



The evolution of ecosystem ascendancy in a complex systems based model



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ABSTRACT

General patterns in ecosystem development can shed light on driving forces behind ecosystem formation and recovery and have been of long interest. In recent years, the need for integrative and process oriented approaches to capture ecosystem growth, development and organisation, as well as the scope of information theory as a descriptive tool has been addressed from various sides. However data collection of ecological network flows is difficult and tedious and comprehensive models are lacking. We use a hierarchical version of the Tangled Nature Model of evolutionary ecology to study the relationship between structure, flow and organisation in model ecosystems, their development over evolutionary time scales and their relation to ecosystem stability. Our findings support the validity of ecosystem *ascendancy* as a meaningful measure of ecosystem organisation, which increases over evolutionary time scales and significantly drops during periods of disturbance. The results suggest a general trend towards both higher integrity and increased stability driven by functional and structural ecosystem coadaptation.

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1. Introduction

Ecosystems are holistically dynamic. Growth and development take place on a range of different scales, ranging from biogeochemical processes to macroecological and evolutionary dynamics. Integrity and health of ecosystems and their relationship to stability and resilience are crucial properties to be understood in the face of today's rates of loss of biodiversity. Extinction and invasion put ecosystems under stress, making the understanding of stability and resilience of ecosystem functionality we rely on even more critical (McCann, 2000). Ecosystem health is usually regarded as three dimensional, including aspects of vigor, organisation and resilience (Costanza, 1992), whereas ecosystem integrity is meant to focus on a longer-term and more comprehensive perspective (Ulanowicz, 1995).

Seeking universal characteristic properties of ecosystem integrity, which may be optimised over time, and measure the complexity, well-being and functionality of an ecological network has been a long-standing goal in ecology. While ecological complexity is often measured in terms of solely structural properties of the trophic topology (see eg. Dunne, 2009), ecological integrity and ecosystem functioning actually depends on the interplay between all species and how they act together. Any measure of ecological

organisation or integrity has thus to account for both structural and functional aspects of the ecological network and integrate the structural constraints with their effect on the functional behaviour of the system.

Ulanowicz (1986) proposes *ascendancy*, a phenomenological measure of ecosystem growth and development, which integrates structural and functional aspects of the network topology and the matter transfer between the species based on information theoretic measures. He hypothesises a trend towards a balance between increased ascendancy and scope for further adaptation for higher developed ecosystems (Ulanowicz, 2014), and reveals parallels to Odum's (1969) characteristics of ecosystem succession. As matter and energy flows are difficult to measure in nature and comprehensive highly resolved data is scarce, a complex systems model of ecosystem evolution (the Tangled Nature Model, Christensen et al., 2002) is used to study the long-term behaviour of ecosystem ascendancy over evolutionary time scales. The complex systems perspective on ecological networks of the Tangled Nature Model bridges the gap between reductionist and holistic approaches, as it incorporates the aim to explain the emergence of the macroscopic properties from the relationship between the microscopic parts (may those be individual organisms or even the biochemical reactions within) and thereby can not only unify different scientific approaches to ecology but also help to understand the interplay between bottom-up and top-down controlling forces in ecosystems. Despite its simplicity and independence of specific parametrisations, the encountered macroecological properties such as the

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species area relationship and the species abundance distribution compare qualitatively well with observations. The generic nature of the Tangled Nature Model and its reliance on very few parameters makes it a useful tool to study general properties of ecosystem evolution and the development of structure and function of ecological networks. (Anderson et al., 2004; Christensen et al., 2002; Hall et al., 2002; Jensen, 2004; Laird et al., 2008; Rikvold, 2007; Rikvold and Sevim, 2007; Rikvold and Zia, 2003) Furthermore, the model emphasises the crucial relevance of species interactions for individual fitnesses as well as community dynamics. Interaction strengths are not, as commonly done, derived and estimated from trophic interactions, but encapsulate all direct and indirect effects, which in reality are almost impossible to measure, and which give rise to the ecological networks in the living world.

2. Methods

2.1. The Tangled Nature Model (TaNa) of evolutionary ecology

The Tangled Nature Model of evolutionary ecology is an individual based stochastic model, in which ecological communities are emergent structures arising from the interactions between individual organisms. The following description of the model follows Christensen et al. (2002) and Laird et al. (2008).

An individual is represented by a vector $S^\alpha = (S_1^\alpha, S_2^\alpha, \dots, S_L^\alpha)$ in the genotype space \mathcal{S} , where the L different “genes” can take the values ± 1 . The genotype space \mathcal{S} hence represents an L -dimensional hypercube and encompasses all possible ways of combining the genes into a genotype sequence. There is no differentiation between genotype and phenotype. The viability of a genotype is determined by the currently perceived environment of a genotype, hence individual fitness is a function of the interactions with all other present genotypes.

