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Katharina Brinck, Henrik Jeldtoft Jensen

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Highlights

- The coadapted emerging ecosystems of the Tangled Nature Model of evolutionary ecology exhibit macroecological properties of real world ecosystems such as degree distributions, trophic levels and connectivity.
- Ecosystem ascendancy, a measure of ecosystem organisation, increases over evolutionary time scales in the model.
- Ecosystem ascendancy is significantly lowered during unstable/disrupted periods.
- The degree of organisation of the model ecosystems matches empirical findings quantitatively.

The evolution of ecosystem ascendancy in a complex systems based model

Katharina Brinck¹, Henrik Jeldtoft Jensen

*Imperial College London, Department of Mathematics, Centre for Complexity Science,
London SW7 2AZ*

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.

¹Corresponding author: k.brinck14@imperial.ac.uk

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Ascendency, Ecosystem Organisation, Evolution, Ecological Networks,
Development, Modelling

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

22 effect on the functional behaviour of the system.

23 Ulanowicz (1986) proposes *ascendency*, a phenomenological measure of
24 ecosystem growth and development, which integrates structural and func-
25 tional aspects of the network topology and the matter transfer between the
26 species based on information theoretic measures. He hypothesises a trend
27 towards a balance between increased ascendency and scope for further adap-
28 tation for higher developed ecosystems (Ulanowicz, 2014), and reveals paral-
29 lels to Odum (1969) characteristics of ecosystem succession. As matter and
30 energy flows are difficult to measure in nature and comprehensive highly re-
31 solved data is scarce, a complex systems model of ecosystem evolution (the
32 Tangled Nature Model, Christensen et al., 2002) is used to study the long-
33 term behaviour of ecosystem ascendency over evolutionary time scales. The
34 complex systems perspective on ecological networks of the Tangled Nature
35 Model bridges the gap between reductionist and holistic approaches, as it
36 incorporates the aim to explain the emergence of the macroscopic properties
37 from the relationship between the microscopic parts (may those be individ-
38 ual organisms or even the biochemical reactions within) and thereby can not
39 only unify different scientific approaches to ecology but also help to under-
40 stand the interplay between bottom-up and top-down controlling forces in
41 ecosystems. Despite its simplicity and independence of specific parametri-
42 sations, the encountered macroecological properties such as the species area
43 relationship and the species abundance distribution compare qualitatively
44 well with observations. The generic nature of the Tangled Nature Model
45 and its reliance on very few parameters makes it a useful tool to study gen-
46 eral properties of ecosystem evolution and the development of structure and

function of ecological networks. (Christensen et al., 2002; Hall et al., 2002; Jensen, 2004; Laird et al., 2008; Rikvold, 2007; Rikvold and Sevim, 2007; Rikvold and Zia, 2003; Anderson et al., 2004) 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.

70 The system consists of $n(S^\alpha, t)$ individuals of genotype S^α and $N(t)$ indi-
 71 viduals in total. In each time step, one individual is randomly chosen to be
 72 annihilated with probability p_{kill} and one other individual is randomly chosen
 73 to reproduce with probability p_{off} . While p_{kill} is constant across genotypes
 74 and over time, p_{off} is time- and species-dependent and controlled by the
 75 weight function²

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

76 where c controls the density-independent magnitude of the interaction
 77 strengths and μ represents the quality of the physical environment and de-
 78 termines the average sustainable population size. J is a matrix of dimension
 79 $(2^L \times 2^L)$ and stores the interaction effects for each pair of genotypes. An
 80 interaction link $J(S^\alpha, S^\beta)$ exists with probability θ_{int} . Self interaction is zero
 81 ($J(S^\alpha, S^\alpha) = 0$), which corresponds to equal intraspecific competition across
 82 species. The non-zero entries of J are for numerical convenience the product
 83 of two uniformly distributed random numbers between -1 and 1 and inde-
 84 pendent for all $J(S^\alpha, S^\beta)$ (and $J(S^\beta, S^\alpha)$). $\Xi(S^\alpha, t)$ can be understood as
 85 the average interaction effect of all individuals S in the genotype space $\mathcal{S}$ on
 86 genotype S^α .

87 Successful asexual reproduction occurs with probability

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

88 and results in two copies of the parent genotype, which undergo mutations

²corresponds to H in previous publications on the TaNa

89 with probability p_{mut} acting independently on each gene, switching its sign
 90 $S_i^\alpha \rightarrow -S_i^\alpha$.

