

Dynamics of life

Self-organisation, co-adaptation & the evolution of resilience in complex ecosystems

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by

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I certify that this thesis, and the research to which it refers, are the product of my own work, and that any ideas or quotations from the work of other people are properly acknowledged.

Katharina Stefanie Theresia Brinck

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Dynamics of life

Self-organisation, co-adaptation & the evolution of resilience in complex ecosystems

Abstract

Ecosystems are highly ordered, non-random systems, yet neither are they designed from a specific construction plan determining their structure and composition, nor are they directly predictable from the traits and behaviour of the species they are comprised of. The order arises from self-organising forces stemming from the interactions between individuals - yet the concrete principles behind self-organisation, the role of community integrity versus single species traits and the feedbacks between species and the systems they form are largely unknown. In this thesis, complex-systems modelling is used as a tool to bridge the gap between microscopic behaviour and emergent macroscopic systems and concepts from information theory are applied to quantify the arising, development and evolution of order within ecological communities. Generally, the information content within an ecosystem, the information content the ecosystem has about itself and its future states as well as the general coadaptation and organisation tend to increase with advanced developmental state. This goes along with a shift from bottom-up control from micro- to the macrolevel in earlier developmental stages to top-down control the system tends to impose on its species and individuals in late-successional stages. Coadaptation, next to individual fitness, also plays a role for species abundance and survival in communities undergoing disturbances, emphasizing the role of community integrity for its persistence. Overall, the results illustrate that species interactions are the guiding force behind ecosystem organisation, that coadaptation shapes functionality, stability and resilience and that ecosystem development is not either guided by fundamental laws *or* global optimisation criteria, but by both - individual fitness and the system's state determine ecosystem development in a dialogue of bottom-up and top-down control.

To life.

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List of Abbreviations, Symbols and Definitions

Abbreviations

TNM	Tangled Nature Model of evolutionary ecology
CTNM	Tangled Nature Model with a correlated genome space
HTNM	Hierarchical version of the Tangled Nature Model
FTNM	Spatial version of the Tangled Nature Model to study community dynamics in the light of habitat fragmentation
qESS	quasi-Evolutionary Stable Strategy of a community
MaxEnt	The statistical inference principle of Maximum Entropy as derived by Jaynes (1957)
MEP	The Maximum Entropy Production hypothesis

Information, Entropy and Graph Theory

$H(X)$	Information entropy of a random variable X and its probability distribution
$MI(X, Y)$	Mutual information of two random variables X and Y
$TE_{X \rightarrow Y}$	Transfer entropy (information flow) from random process X to random process Y
$C(x) = \frac{F}{\sum_y d(x, y)}$	Closeness centrality of node x , where F is the total number of nodes in the graph and $d(x, y)$ is the distance between node x and node y

T_{ij}	Flow from node i to node j during a defined time frame
$T_{i.} = \sum_j T_{ij}$	Total outflow of node i
$T_{.j} = \sum_i T_{ij}$	Total inflow to node j
$T_{..} = \sum_{ij} T_{ij}$	Total network throughflow
$H_N = - \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{T_{ij}}{T_{..}}$	Entropy of network flows
$MI_N = \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}}$	Average mutual information of network flows
$C_N = T_{..} \cdot H_N$	Capacity of a network
$A_N = T_{..} \cdot MI_N$	Ascendency of a network
$OH_N = T_{..} \cdot (H_N - MI_N)$	Overhead of a network
$F_N = -e^{\frac{MI_N}{H_N}} \ln \frac{MI_N}{H_N}$	"Fitness" of a network

Variables in the Tangled Nature Model

M	Maximum species diversity (number of potentially co-occurring species in the community)
L	Number of genes which define a species
S_i^α	Gene expression, usually in $\{-1, 1\}$
S^α	Species α . A species is either defined by a genotype ($S^\alpha = (S_1^\alpha, S_2^\alpha, \dots, S_L^\alpha)$) or as a positive integer ($S^\alpha \in \{1, \dots, D_{\max}\}$).
$\mathcal{S} = (S^\alpha, S^\beta, S^\gamma, \dots)$	The species or genotype space (pool of all potentially occurring species in the community)
$d_{\max}(S^\alpha)$	Maximum dispersal distance of species S^α
$d_{\text{global.max}}$	Maximum possible dispersal distance across all species in the community
$E(S^\alpha)$	Intrinsic fitness of species S^α
$J(S^\alpha, S^\beta)$	Interaction effect of species S^β on species S^α
θ_{int}	Expected fraction of non-zero interactions in J
θ_{PP}	Expected fraction of primary producers in the species pool $\mathcal{S}$