The system consists of $n(S^\alpha, t)$ individuals of genotype S^α and $N(t)$ individuals in total. In each time step, one individual is randomly chosen to be annihilated with probability p_{kill} and one other individual is randomly chosen to reproduce with probability p_{off} . While p_{kill} is constant across genotypes and over time, p_{off} is time- and species-dependent and controlled by the weight function¹

$$\Xi(S^\alpha, t) = \frac{c}{N(t)} \sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t) - \mu N(t) \quad (1)$$

where c controls the density-independent magnitude of the interaction strengths and μ represents the quality of the physical environment and determines the average sustainable population size. J is a matrix of dimension $(2^L \times 2^L)$ and stores the interaction effects for each pair of genotypes. An interaction link $J(S^\alpha, S^\beta)$ exists with probability θ_{int} . Self interaction is zero ($J(S^\alpha, S^\alpha) = 0$), which corresponds to equal intraspecific competition across species. The non-zero entries of J are for numerical convenience the product of two uniformly distributed random numbers between -1 and 1 and independent for all $J(S^\alpha, S^\beta)$ (and $J(S^\beta, S^\alpha)$). $\Xi(S^\alpha, t)$ can be understood as the average interaction effect of all individuals S in the genotype space \mathcal{S} on genotype S^α .

Successful asexual reproduction occurs with probability

$$p_{off}(S^\alpha, t) = \frac{\exp(\Xi(S^\alpha, t))}{1 + \exp(\Xi(S^\alpha, t))} \in (0, 1) \quad (2)$$

and results in two copies of the parent genotype, which undergo mutations with probability p_{mut} acting independently on each gene, switching its sign $S_i^\alpha \rightarrow -S_i^\alpha$.

An initial population of size N_{init} is randomly distributed over the genotype space; the initial configuration does not qualitatively influence the long-term dynamics. A generation consists of

$N(t)/p_{kill}$ time steps, which corresponds to the average time taken to kill all living individuals.

Evolutionary dynamics acting on the individual genotypes give rise to species, forming long-term persisting quasi-stable mutually interacting communities (quasi-Evolutionary Stable Strategies or qESS), interrupted by brief periods of hectic reorganisation and transition to a new qESS

2.2. A hierarchical version of the TaNa

In the Tangled Nature Model, reproductive success is determined by the fitness of an individual, which is a function of its interaction with the environment. Fitness in a given environment is hereby however not an arbitrary suitability, but shaped entirely by the species present in the system, emphasising the importance of biotic over abiotic interactions. The interactions however do solely influence the probability of reproduction of an individual and do not necessarily imply any direct interactions that include the transfer of matter or energy between compartments. To study the relation between flow and structure in ecological networks which are shaped by an interacting environment, the Tangled Nature Model is extended in a way that hierarchical systems with energy transfer emerge. This approach allows for studying quantified food webs based on the TaNa. Different interpretations of the networks arising in the TaNa have been studied by Rikvold (2007) and Rikvold and Sevim (2007).

Starting from the classical Tangled Nature Model, species are additionally classified as primary producers with probability θ_{pp} . Predator-prey relationships are arbitrarily predefined just like the indirect interactions, where each consumer (hence a species which is not classified as a primary producer) is assigned a list of potential prey species, each of which is included with probability θ_{feed} . Indirect interaction strengths as denoted in J and predator-prey interactions are thereby independent of each other, which is in agreement with the findings of no correlation between interaction strengths effects on community stability and the respective link flow along a certain link (de Ruiter et al., 1995). The weight function which determines offspring probability is defined as

$$\Xi_{PP}(S^\alpha, t) = \frac{c}{N(t)} \sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t) - \mu N_P(t) \quad (3)$$

$$\Xi_C(S^\alpha, t) = \frac{c}{N(t)} \sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t) - \frac{\mu_C}{N_{prey}^\alpha(t)} n(S^\alpha, t) \quad (4)$$

for primary producers and consumers respectively (compare Eq. (1)). Here, $N_P(t)$ denotes the current number of primary producers, N_{prey}^α the number of prey individuals of consumer α and μ_C scales the carrying capacity of consumers relative to their prey abundance.

The dynamics occur exactly the same way as in the original Tangled Nature Model, with the extension that whenever a consumer reproduces, it depletes one randomly chosen individual from its pool of prey. If the consumer fed on a primary producer S^α , the primary producer immediately gets the chance to regrow with probability $p_{off}(S^\alpha, t)$. Thereby the population of primary producers still undergoes fluctuations (due to stochastic reproduction both during the reproduction phase and after consumption by a predator), but it regrows faster after a predation event than non-primary producing prey. This accounts for the effects of grazing, where the primary producer can regrow quickly and without reproduction, opposed to true predation, which generally leads to death of the prey.

Energy flow in the evolving species network is measured by counting the number of predation events between each pair of species during each generation. One predation event corresponds to one unit of biomass exchange between the respective species.

¹ Corresponds to H in previous publications on the TaNa.

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