91 An initial population of size N_{init} is randomly distributed over the geno-
 92 type space; the initial configuration does not qualitatively influence the long-
 93 term dynamics. A generation consists of $N(t)/p_{kill}$ time steps, which corre-
 94 sponds to the average time taken to kill all living individuals.

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

99 *2.2. A hierarchical version of the TaNa*

100 In the Tangled Nature Model, reproductive success is determined by the
 101 fitness of an individual, which is a function of its interaction with the envi-
 102 ronment. Fitness in a given environment is hereby however not an arbitrary
 103 suitability, but shaped entirely by the species present in the system, empha-
 104 sising the importance of biotic over abiotic interactions. The interactions
 105 however do solely influence the probability of reproduction of an individual
 106 and do not necessarily imply any direct interactions that include the transfer
 107 of matter or energy between compartments. To study the relation between
 108 flow and structure in ecological networks which are shaped by an interacting
 109 environment, the Tangled Nature Model is extended in a way that hierarchi-
 110 cal systems with energy transfer emerge. This approach allows for studying
 111 quantified food webs based on the TaNa. Different interpretations of the
 112 networks arising in the TaNa have been studied by Rikvold et al. (Rikvold,
 113 2007; 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

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

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

for primary producers and consumers respectively (compare Equ. 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

132 fed on a primary producer S^α , the primary producer immediately gets the
 133 chance to regrow with probability $p_{off}(S^\alpha, t)$. Thereby the population of pri-
 134 mary producers still undergoes fluctuations (due to stochastic reproduction
 135 both during the reproduction phase and after consumption by a predator),
 136 but it regrows faster after a predation event than non-primary producing
 137 prey. This accounts for the effects of grazing, where the primary producer
 138 can regrow quickly and without reproduction, opposed to true predation,
 139 which generally leads to death of the prey.

140 Energy flow in the evolving species network is measured by counting the
 141 number of predation events between each pair of species during each gener-
 142 ation. One predation event corresponds to one unit of biomass exchange be-
 143 tween the respective species. $T_{ij}(t)$ stands for the amount of energy/biomass
 144 transfer from species i to species j during generation t . To enhance readabil-
 145 ity, the dependence on t is disregarded in the rest of the paper.

146 The computationally extensive simulations are run on the Imperial Col-
 147 lege High Performance Cluster (HPC, 2016).

148 *2.3. Measuring ecosystem organisation*

149 Ecosystem organisation is quantified using information theoretic measures
 150 based on the flow pattern in the network, which itself is constrained by the
 151 topology. Network flow is generally based on exchange of matter between
 152 species and measured in the model in terms of biomass units passed between
 153 species due to trophic activity.

154 Following Ulanowicz's work (compare eg. Ulanowicz (2011)), the capacity
 155 C of the network is defined in terms of the entropy H of the distribution flows
 156 across the network

$$H = - \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{T_{ij}}{T_{..}} \quad (5)$$

157 times the total throughflow $T_{..}$

$$C = - \sum_{i,j} T_{ij} \ln \frac{T_{ij}}{T_{..}} \quad (6)$$

158 where T_{ij} is the flow from species i to j and $T_{i.}$ and $T_{.j}$ denote the total
159 outflow of species i and the total inflow to species j respectively:

$$\begin{aligned} T_{i.} &= \sum_k T_{ik} \\ T_{.i} &= \sum_l T_{li} \\ T_{..} &= \sum_{i,j} T_{ij} \end{aligned} \quad (7)$$

160 $\ln(x)$ denotes the natural logarithm of x .

161 The average mutual information in a network is defined as

$$MI = \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}} \quad (8)$$

162 While MacArthur (1955) hypothesises that the average entropy H in-
163 creases in ecosystems over time, Rutledge et al. (1976) argue that due to
164 stability aspects,

$$R = H - MI \quad (9)$$

165 should increase during the development of ecological networks. Ulanowicz
166 synthesises characteristics of ecosystem maturity layed out by Odum (1968)

167 and ideas about autocatalysis and intrasystemic feedbacks in the measure of
 168 ascendancy A as the product of the mutual information MI and the total
 169 throughflow $T_{..}$.

$$A = \sum_{i,j} T_{ij} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}} \quad (10)$$