θ_{feed}	Expected fraction of prey species of a certain consumer in the species pool
R	Carrying capacity of the community
w	Scaling factor for the relative importance of the interaction effects for the offspring probability of a species
c	Scaling factor for the carrying capacity of consumers relative to their prey abundance
N_{init}	Initial number of individuals in the community
F	Number of patches in the landscape
$\hat{t}$	Time step of landscape fragmentation
$N(t)$	Total number of individuals in the community at time t
$N_{\text{PP}}(t)$	Number of individuals of species at time t which are primary producers
$N_{\text{prey}}^{\alpha}(t)$	Number of individuals at time t which belong to those species which species S^{α} predates on
$D(t)$	Total number of species in the community at time t
$n(S^{\alpha}, t)$	Number of individuals of species S^{α} at time t
NG	Number of time steps or generations the model is run for

The subscript $_f$ denotes that the measure is to be understood with respect to patch f .

Definitions in the Tangled Nature Model

$J_{\text{sum}}(S^{\alpha}) := \sum_{S \in \mathcal{S}} J(S^{\alpha}, S)$	Degree of coadaptation to a hypothetical balanced community in which all species have equal abundance
---	---

$$\tilde{J}(S^\alpha, t) := \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t)}{N(t)}$$

Degree of coadaptation of an individual of species S^α to the community at time t (defined as the average interaction effect other individuals impose on S^α)

$$\Xi(S^\alpha, t) = w \cdot \tilde{J}(S^\alpha, t) - \frac{N(t)}{R}$$

Weight function which controls the offspring probability of species $S^{\alpha*}$

$$\Xi_{PP}(S^\alpha, t) = w \cdot \tilde{J}(S^\alpha, t) - \frac{N_{PP}(t)}{R}$$

Weight function which controls the offspring probability of primary producer S^α

$$\Xi_C(S^\alpha, t) = w \cdot \tilde{J}(S^\alpha, t) - \frac{n(S^\alpha, t)}{c \cdot N_{prey}^\alpha(t)}$$

Weight function which controls the offspring probability of consumer species S^α

$$\Xi_E(S^\alpha, t) = w_E \cdot E(S^\alpha) + w_J \cdot \tilde{J}(S^\alpha, t) - \frac{N(t)}{R}$$

Weight function which controls the offspring probability of species S^α if species have an intrinsic fitness E

$$P_{off}(S^\alpha, t) = \frac{\exp(\Xi(S^\alpha, t))}{1 + \exp(\Xi(S^\alpha, t))}$$

Offspring probability of species S^α

$$P_{death}$$

Probability of death of a species

$$P_{mut}$$

Probability of mutation of a gene or a species

$$P_{mig}$$

Probability of a species of migrating from one patch to another

$$P_{imm}$$

Immigration rate to the community of any species

$$P_{imm.frag}$$

Immigration rate to the community of any species after fragmentation

*corresponds to H in previous publications on the TNM

Preface

"There are many windows through which we can look out into the world, searching for meaning. Most of us, when we ponder on the meaning of our existence, peer through but one of these windows onto the world. And even that one is often misted over by the breath of our finite humanity. We clear a tiny peephole and stare through. No wonder we are confused by the tiny fraction of a whole that we see."

Jane Goodall
Through a window (2010)

Most of scientific progress across all disciplines over the last centuries has been achieved by looking at the world through the window of a reductionist worldview. The reductionist hypothesis claims that natural phenomena can be reduced to a small set of fundamental laws, being the research focus of particle physicists, logicians and a few others. Scientific disciplines form a hierarchy, where social sciences obey the laws of psychology which obeys the laws of biology which obeys the laws of chemistry which obeys the laws of physics - with any further fine-graining being possible.

The reductionist hypothesis is widely accepted among scientists and has certainly proven useful for the integrity of knowledge and scientific progress. However, the idea that phenomena *obey* common fundamental laws of lower hierarchy disciplines does not immediately imply, that these higher order phenomena can also be *constructed* from these. A set of microscopic entities and their behaviour can give rise to many different macroscopic states - and some macroscopic states influence the microscopic entities to behave differently than they would have, given only the fundamental laws they follow ([Hendry, 2010](#)).

