jensen, Department of Mathematics, Imperial College London, South Kensington Campus, London SW7 2AZ, UK. Voice: +44 0 20 759 48541; fax: +44 0 20 7594 85 17. h.jensen@imperial.ac.uk

We discuss the relevance of studying ecology within the framework of Complexity Science from a statistical mechanics approach. Ecology is concerned with understanding how systems level properties emerge out of the multitude of interactions among large numbers of components, leading to ecosystems that possess the prototypical characteristics of complex systems. We argue that statistical mechanics is at present the best methodology available to obtain a quantitative description of complex systems, and that ecology is in urgent need of "integrative" approaches that are quantitative and nonstationary. We describe examples where combining statistical mechanics and ecology has led to improved ecological modeling and, at the same time, broadened the scope of statistical mechanics.

Key words: complexity; statistical mechanics; emergence; evolution; ecology

Introduction

Does the concept of "Complexity" bear any specific meaning or is it just synonymous with complicated and yet not comprehended phenomena? We will argue that it is possible and useful to use the term "Complexity Science" in a specific and reasonably well-defined way. It is useful because a number of common trends and implications become clear when a phenomenon is classified as part of "Complexity Science." The science of complexity emphasises the interactions between components. It stresses that components, most often, are heterogeneous and evolve in time. Complexity is concerned with the emergent properties at systems level originating from the underlying multitude of microscopic interactions.

In an attempt to make our discussion more clear we will immediately describe the way we use some terms central to our exposition. We hurry to stress that these descriptions are not meant to be exhaustive final philosophical definitions, but rather intended to lower the risk of misunderstanding when we deal with terms frequently used to mean different things by different people. And now our specifications.

Complex Systems consist of a large number of interacting components. The interactions give rise to emergent hierarchical structures.

The components of the system and properties at systems level typically change with time. A complex system is inherently open and its boundaries often a matter of convention.

Statistical Mechanics seeks to understand how properties at systems level emerge from the level of the system-components and their interactions. This often involves the application of probability theory, and a number of mathematical techniques. Throughout, we draw a distinction between statistical mechanics and statistical physics. The latter is mainly concerned with the microscopic foundation of thermodynamics and, for example, phenomena such as phase transitions and superconductivity. We consider here statistical mechanics as a mathematical methodology, which can be applied to many different sciences including economics, population biology and sociology, to name a few.

Ann. N.Y. Acad. Sci. 1195 (2010) E19-E26 © 2010 New York Academy of Sciences.

Complexity, collective effects, and modeling of ecosystems

Statistical mechanics is a powerful transdisciplinary methodology for the study of emergent phenomena at a macroscopic level caused by the many interactions taking place at a microscopic level. It provides a framework within which it is possible to encapsulate the myriad of degrees of freedom of a system at a microscopic level, into just a few degrees of freedom at a macroscopic level. In its current form statistical mechanics does not hold all the answers for all the complex systems, however, we argue that it is at present the best methodology available to obtain a quantitative description of complex systems. By systematically applying it to fields outside its traditional range of application in physics, statistical mechanics can be developed further, in addition to simultaneously contributing to the understanding of those fields, such as ecology. The importance of this feedback loop cannot be overestimated. It can also provide a starting point for the possible development of new mathematical techniques.

Along these lines, the research programme in search for the "laws" of ecosystems described by Jørgensen and collaborators,¹ looks into finding a rigorous set of laws that govern the dynamics at the macrolevel. This is a first attempt into establishing a methodology for ecological complexity. At the moment the analysis is mainly qualitative, and we suggest that the second step towards that goal would be the implementation of techniques from statistical mechanics, in order to obtain a rigorous mathematical formalism and modeling.

The paper is organized as follows. In the next section, we will for concreteness illustrate our arguments by briefly describing a complexity inspired model of evolutionary ecology called the Tangled Nature model. This will allow us to demonstrate how macroevolution can be modeled as emerging from the interacting microevolution, which consists of individual organisms influencing each other and undergoing reproduction which is prone to mutation. We will discuss feedback, emergence, network structures, and the intermittent temporal mode of macroevolution in contrast to the steady smooth pace of dynamics at the level of individuals. We will also briefly touch on the modeling of ecological observables, such as the Species Abundance Distribution (SAD), Species Area Laws, and the relationship between interaction and diversity.