170 Capacity minus ascendancy is called overhead OH

$$OH = C - A. \quad (11)$$

171 While Ulanowicz originally hypothesised ecosystems to evolve to ever
 172 higher values of ascendancy, more recent considerations and empirical find-
 173 ings led to the proposition of adaptive evolutionary systems to balance be-
 174 tween their degree of organisation $\frac{MI}{H}$ (constraints ensuring function and
 175 integrity of the system) and their degree of disorganisation $-\ln \frac{MI}{H}$ (scope
 176 for adaptation and flexibility in face of disturbances) and therefore cluster
 177 around maximal "fitness"

$$F = -e^{\frac{MI}{H}} \ln \frac{MI}{H} \quad (12)$$

178 where they are "best poised for further evolution" (Ulanowicz, 2014).

179 $e = \exp(1)$ scales F to the range between 0 and 1.

180 All measures are compared according to their evolution through the adap-
 181 tive dynamics of the Tangle Nature Model.

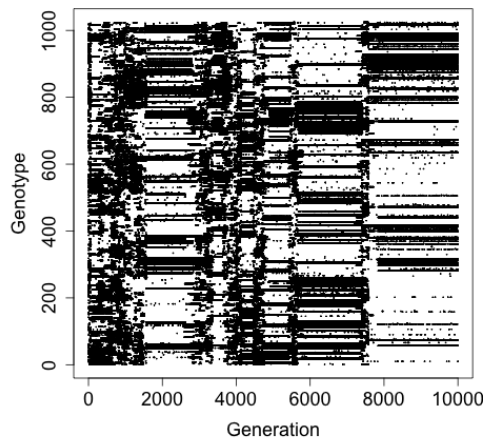


Figure 1: Occupation of the genotype space over time. Alternating stable (qESS) periods interrupted by transitions are clearly visible.

3. Results

3.1. Evolutionary intermittent dynamics

Just as in the original version, also in the hierarchical Tangled Nature Model, species emerge from the microscopic interactions of genotypes and form quasi stable communities, interrupted by transition periods of hectic reorganisation (Fig. 1). Unless otherwise stated, the parameters were chosen as follows: $\theta_{int} = 0.8$, $\theta_{feed} = 0.5$, $\theta_{PP} = 0.5$, $L = 10$, $N_{init} = 500$, $c = 0.012$, $\mu = 0.01$, $\mu_C = 20$, $P_{kill} = 0.02$, $P_{mut} = 0.0002$. This is a generic set of parameters which leads to alternating stable (qESS) periods interrupted by transitions with a computationally feasible system size, and is not adjusted with regards to the resulting trophic network architecture and flow (more detailed discussion in chapter 3.2).

Species diversity remains about constant, both if considering only species

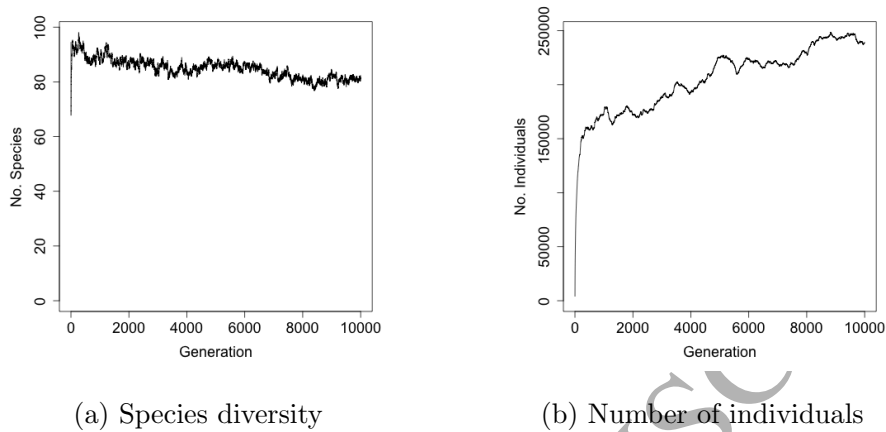


Figure 2: Development of the number of individuals and species over time, averaged over 100 runs

with an abundance above a threshold value (hence neglecting mutants who appear and go extinct immediately again) and if considering all present species (Fig. 2a). The average number of individuals increases over time (Fig. 2b), reflecting the fact that the system during the course of evolution optimises the interactions between species and hence can sustain more biomass.