This crucial difference between the reductionist and the constructivist hypothesis, brought up and discussed elegantly by [Anderson \(1972\)](#), is an important motivation for complexity research. If macroscopic phenomena around us obey fundamental microscopic laws, but cannot be predicted directly from them, we

Preface

need to bridge the gap between levels of emergence in a non-constructivist way. Complex systems modelling is the only tool we currently have to explore which specific microscopic rules and which boundary conditions ensure, that systems with similar properties to the ones we observe in nature emerge.

If ecology was less complex, a few most "fit" species would win the war of competition and the outcome could be predicted from single species traits, cells or DNA. But dynamics, decay and multidimensional interactions give rise to the complex and beautiful world around us. This thesis looks at different aspects of this complex self-organisation in ecosystems, aiming to bridge the gap between microscopic behaviour of individuals and the emerging macroscopic ecosystems, and widening the window complexity scientists opened next to the reductionist window in the progression of science.

"It turns out that an eerie type of chaos can lurk just behind a facade of order and yet, deep inside the chaos lurks an even eerier type of order."

Douglas R. Hofstadter
*Metamagical Themas: Questing for the
Essence of Mind and Pattern* (1985)

1

Introduction

Chaos and order are ubiquitous in the living world around us. A multitude of ecological and evolutionary processes shape the various patterns of interacting individuals, populations and species and contribute to the variety, heterogeneity and diversity of nature. All this diversity however acts by no means chaotic. Complicated interaction patterns along with evolutionary, functional and developmental constraints give rise to emerging self-organisation in ecological systems, leading to ecosystem integrity.

To explain emerging characteristics of complex ecosystems, classical theoretical ecology often deals with detailed processes and mechanisms, coupled with multitudinous species traits and behaviours, which all operate within stochastic environments. This approach is useful for detailed descriptions of specific local ecosystems, but it impedes the formation of ecological theory across individuals and species as well as spatial and temporal scales.

The aim of this dissertation project is to enhance the understanding of the governing principles behind the self-organisation of ecological systems in a more general sense, by looking at information contained and transferred in ecological systems.

1. Introduction

1.1. Motivation and scientific context of the dissertation

Ecosystems are understood as emerging structures from microscopic complex interactions of individuals and species (Fig. 1.1).

The information content within such a macroscopic ecosystem (A), the information the microscopic entities contain about the system (B) as well as the information transfer between the micro- and the macrolevel (C) are assessed. Therefore, mathematical concepts from information theory are applied to simulated data from agent based dynamical systems modelling (D), to gain better understanding of where ecosystems are located between order and chaos and what shapes their development over successional and evolutionary time scales. Note that while the system (A) is an emergent structure of the building blocks' (individuals' and species') interactions at the microscopic level (B), those building blocks can be emergent structures themselves - a "species" is by no means defined unambiguously. This relation and complication will be discussed in more detail in the second to last epistemological chapter.

The overall research is located at the intersection of ecology, mathematics, complexity science and philosophy, touching on all disciplines briefly but mainly aiming to build bridges between them.

1.1 Motivation and scientific context of the dissertation

1.1.1 Complexity, self-organisation and emergence

According to George Cowan, the founder of the Santa Fe Institute, the 21st century is the century of complexity science ([Waldrop, 1992](#)). Complex dynamics

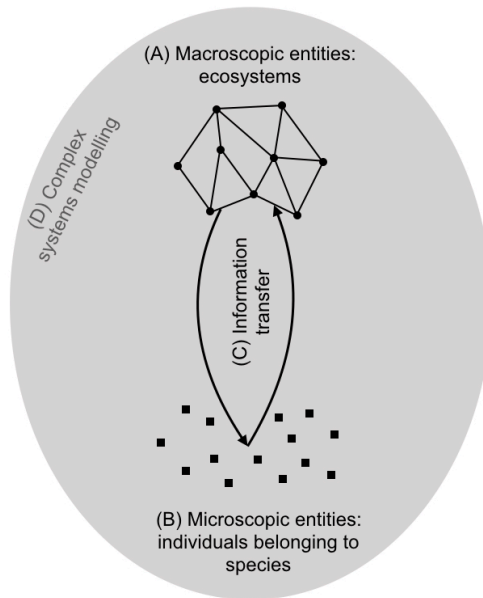


Figure 1.1: Ecosystems as complex systems - the scope of this thesis

1. Introduction

1.1. *Motivation and scientific context of the dissertation*

govern financial markets, trade and consumer behaviour, they steer communities, social networks and opinion transfer, and they play a key role for all life - from gene expression over homeostasis up to the emergence of consciousness in living organisms. A clear consensus on the definition of a complex system is still missing, but it is widely agreed upon that complex systems have three key components:

- Complex systems consist of a large number of agents.
- Those agents are connected with each other through dynamic interactions.
- Those interaction give rise to emergent, self-organised behaviour.