In the Discussion Section, we will mention two examples of research presented at the Symposium on Complexity, Collective Effects and Modelling of Ecosystems: formation, function and stability at the Beijing Eco Summit 2007. These examples illustrate how a complexity science viewpoint may shape the approach of ecological research projects. The first example is John Crawford's contribution on "The Self-organization of life in Earth." This work looks at the soil-microbe system, and at the development of models on evolutionary ecology, that can be applied to this dynamical system. The second example is Cédric Gaucherel's work on "Theoretical analysis of dynamic patchy landscapes," which looks at landscape models constructed within the framework of statistical mechanics.

Tangled Nature model

Description of model

The Tangled Nature model is defined at the level of interacting individuals. It is an attempt to identify possible simple mechanisms behind the myriad of complicated interactions, feedback loops, contingencies, etc., as one moves from the short time reproductive dynamics at the level of individuals, to the long time systems level behavior. The strategy is to keep the model sufficiently simple to enable analysis, and to pinpoint the details or assumptions in the model that are responsible for the specific behavior at the systems level. One major concern of the model has been to understand how the smooth continuous pace of the reproductive dynamics at the level of individuals, can lead to intermittent or punctuated dynamics at the level of high taxonomic structures. To be able to address such issues, the model considers individuals as represented by a single sequence with individual number α , denoted by $\mathbf{S}^{\alpha} = (S_1^{\alpha}, S_2^{\alpha}, ..., S_L^{\alpha})$ belonging to a sequence space S, where all $S_i^{\alpha} \pm 1$. These sequences undergo simple reproduction during which a given sequence duplicates itself, and while this happens, components of the sequence may mutate, represented by the offspring having a different sign from the mother, that is, $S_i^{\gamma} = -S_i^{\alpha}$, where γ denotes the index for the daughter, and α the one for the mother. The aim of the model is to understand the macrodynamics emerging at the systems level. This is done by analyzing the dynamics of the occupancy in this sequence or type space. Taxonomic structures, such

Jensen & Arcaute

as species formation, emerge as aggregations in the density of occupied sites $n(\mathbf{S}, t)$ in the type space. This is very much in accordance with Mallet's definition of species.² A species will be identified as a local peak in the density $n(\mathbf{S}, t)$ and species formation will correspond, for example, to the splitting of such a peak into two peaks. Macroscopic ecological measures such as SADs are derived from the structure of $n(\mathbf{S}, t)$.

Let us now sketch the mathematical details of the model. For in depth studies of the model, please refer to references 3–6. The size of the type space is set by the length, L, of the sequences; a typical value used is L = 20 leading to about one million different genotypes. The sites in the genome space are supposed to represent all possible ways of constructing a "genome." Many sequences may not correspond to viable organisms. The viability of a genotype is determined by the evolutionary dynamics. All possible sequences are available for evolution to select from. We will see that a natural species concept arises from the dynamics, in which each species is separated in genotype space.

The system consists of N(t) individuals, and a time step consists of one annihilation attempt followed by one reproduction attempt. A reproduction event is successful with varying probability p_{off} , defined later, and an annihilation attempt is successful with constant probability p_{kill} . The killing probability is considered a constant independent of type for simplicity. It would obviously be more realistic to let p_{kill} depend on the type of the individual considered. However, this does not change the overall behavior at systems level. One generation consists of $N(t)/p_{kill}$ time steps, which is the time taken (on average) to kill all currently living individuals. The dynamics leads to a population size, which remains nearly constant on short timescales. The individuality of the specific types, or sequences, is given by their ability to reproduce. Because we are interested in the collective, or complexity, aspects of evolution, the Tangled Nature model stresses the mutual influence among different types of organisms. This is done by assuming that each individual of type S is able to reproduce, when selected for reproduction, with a probability $p_{off}(\mathbf{S}, t)$ that depends on the sequence S and the configuration of other types in the type space. The reproduction probability, p_{off} , is determined by a weight function $H(\mathbf{S}^{\alpha}, t)$:

Complexity, collective effects, and modeling of ecosystems

$$H(\mathbf{S}^{\alpha}, t) = \frac{k}{N(t)} \left(\sum_{\mathbf{S} \in S} J(\mathbf{S}^{\alpha}, \mathbf{S}) n(\mathbf{S}, t) \right) - \mu N(t),$$
(1)

where k controls the strength of the interaction (large k means a large interaction), N(t) is the total number of individuals at time t, the sum is over the 2^L locations in **S** and $n(\mathbf{S}, t)$ is the number of individuals (or occupancy) at position **S**. Two positions \mathbf{S}_a and \mathbf{S}_b in genome space are coupled with fixed but random strength $J(\mathbf{S}_a, \mathbf{S}_b)$ which can be either positive, negative, or zero. This link exists (in both directions) with probability θ , that is, θ is simply the probability that any two sites are interacting. If the link exists, then $J(\mathbf{S}_a, \mathbf{S}_b)$ and $J(\mathbf{S}_b, \mathbf{S}_a)$ are both generated randomly and independently, and such that they belong to (-1, 1). To study the effects of interactions *between* species, we exclude self-interaction so that $J(\mathbf{S}_a, \mathbf{S}_a) = 0$.

The conditions of the physical environment are simplistically described by the term $\mu N(t)$ in Eq. (1), where μ determines the average sustainable total population size, that is, the carrying capacity of the environment. This is an example of how the question of the openness and "surroundings" of ecosystems arises in a natural way in the present statistical mechanics like formalism. An increase in µ corresponds to harsher physical conditions. We use asexual reproduction consisting of one individual being replaced by two copies mimicking the process of binary fission seen in bacteria. We allow for mutations in the following way: with probability p_{mut} per gene we perform a change of sign $S_i^{\alpha} \rightarrow -S_i^{\alpha}$ during reproduction. Successful reproduction occurs with a probability per unit time, $p_{off}(\mathbf{S}^{\alpha}, t) \in [0, 1)$, given by

$$p_{off}(\mathbf{S}^{\alpha}, t) = \frac{\exp[H(\mathbf{S}^{\alpha}, t)]}{1 + \exp[H(\mathbf{S}^{\alpha}, t)]}.$$
 (2)

This function is chosen for convenience, since the specific functional form has no effect on the dynamics of the model—any smoothly increasing function that maps $H(\mathbf{S}^{\alpha}, t)$ to the interval (0,1) will do. Let us mention that this basic quantity is deliberately taken by the Tangled Nature model to be a context dependent reproduction probability rather than a fitness function. One reason why this is done is to try to avoid some of the dangers and subtleties inherent to the fitness concept.⁷

Eq. (1) can be understood as the interaction of an individual with all the others, with a term $\mu N(t)$ which determines the total population and controls fluctuations. The interaction strength k gives the magnitude of the total interaction. We can tune the effective 'resource' density (and hence the population density) with the parameter μ . The total population remains approximately constant over ecological timescales (and actually increases over evolutionary timescales). Setting self-interaction to zero is equivalent to considering that all types interact equally with their own species (one can rescale p_{kill} and μ to accommodate this). This constraint is imposed in order to focus on the effect of interactions between different types. To study the relation between diversity and the strength of the interactions, there is a version of the model in which different strengths of intraspecific interactions are included.8 Obviously it is impossible to design the details of the interaction matrix $J(\mathbf{S}_a, \mathbf{S}_a)$ in a realistic way. What can be accomplished is to study qualitative questions, such as what is the effect of having very few interaction links between sequences compared with many interaction links.⁴ Or one can address the effect of correlations in the allowed interactions?9

After a short transient period the initial state becomes irrelevant. There are two very different initial conditions that consist in placing the entire population at time zero in: (i) one position in type space, or (ii) on random positions, that is, a random collection of initial types. Because both configurations are badly adapted to the interaction matrix $J(S_a, S_a)$, in both cases the population will typically collapse to one single position in type space. Eventually the population size will have decreased enough to make the $-\mu N(t)$ term sufficiently small to allow p_{off} to grow to a value that ensures a nonvanishing reproduction rate. When this happens the population will, due to mutations, start to spread out from its initial position into the surrounding genotype space. And as this happens, natural selection will ensure that only certain configurations of occupied sites are viable. These are configurations for which the mutual interactions between the types lead to offspring probabilities that, for a significant part of the occupied types, are able to balance the killing probabilities, that is, $p_{off}(\mathbf{S}, t) = p_{kill}$ for some set of types S.