3.2. Parameter space

Whilst the initial distribution of genotypes does not change the model behaviour, different parameters influence the exhibited pattern of dynamics. The combination of μ , μ_C and P_{kill} defines a baseline "carrying capacity" of the non-adapted system and is chosen such that the number of individuals remains in the low 6-digit regime to limit computational time. c and P_{mut} influence the coadaptation of communities and are chosen within the regime

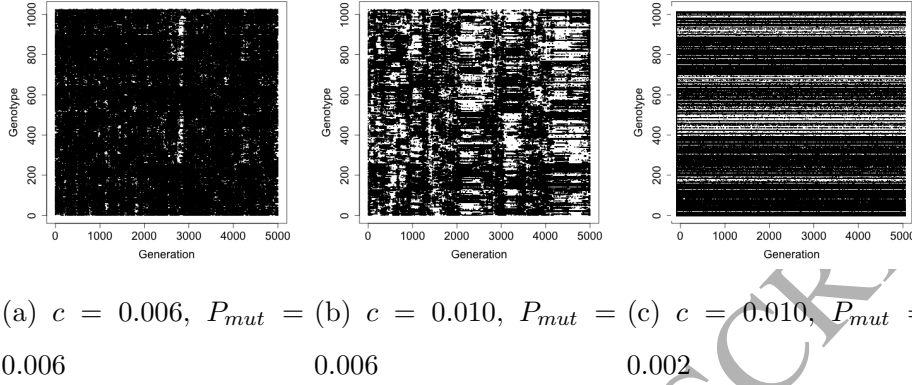


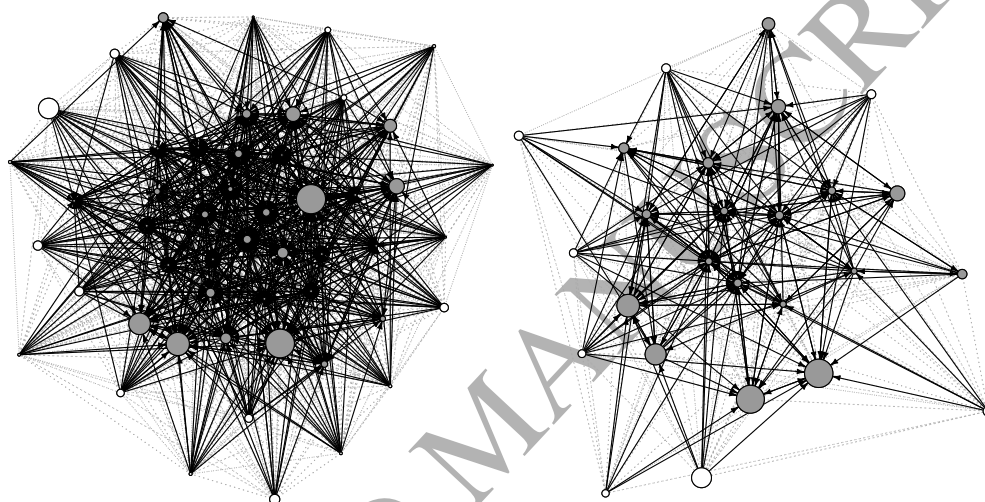
Figure 3: Occupation of the genotype space over time in the hierarchical TNM.

which allows for the establishment of qESS communities. Varying this set of parameters can lead to either hectic communities, in which no coadapted communities stabilise, or to the formation of one stable community with a few appearing and disappearing mutant species but no hectic phases followed by reorganisation. This effect has been explored in depth in di Collobiano et al. (2002) for the original version of the Tangled Nature Model and is mirrored in the hierarchical version (Fig. 3) The choice of those parameters which influence the trophic network, biomass exchange and chain length (θ_{feed} , θ_{PP}) is generic.

3.3. Ecosystemic properties

Based on the interaction network and the trophic links, ecological networks emerge (Fig. 4). As energy cycling isn't restricted, no clear tree-shaped layout is visible.

To compare and characterise ecosystem topologies, one often makes use of the number of trophic levels and by the degree distribution.



(a) Full network, including rare mutants

(b) Subset (species with $n > 10$)

Figure 4: Species network after 10000 generations in an equilibrium state. Vertex colour denotes if the species is a primary producer (white) or a consumer (gray); vertex size equal the log of the number of individuals. Dotted gray lines represent J-interactions (both positive and negative), solid black lines are trophic interactions (the arrows point in the direction of energy transfer).