Often, the emergent structures are hierarchical or exhibit other characteristics of organisation which are not inherent to the agents themselves, and they typically change over time. Complex systems are open and their boundaries often defined by conventions rather than a property of the system itself ([Jensen, 2009](#)).

The key to complex systems research lies in the self-organized appearance of emergent phenomena. The term emergence originates from philosophy, going back at least to Aristotle's phrase about the whole being greater than the sum of its parts ([Aristotle, n.d.](#)). In a complex systems setting, it refers to effects appearing in complex systems leading to patterns grounded in but a priori unpredictable from the multiplicity of simple interactions of the system's constituents. Emergent phenomena and complex systems are thus two sides of the same coin: while complex systems are defined by appearance of emergent phenomena, emergent phenomena are just those phenomena, which result from complex interactions. Often but not necessarily, those emerging complex systems include self-organising properties; the terms complexity, emergence and self-organisation are regularly even used synonymously or at least closely entangled. Examples for emergent properties in biology are swarm dynamics of birds and fish, which arise from simple interaction rules between individuals, the mind as being emergent from brain physiology and processes, life itself as being emergent from thermodynamic principles (compare chapter 1.6.1), the complexity of organisms emerging from selection and evolution, as well as the assembly of ecosystems, culminating in the Gaia hypothesis of a complex, self-regulating earth system ([Lovelock, 1972](#); [Ryan, 2007](#)).

1. Introduction

1.1. *Motivation and scientific context of the dissertation*

Complex dynamics occur on all sorts of scale, from physics over chemistry up to biology, with ecosystems being on an outer arm of a hierarchy of emerging levels - containing components from all essentially all subdisciplines. From a reductionist perspective, what happens on an ecosystem level can be reduced to fundamental laws, but from a complexity perspective we know, that this doesn't equal a constructionist understanding - deducting and predicting the universe from laws acting at the lowest is not possible ([Anderson, 1972](#)). Nevertheless, to understand the organisation of ecosystems requires an understanding of which species and processes their development and evolution - which are those "fittest" species which dominate the ecosystems of our planet?

1.1.2 **Evolution through natural selection - a brief historical overview**

Darwinian evolutionary research tradition is built on natural selection on heritable variation as the fundamental principle for order and diversity. Ecosystems/species networks are regarded as the simple result of a fight for the "survival of the fittest"* on lower scales. In recent years, with the rise of complex systems sciences, the need for integrative and process oriented approaches to capture ecosystem growth, development and organisation, has been addressed from various sides ([Odum, 1977](#); [Kauffman, 1993](#); [Lovelock, 2003](#); [Jorgensen et al., 2007](#)). Regarding ecosystems as non-reductionistic systems raises the question, which general principles guide the development of an ecological network itself. In such a strongly-emergent system, fitness is rather regarded as a potential for the system than an intrinsic property of a species.

Darwinism

The introduction of the concept of evolution to the science of biology constituted one of the most severe paradigm shift in the history of biological science. Building on the ideas of Erasmus Darwin, that life forms have not been created but evolved from a first "blobb" of live, his grandson Charles Darwin was able to find a

*The problems around the meaning of this popular phrase are discussed in the section starting on page 28.

1. Introduction

1.1. Motivation and scientific context of the dissertation

mechanism to evolution: natural selection - the struggle for existence ([Bethell, 1976](#)).

Over the course of time, many discussions and extensions of the originally proposed theory of Darwin have been added to the discourse, but the fundamental principle underlying evolutionary theory has remained unchanged: (i) organisms are characterised by traits which are transmitted from parent to offspring (*heritability*), (ii) offspring numbers exceed resource availability, leading to *competition*, and (iii) the better the traits of an organism are suited to the specific environment, the higher the chances for survival and reproduction (*selection*).

Neo-Darwinism and the Modern Synthesis

The rediscovery of Mendelian inheritance and its introduction to Darwinian evolutionary theory brought a first phase of synthesis in the 1920s/30s. The discovery of population genetics shifted the understanding of the concept of natural selection from acting on the phenotype to acting on gene frequencies. This major shift of perspective gave rise to Neo-Darwinism based on the so called "Modern Synthesis". The major novelties are summarised in Table 1.1.