The dynamics in type space is characterized by a two-phase switching, consisting of long periods of relatively stable configurations (quasi-Evolutionary Stable Strategies or q-ESSs) (Fig. 1) interrupted by brief spells of reorganization of occupancy called transitions. Transition periods are terminated when a new q-ESS is found, as discussed in reference 3. The intermittent macrodynamics is not in a stationary state. When one considers very many realizations of the dynamics it turns out that the transition rate between q-ESS decreases with the age of the system.⁶ This happens because selection is able to pick out configurations in type space that tend to possess more beneficial links (i.e., positive $J(\mathbf{S}_a, \mathbf{S}_a)$ bonds), than is the case between a randomly selected set

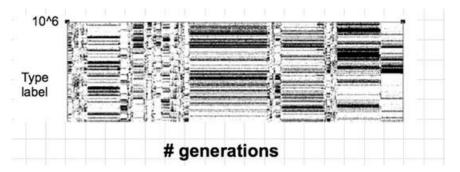


Figure 1. Intermittent evolution of the occupancy in type space. Time, measured in generations, is along the *x*-axis. The $\sim 10^6$ different types are labeled up along the *y*-axis. Whenever a type is occupied a dot is placed at its label. Long stretches of parallel lines indicate epochs during which the main composition in type space remains essentially the same. Figure courtesy of Matt Hall.

Jensen & Arcaute

of types. We consider this directedness of the long time systems level dynamics to be prototypical of complex systems.¹⁰

Emergent ecological measures

As we move from the level of individuals to the systems level, "species" can be well-defined as the highly occupied genotype points called "wildtypes," which are separated in genotype space. Each wildtype is surrounded by a "cloud" of mutant genotypes with low occupancy. Thus, we can take a natural definition of diversity: the number of wildtypes in the system. It is interesting to study how the SAD depends on the assumed properties of the interaction matrix $J(\mathbf{S}_a, \mathbf{S}_a)$. It was found by reference (4) that the often observed log-normal shape of the SAD is reproduced by the evolutionary dynamics of the Tangled Nature model under certain conditions. Namely, when each type is potentially able to interact with a large number of other types. In this case, the adapted configurations consist of populations of species that form one large interconnected cluster, and the SAD evolves with time towards a lognormal like form. If $J(\mathbf{S}_a, \mathbf{S}_a)$ only allows a type to interact with few other types (i.e., few nonzero elements in the *I* matrix), the population in the type space splits up into separate groups, and the SAD does not develop a form resembling a log-normal distribution.

Considered from this perspective, the SAD might be thought of as containing information about the properties of the network of all possible interactions between organisms.

Let us focus on the properties of the network of interactions^{*a*} of extant species. The evolutionary dynamics performs a collective adaptation on the coexisting types in type space. As selection and adaptation act generation after generation, a subset of sites in type space becomes occupied. This subset is selected such that the mutual interactions allow each of the extant species to counter balance the depletion of its population, caused by death (p_{kill}) and mutations (p_{mut}), by a suffciently large offspring production ($p_{off}(\mathbf{S}, t)$). Complexity, collective effects, and modeling of ecosystems

The network of interactions between these coexisting types possesses some interesting emergent properties. The typical coupling strength between extant types is more mutualistic than the coupling between arbitrary types S_a and S_b , chosen at random in type space irrespectively of the types being extant or not.^{4,9} This effect is significantly bigger when the coupling matrix $J(\mathbf{S}_a, \mathbf{S}_b)$ is correlated for sites \mathbf{S}_a and \mathbf{S}_b that reside in the same vicinity of type space. A correlated coupling matrix is more realistic because it corresponds to assuming that similar organisms have a certain similarity in the way they interact with the surrounding ecosystem. The degree distribution of the network of extant species is sensitive to the amount of correlations imposed on type space. When correlations are present, we typically observe exponential degree distributions of the network of interactions between extant types. In contrast, uncorrelated interaction matrices lead to binomial degree distributions, as it is observed in networks where edges are placed at random. This example indicates how some properties at systems level may be caused by generic mechanisms for emergent collective behavior.