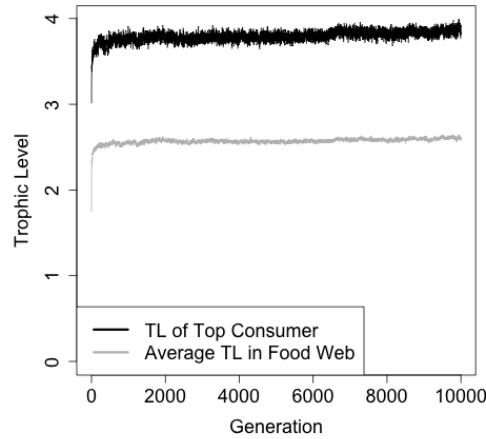


Figure 5: Development of the trophic level (TL) of the top consumers (maximum trophic position, black) and the average trophic level (grey) over time, averaged over 100 runs

In the hierarchical Tangled Nature Model with the given parameters, the average trophic position of a species is 2.60, with the average maximum trophic position being 3.84 (50 runs). The trophic position is defined as the length of the shortest path from the energy source (hence primary producers occupy trophic position 1) and doesn't show any in- or decreasing trend in the long-term average (Fig. 5).

The degree distribution across the nodes of the trophic ecological network in a mature quasi stable period is visualised in Fig. 6a and on a log-log-plot in Fig. 6b.

Ecosystem connectivity, the fraction of present links relative to the potential number of links (L/S^2), has long been studied to detect patterns in food web structure. In the Tangled Nature Model, average connectivity doesn't change over time but varies around 0.04 (Fig. 7).

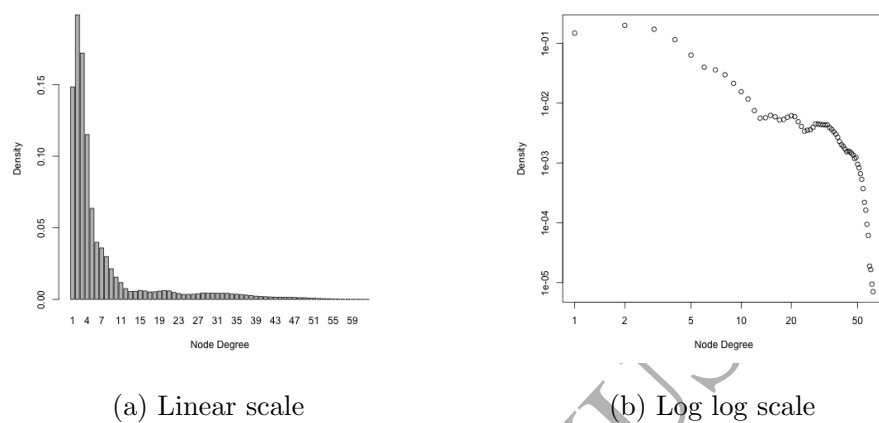


Figure 6: Degree distribution of the trophic interactions across generations in qESS

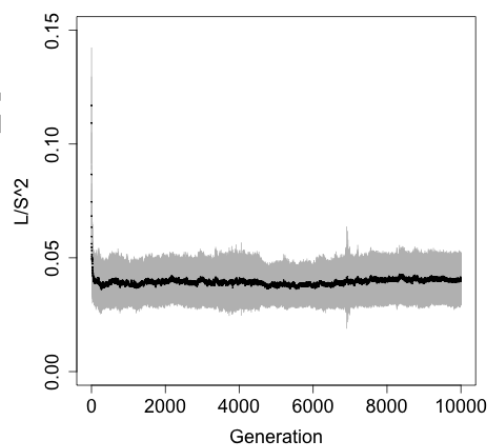
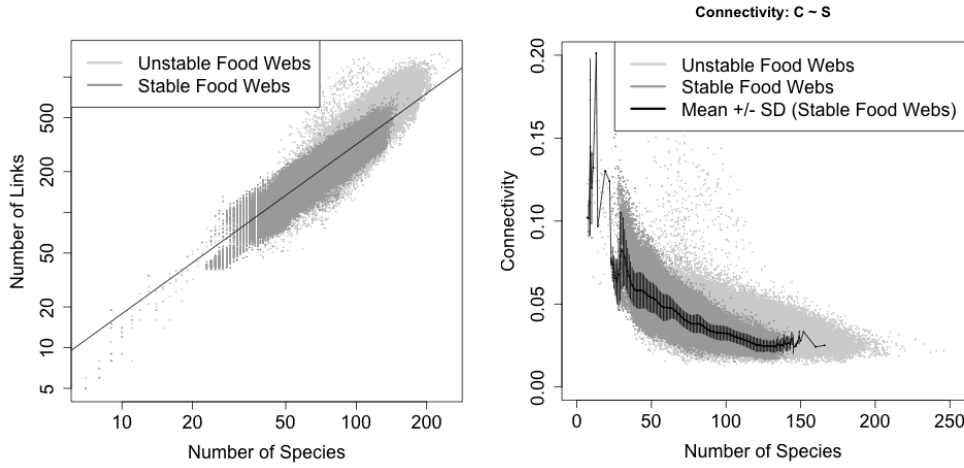