Darwinism	Neo-Darwinism
Evolution = interplay between organism and environment	Evolution = changes in gene frequencies
Survival of the adequate	Survival of the fittest
Species are species	Species are demographic accidents
Evolutionary outcomes are generally gradual	All evolution is inherently gradual
Fitness space is sloppy	Fitness space is highly optimized
Survival is paramount (he who lives longest wins)	Optimal is paramount (he who dies with the best toys wins)

Table 1.1: Comparison of the main perspectives on evolution according to Darwinism vs. Neo-Darwinism/The Modern Synthesis (aggregated from [Brooks, 2011](#))

The deeper understanding of the mechanisms behind inheritance through population genetics helped to develop evolutionary theory from being conceptual and somewhat philosophical to a proper scientific theory, which allows for the derivation of testable hypotheses on a fairly detailed level. At the same time however, the claims became much more rigid. The modern synthesis has a strongly

1. Introduction

1.1. *Motivation and scientific context of the dissertation*

reductionist and also constructivist perspective, claiming to be able to explain all of biological order and diversity from natural selection acting on genetic code. This perspective allows for more concrete derivations, but doesn't leave room for important biological dynamics.

Criticism of the Modern Synthesis

There are two major areas of biology which the Modern Synthesis fails to address. First, in the Neo-Darwinistic perspective, there is little to no room for the role of ontogeny. The theory directly maps genomes to adult genotypes (on which selection acts), which doesn't take into account the fact, that these genomes need to develop into an independently viable organism first, before natural selection having a chance to act on them. This shortcoming contributed to the development of the field of Evo-Devo (evolutionary developmental biology).

Second, the claim that all evolution is gradual contradicts findings from palaeontology, which support much better the concept of periods of stasis, during which species undergo little evolutionary change, interspersed with periods of rapid change leading to cladogenesis. This perspective has become known as punctuated equilibrium ([Eldredge and Gould, 1972](#)) and a variety of explanatory mechanisms have been suggested (see eg. [Bokma, 2015](#)).

One other major shortcoming of the Modern Synthesis is the integration of the biological environment. In complex ecological systems, selection acts upon each component and process - through the environment and through the system itself - chance, self-organisation and selection form a complex interplay. These considerations have lead to the integration of complex systems sciences, thermodynamics and ecology, which should lead to an extended synthesis within the Darwinian research tradition.

Despite all criticism of the Modern Synthesis, the fact that it is natural selection, which acts as the "major source of biological order, adaptation, information and novelty through its action on heritable variation, which defines the Darwinian Research Tradition" ([Weber, 2011](#)), unites the different extensions and approaches. Only what natural selection is comprised of depends on the characteristics of

1. Introduction

1.1. *Motivation and scientific context of the dissertation*

the particular line of research - "nature" may include the surrounding during the whole of organismal development, the functionality of traits not only in an environment but within the set of traits the single organism is comprised of, or the whole abiotic and biotic environment formed by a complex ecosystem. Certainly either definition is valid. The important question remains whether "natural selection" is still the most useful term ([Weber, 2011](#)).

The necessity of a better understanding of fitness

What has been described so far leads to the conclusion that fitness as a suitability to the natural conditions which impose selection depends a lot on how specifically "nature" is defined. However there is a further twist in the concept of fitness.

Fit individuals are defined as those individuals who are best adapted to survive. Stating that fitter individuals have a higher chance of survival and reproduction is hence a truism: Who is fit? Those who survive. Who survives? Those who are fittest ([Bethell, 1976](#)). Fitness is hence not an intrinsic trait of an organism (depending on its environment), it is simply a paraphrase of the fact that some individuals survive longer or contribute more to the next generation than others.

The origin of this tautology can be understood by looking at where Darwin generated some of his ideas: from a breeding analogy. If a certain trait like long wool is desired from an external perspective, having that particular feature makes one fitter. In the wild however, there are no extrinsically defined trait optima - simply those traits are desired, which in the current environment function best. The lack of "fitness" as an intrinsic feature makes the theory of the survival of the fittest untestable!

Different allies have been explored to resolve this apparent contradiction, which all require careful and thoughtful argumentation (see eg. [Hunt, 2014](#)). Here this difficulty shall be used as an opportunity to look at fitness from a profoundly different perspective.