A similar situation is encountered when the qualitative behavior of spatial properties is investigated. Spatial aspects are obviously of the greatest ecological importance. A simple quantity to start out with is the Species Area Relation (SAR). By placing a copy of the Tangled Nature model on each site of a two dimensional lattice, one can make a simplistic model combining evolutionary dynamics with spatial dispersion. Such a model was studied in¹¹ and a power-law SAR is observed. The evolutionary dynamics produces a high degree of spatial diversity even when the same type space is placed on each site of the spatial lattice.

Complexity science stresses that the interaction between the components is responsible for the emergent properties at systems level. Sometimes for tractability reasons, models might oversimplify the components compared with reality, and still it happens that such simple models are able to capture certain qualitative aspects. An attempt in this direction was made in,⁸ where the relationship between interactions among different types and the diversity of types was discussed. The inspiration behind this study came from molecular evolution experiments on E. coli, in which the relation between fitness plasticity and diversification was addressed.¹² The

^{*a*} The nodes of the network under consideration consist of occupied positions in type space. There is an edge between two nodes S_a and S_b if the two types interact, i.e. if $J(S_a, S_b)$ or $J(S_b, S_a)$ is non-zero.

model used a version of the Tangled Nature model in which each type was assigned an amount of selfinteraction. This was achieved by supplementing the weight function in Eq. (1) by an extra term proportional to an intrinsic fitness $E(\mathbf{S}^{\alpha}, t)$. It was found that diversity rapidly increased when the typical interaction strength, set by the parameter k in Eq. (1), exceeded a certain value, determined by the properties of the intrinsic fitness.

Discussion

We have proposed that complexity science can be seen as a coordinated attempt to understand how emergent collective behavior at systems level arises due to the multitude of interactions between the components. From this perspective we have argued that complexity science offers a particularly relevant approach to ecology. Above we tried to illustrate our point of view with some theoretical examples taken from the Tangled Nature model's study of evolutionary ecology. Let us now conclude with a couple of examples that are closely related to observations, where we believe that the complexity science's perspective has made a difference.

Our first example is the soil-microbe system. In the study of such systems, there is an urgent need to develop models on evolutionary ecology that integrate function and diversity, and that are dynamical,¹³ since at present many of the current models for soil are static. The soil-microbe system is an extremely rich and intricate system that has not yet been fully understood, and moreover is of great relevance to agriculture, waste management and the water industry to mention a few.¹⁴ Crawford and collaborators believe that any model describing the system should integrate biochemistry and biophysics, since from the interactions between the biotic and abiotic factors, the structure, the functionality and the dynamical behavior of the soil emerge.

The soil-microbe complex is a self-organized system capable to adapt, therefore, within the many different approaches that currently exist,¹³ they suggest the development of models of evolutionary ecology that have the same aspects as those described by the Tangled Nature model: evolutionary processes, population dynamics, feedback loops, interactions, etc. In addition, the ecosystem functioning needs to be included, since it is the relation between diversity and function that is mostly ignored in other soil models. Experimental techniques to measure this connection need therefore to be developed. They argue that the ecosystem-level behavior of the soil microbe system is the outcome of the behavior at the organism's level, which is natural if the system is classified as a complex system. In addition, this viewpoint stresses the importance to include evolutionary processes when looking at ecology, since these are crucial for the understanding of ecological function. For example, in the soil-microbe system, the activity of the microbes changes the structure of the soil by affecting its rates of oxygen diffusion and porosity, while the substrates in the soil affect the activity of the microbes.

Crawford and collaborators have identified important properties of soil systems by applying statistical mechanics to their research,¹⁵ however, they also recognize the need of an extended methodology, where interdisciplinarity is crucial. They emphasize that there is no unique discipline that is able by itself to understand the soil.¹⁴

Our second example is the modeling of landscapes. Models explaining and being able to predict the shape of landscapes are extremely important to prove ecological hypotheses, and for the implementation and development of market and land planning policies. Gaucherel *et al.*¹⁶ argue that in many systems, the most relevant factors causing the dynamical changes of landscapes are human driven. For this reason they urge for the development of models that integrate biophysical and socio-economical factors.