Figure 7: Average connectivity over time (black: mean, grey: standard deviation, $n = 100$)



(a) $L \sim S$. Line represents a statistical model fitted to the stable data points, sends mean C ($\pm$ SD) for stable food webs $L \sim S^{1.25}$

(b) $C \sim S$, where $C = L/S^2$. Line represents mean C ($\pm$ SD) for stable food webs

Figure 8: Relationship between the number of trophic interaction links and the number of species

236 Much debate has been around the relationship between the size of an
 237 ecosystem and its connectivity (Dunne, 2009). While early results suggested
 238 scale invariance (hence approximately constant L/S) or constant connectivity
 239 (constant $C = L/S^2$), later studies report power law relationships in the form
 240 of $L = \alpha S^\beta$ with different exponents β . (Dunne et al., 2002b; Dunne, 2009).
 241 While during stable periods, a clear power law relationship between L and
 242 S (exponent = 1.25) can be detected, unstable systems show more scatter
 243 (Fig. 8a). The corresponding relationship between connectivity and diversity
 244 (Fig. 8b) mirrors previous findings on the characteristics of the interaction
 245 network in the Tangled Nature Model (Laird and Jensen, 2006).

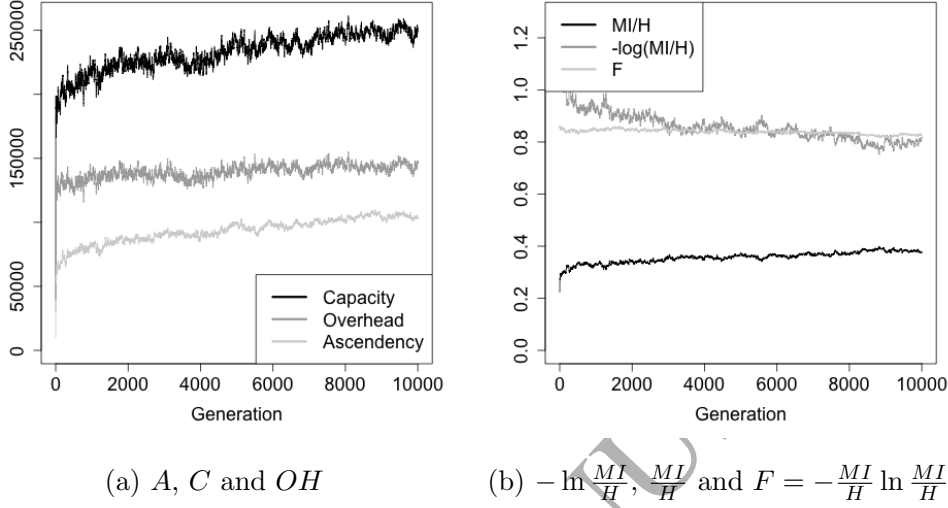


Figure 9: Ecosystem organisation: development of ascendency A , capacity C and overhead OH (left) and relative mutual information $\frac{MI}{H}$, its inverse $-\ln \frac{MI}{H}$ and the scaled product $F = -e^{\frac{MI}{H}} \ln \frac{MI}{H}$ (right) over time, averaged over 100 runs

246 3.4. Ecosystem organisation

247 Measures of ecosystem capacity and ascendency show a slight increase
 248 over time, whereas the overhead remains constant on average. (Fig. 9a).

249 The relative mutual information $\frac{MI}{H}$, representing the organisation of the
 250 system, increases slightly over time to values around 0.4, while a version of
 251 its inverse, $-\ln \frac{MI}{H}$, a potential measure for disorganisation, decreases on
 252 average (Fig. 9b). The product $F = -\frac{MI}{H} \ln \frac{MI}{H}$, which has been suggested
 253 to describe the system's fitness (Ulanowicz, 2014), remains more or less con-
 254 stant.

255 Comparing the distribution of ascendency values between hectic and sta-
 256 ble periods shows a clear shift towards higher ascendency during qESS peri-

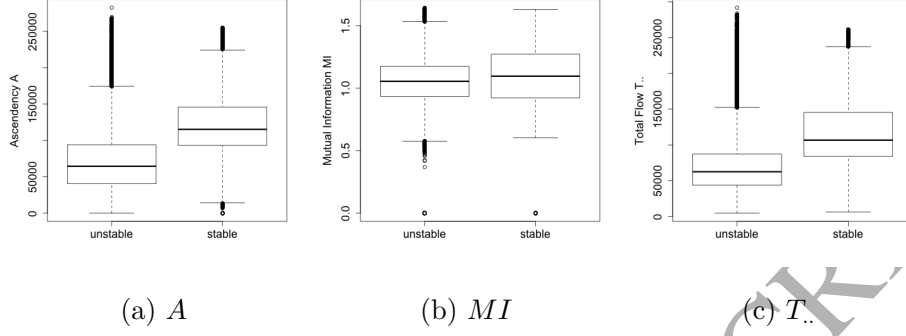


Figure 10: Box-Whisker-Plots of ascendancy A , mutual information MI and total flow $T_{..}$ during hectic and stable periods (50 runs, 352057 stable data points, 147943 hectic data points). The boxes show the median (solid line in the middle of the box), the lower and upper quartile ($Q1$ and $Q3$, boundaries of the box), the upper (minimum of $\max(\text{data})$ and $Q3 + 1.5 * (Q3 - Q1)$) and lower (maximum of $\min(\text{data})$ and $Q1 - 1.5 * (Q3 - Q1)$) whisker as well as outliers (circles). For all three measures, differences between unstable and stable periods are significant ($p < 2.2 \cdot 10^{16}$).

ods Fig. 10a, with a mean ascendancy A of $11.7 \cdot 10^4$ ($SD = 4.5 \cdot 10^4$) during
 stable and of $7.1 \cdot 10^4$ ($SD = 4.6 \cdot 10^4$) during hectic periods. This effect is
 partly caused by the average mutual information MI (mean stable periods:
 1.07 ($SD = 0.31$), mean hectic periods: 0.99 ($SD = 0.33$), Fig. 10b), and
 more strongly influenced by the change of total flow (mean stable periods:
 $11.6 \cdot 10^4$ ($SD = 4.4 \cdot 10^4$), mean hectic periods: $7.1 \cdot 10^4$ ($SD = 4.1 \cdot 10^4$), Fig.
 10c). The difference of MI , $T_{..}$ and A comparing hectic and stable periods
 is highly significant ($p < 2.2 \cdot 10^{16}$ for all three measures).

265 4. Conclusions

266 Previous studies have confirmed that despite the simplicity of the Tangled
 267 Nature Model, the model is well capable of reproducing complex macroe-
 268 cological patterns found in nature such as the log-normal shaped species-
 269 abundance distribution, a power law relation between area and species diver-
 270 sity and exponential degree distributions of the indirect interaction network
 271 (Hall et al., 2002; Laird and Jensen, 2006; Laird et al., 2008; Lawson and
 272 Jensen, 2006). A most notable feature is the intermittent nature of macro-
 273 evolution, denoted as punctuated equilibrium by Eldredge and Gould (1972),
 274 which, as shown here, can also be reproduced in the hierarchical version of
 275 the model. In the course of co-evolution, the realised indirect interaction
 276 strengths tend to become more positive (di Collobiano et al., 2002), allow-
 277 ing for the support of a higher number of total individuals in the system
 278 (compare Equ. 1 and Fig. 2b), which is in accordance with previous pro-
 279 posals and findings (compare eg. Fath and Patten (1998)). The TaNa has
 280 also been used to study predator prey interactions and therefrom resulting
 281 (non-quantitative) model food webs (Rikvold, 2010). The presented results
 282 from the quantitative hierarchical TaNa additionally reveal an average food
 283 chain length of 2.6 (Fig. 5), agreeing well with empirical observations of av-
 284 erage chain lengths mainly lying between 2 and 3 (Briand and Cohen, 1987).
 285 Maximum chain lengths can in reality reach up to 10 species or more, but in
 286 the majority of the cases don't exceed 4 (Briand and Cohen, 1987), which is
 287 in agreement with the presented findings. Much debate has been around the
 288 relationship between complexity and stability of ecological networks. From
 289 May's model studies suggesting larger food webs to be less connected in order