They propose a generic modeling platform: "L1," that can be used to look at the patterns resulting from specific processes. This can therefore be applied as a tool to assess environmental policies and technological implementations at different landscape scales. The platform simulates the dynamical evolution of a landscape as a result of the feedbacks and interactions between the elements composing the landscape. Following the methodology of statistical mechanics, the objects are modeled by introducing only the relevant aspects that give rise to such emergent structures, and not by parametrising all of their degrees of freedom.

In their approach, Gaucherel *et al.* stress the crucial role of feedback and scales in ecological systems. On the one hand, the landscape is an emergent structure, product of the interactions between the many different components, see for example the role of

Jensen & Arcaute

farm systems in human driven landscapes.¹⁶ On the other, their models give rise to hierarchical structures that feed back into the system. For example, the landscape itself determines important aspects of habitats and ecosystems at different scales. This is illustrated in,¹⁷ where the authors look at the relationship between the characteristics of the habitat given by the landscape, and particular characteristics of the inhabitant species, such as their spatial distribution, their morphology, etc. Using their framework, one can investigate at different locations, times and scales, the ecological relationships. They apply their model to look at the link between agricultural activities, landscape shape, and some characteristics of carabid beetles, such as their abundance and their body size. They proved that some correlations are only valid for certain specific locations and scales, contrary to what was believed using other techniques unable to give spatial and scaling precision.

An explicit outline of how the methodology from statistical mechanics is implemented in this approach to landscape modeling can be found in.¹⁸ There the authors construct a neutral model for patchy landscapes using the Gibbs process to describe the interactions between the different components of the landscape. A neutral model is a model that simulates the landscape properties and patterns that are not the outcome of a particular ecological process. Therefore, using these models a distinction can be drawn between structures caused by random processes and those obtained through real processes. In addition, such models give rise to virtual landscapes that can be used to study real mosaics, such as forest landscapes.¹⁸ For this or other specific applications, the neutral model is implemented in the L1 platform mentioned above, where the particularities of the system can be entered.

The project to establish a systems perspective on ecology as laid out in the book *A New Ecology* by Jørgensen and collaborators in¹ can, in our opinion, be seen as a prototypical example of the objectives aimed at when taking inspiration from the methodology of statistical mechanics and applying it to complex systems. Jørgensen *et al.* argue that laws at the emergent systems level may exist and the authors suggest a list of laws they believe ecosystems obey. They make clear that it is a grand task to identify these laws and that their list is to be thought of as a starting point. If we embed these laws within the statistical mechanics framework, they describe the expected properties of a complex system. For example, Jøgensen *et al.* mention that ecosystems have openness, connectivity, complex dynamics, and that their dynamics is directed. These properties are totally in agreement with the features of complex systems highlighted by applying methods from statistical mechanics to their analysis.

In addition, within the Tangled Nature model, interconnectedness and interaction become a focal point of the description when one thinks in terms of the emergent networks of interactions between extant species. Furthermore, within the mathematical formulation of dynamical systems, there is a term encoding the carrying capacity and resources, which represents an open system. Ecosystems are therefore correctly taken into account as open within this formalism. The Tangled Nature model was formulated by including what appears to be minimal assumptions for the dynamics; namely reproduction prone to mutations and livelihoods of the individual types that are influenced by other coexisting types. As a result the model produces a slowly adapting nonstationary directed dynamics at the macroscopic systems level. This is certainly in agreement with properties of ecosystems encoded in the form of a law by Jørgensen et al. and, moreover, it appears to be in agreement with records of macroevolution.¹⁹ The nonstationary directional nature of the Tangled Nature model has been suggested to be an example of generic properties of complex systems dynamics as observed in a number of very diverse phenomena by Anderson et al.¹⁰ Here, it was suggested that the directional gradual relaxation can be viewed as a release of a generalized strain originating in starting from a badly adjusted initial configuration. The Tangled Nature model suggests that in the case of ecosystems, selection and adaptation manage to direct the dynamics towards a selections of species better adjusted to coexist.