290 to be stable May (1973) over suggested "link-species scaling laws" ($L/S \approx 2$,
 291 Cohen and Newman (1985)), more comprehensive recent data with higher
 292 resolution indicate power law scaling ($L = \alpha S^\beta$) across a wide range of food
 293 web types (Dunne et al., 2002a; Dunne, 2009).

294 Stable food webs produced by the Tangled Nature Model exhibit a clear
 295 power law relationship with an exponent of 1.25 ($R^2 = 0.82$, Fig. 8a), which
 296 is in line with most recent findings of real world food web topologies. The
 297 Tangled Nature Model hence has shown to be well suitable for reproducing
 298 structural properties of real-world ecological networks and can therefore be
 299 analysed with regard to ecosystem organisation and integrity.

300 Quantifying ecosystem integrity, growth and development is a controver-
 301 sial undertaking and depends substantially on the assumptions made as well
 302 as the properties of the specific system. Ideally one would like to measure
 303 ecosystem structure and flow in a real world ecosystem, tracing all species
 304 interactions as well the transfers and losses of nutrients and energy between
 305 them, relate these properties to observations of functionality, stability and
 306 resilience and assess which measures might function best in capturing all
 307 these characteristics. As such comprehensive knowledge is unattainable in
 308 reality, generic models of evolutionary ecology can help to illuminate these
 309 practical questions even within a theoretical setting. The presented results
 310 show, that ecosystem ascendancy as a measure of growth and development
 311 indeed increases over evolutionary time scales, as the overall capacity for the
 312 flow pattern increases (Fig. 9a). Ecosystems therefore apparently tend to
 313 extend their scope for organisation or integrity, as well as the actual realised
 314 ascendancy, while the difference of the two measures, the overhead, remains

more or less constant over time. This supports the idea of Rutledge et al. (1976), who proposed the difference between flow entropy and mutual information (so $C/T_{..}$) as a measure of stability. As in the Tangled Nature Model, the system is subject to continuous disturbances in the form of constant mutation rates, the amount of buffering is not expected to change over time.

Apart from an overall increase in network capacity and ascendancy over time, ascendancy is significantly higher during stable periods compared to periods of hectic transitions and rearrangements (Fig. 10a). This is both accounted for by significantly higher mutual information and significantly higher overall flow rates during stable compared to hectic periods (Fig. 10b and 10c). These findings indicate a clear difference in ecosystem integrity and functioning between stable, well-functioning communities, and communities, which are rearranging due to external or internal disturbances. Furthermore, as results reveal a trend towards overall increasing ecosystem ascendancy, the work supports the usefulness of ascendancy as a measure of growth and development.

While Ulanowicz (1986) originally expected ecosystems to ever increase their ascendancy as they grow and develop, more recent findings showed that real world ecosystems tend to cluster around relative values of ascendancy $\frac{A}{C} = \frac{MI}{H}$ of 0.4 (Ulanowicz, 2014). This value of ascendancy maximises the function $F(\frac{MI}{H}) = -\frac{MI}{H} \ln \frac{MI}{H}$ and implies that adaptive evolutionary systems evolve to both ensure a certain degree of organisation, while at the same time maintaining enough scope for further adaptation and rearrangement of flows in case of disturbances. Interestingly and even though the exact choice of F

is somewhat arbitrary, also the TaNa model ecosystems evolve to values of $\frac{MI}{H}$ around 0.4 (Fig. 9b). The relative contribution of mutual information F depends both on topology and dynamics on the network and is therefore much more than a mathematical artefact. Reasons and implications for why F clusters around 0.4 both real world and in model ecosystems should be the result of future work.

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