In conclusion, it is useful to identify systems under the label "Complex Systems," since this indicates that the machinery of statistical mechanics can be applied to try to describe the system's dynamics and evolution. In ecology, there is an urgent need for "integrative" approaches that are nonstationary, and statistical mechanics can provide an initial mathematical framework, subject to modification and adaptation as one navigates deeper into the mysteries of complex systems. Complexity, collective effects, and modeling of ecosystems

Acknowledgments

We wish to thank the participants in the Symposium on *Complexity, Collective Effects, and Modelling of Ecosystems* for interesting discussions at the Beijing Eco Summit 2007. HJJ is grateful to P. Anderson, K. Christensen, S. A. di Collobiano, M. Hall, S. Laird, and D. Lawson for stimulating collaboration. Work on the Tangled Nature model has received funding from the EPSRC both through studentships and projects.

Conflicts of interest

The authors declare no conflicts of interest.

References

- 1. Jørgensen, S.E. *et al.* 2007. A New Ecology. *Systems Perspective*. Elsevier.
- Mallet, J. 1995. A species definition for the Modern Synthesis. *Trends Ecol. Evol.* 10: 294–299.
- Christensen, K., S.A. di Collobiano, M. Hall & H.J. Jensen. 2002. Tangled nature: a model of evolutionary ecology. J. Theor. Biol. 216: 73–84.
- Anderson, P. & H.J. Jensen. 2005. Network properties, species abundance and evolution in a model of evolutionary ecology. *J. Theor. Biol.* 232: 551–558.
- di Collobiano, S.A., K. Christensen & H.J. Jensen. 2003. The tangled nature model as an evolving quasi-species model. J. Phys. A 36: 883–891.
- Hall, M., K. Christensen, S.A. di Collobiano & H.J. Jensen. 2002. Time-dependent extinction rate and species abundance in a tangled-nature model of biological evolution. *Phys. Rev. E* 66: 011904-1–011904-10.
- Ariew, A. & R.C. Lewontin. 2004. The confusion of fitness. Br. J. Phil. Sci. 55: 347–363.
- 8. Lawson, D.J., H.J. Jensen & K. Kaneko. 2006. Diversity as

a product of interspecial interactions. *J. Theor. Biol.* **243**: 299–307.

- Laird, S. & H.J. Jensen. 2006. The tangled nature model with inheritance and constraint: evolutionary ecology restricted by a conserved resource. *Ecol. Complexity* 3: 253–262.
- Anderson, P.E., H.J. Jensen, L.P. Oliveria & P. Sibani. 2004. Complexity 10: 49–56.
- Lawson, D.J. & H.J. Jensen. 2006. The species area relationship and evolution. J. Theor. Biol. 241: 590–600.
- Kashiwagi, A., W. Noumachi, M. Katsuno, *et al.* 2001. Plasticity of fitness and diversification process during an experimental molecular evolution. *J. Mol. Evol.* 52: 502–509.
- Crawford, J.W., J.A. Harris, K. Ritz & I.M. Young. 2005. Towards an evolutionary ecology of life in soil. *Trends Ecol. Evol.* 20: 81–87.
- Young, I.M. & J.W. Crawford. 2004. Interactions and selforganization in the soil-microbe complex. *Science* 304: 1634–1637.
- Zhang, X.X., S.N. Johnson, P.J. Gregory, *et al.* 2006. Modelling the movement and survival of the root-feeding clover weevil, sitona lepidus, in the root-zone of white clover. *Ecol. Model.* **190:** 133–146.
- Gaucherel, C., N. Giboire, V. Viaud, *et al.* 2006. A domain-specific language for patchy landscape modelling: the brittany agricultural mosaic as a case study. *Ecol. Model.* 194: 233–243.
- Gaucherel, C., F. Burel & J. Baudry. 2007. Multiscale and surface pattern analysis of the effect of landscape pattern on carabid beetles distribution. *Ecol. Indicators* 7: 598– 609.
- Gaucherel, C., D. Fleury, D. Auclair & P. Dreyfus. 2006. Neutral models for patchy landscapes. *Ecol. Model.* 197: 159–170.
- Newman, M.E.J. & P. Sibani. 1999. Extinction, diversity and survivorship of taxa in the fossil record. *Proc. R. Soc. Lond. B* 266: 1–7.

Jensen & Arcaute