Let's define an organism as "fit" if it fits in the system. This perspective requires an inherently dual look at fitness. Fitness is never alone a characteristic of an individual (may it be intrinsic or extrinsically imposed by the surrounding). It

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is always at the same time also a measure of how well the organism is able to contribute to the overall functionality of the system. This perspective opens up the possibility of examining global fitness criteria acting on the system itself and linking them to local fitness optimisation. Fitness is then transferred through an ecological network, linking to ideas of feedback cycles and autocatalysis.

The suggested new look on fitness requires the examination of the whole interacting ecosystem simultaneously, to be able to link individual fitness, their propagation through the network and network functionality. Complex systems science studies how the interactions between microscopic entities give rise to collective macroscopic behaviour, which is not intrinsically predictable from the actions on the microscale. Even though the perspective of the systems ecologist is from a top-down perspective, observing the macroscopic development of an ecological community, the goal is still to find (most simple) rules acting on the microscopic level, which, together with the selective pressure of the system's behaviour, can give rise to the overall macroscopic state of the system. The spontaneous appearance of macroscopic structure or pattern without any external force, resulting, but being a priori not predictable from the stochastic interactions on the microscale of a complex system, is referred to as emergence. In the framework of complex systems modelling, ecosystems can be regarded as open complex systems far from equilibrium, which are stabilised by "self-organising autocatalytic structures, that serve as pathways for the dissipation of unusable energy" (Weber et al., 1989). Autocatalytic feedbacks within a system are responsible agencies for the selection for growth enhancing systemic configurations and act as a self-organising driver in ecosystem formation, evolution and development (Ulanowicz, 1979).

1.1.3 So what is an ecosystem?

So ecosystems, as fundamental entities of ecology (Lindeman, 1942), are more than "a community of living organisms in conjunction with the non-living components of their environment" (Wikipedia, 2018). As emergent structures, they behave in line with population and evolutionary dynamics acting on species and individuals, but don't necessarily need to be constructable from those. As An-

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Anderson (1972) pointed out in his famous essay *More is Different*, "the elementary entities of solid state physics obey the principles of particle physics, yet solid state physics is not just applied particle physics. Likewise, cells consist of molecules, but cell biology is not applied molecular biology, and psychology is not applied physiology. At each hierarchical stage, entirely new concepts, principles, and generalizations are necessary" (Bokma, 2015). Building upon Anderson's ideas, Nurse (2008) points out the necessity for understanding information transfer in biological systems, where "studies at higher system levels are likely to inform those at the simpler level of the cell and vice versa".

Ecosystem growth and development take place on a range of different scales, ranging from biogeochemical processes to macroecological and evolutionary dynamics. According to Jorgensen et al. (2007), complex ecosystems can be disentangled into several fundamental characteristics.

1. Ecosystems are open systems, exchanging energy, mass and information with their environment, which allows them to maintain themselves far from thermodynamic equilibrium.
2. Ecosystems are ontically inaccessible, meaning that their size and complexity impedes the predictions of detailed ecosystem behaviour.
3. Ecosystems have directed development towards increased feedback and autocatalysis, guiding their intrinsic change and responses to external influences.
4. Ecosystems have network connectivity including synergistic properties, which provides the origin of emergent phenomena.
5. Ecosystems are organized hierarchically, where changes in one compartment can either be multiplied or levelled out on other levels.
6. Ecosystems grow and develop, by gaining biomass and structure, enlarging the networks and increasing their information content.
7. Ecosystems have complex responses to disturbance, which demand the understanding of ecosystem properties such as adaptation, biodiversity, resistance and connectedness, to explain and predict ecosystems' reactions to external influences (Jorgensen et al., 2007).

Ecosystems are holistically dynamic, and the emergence of living systems hence

has to be understood as a process rather than a single event (Weber and Depew, 2004). Self-organisation is not a mathematical abstract concept but a real phenomenon. Selection on individual fitness has shaped the ecosystems on our planet - but also only individuals, which "fit" in the system, which served the overall system functionality and resilience could persist in the context of their ecology. Searching for global criteria of ecosystem health, organisation or integrity does hence by no means require a metaphysical view on living systems - it is simply a fact, that only those systems comprised of components which do serve the system's persistence, are the ones which persist in the long term.

1.2 Thesis aim

The aim of this dissertation project is to enhance the understanding of the governing principles behind the self-organisation of ecological systems which ensure sustainability and resilience in the natural world, by assessing the development and evolution of information content in complex model ecosystems.

The following questions will be addressed.

1. *How can the degree of self-organisation in ecological systems be quantified?*

Making use of graph theory, information theory and ecological network theory, different well-known, non-famous and new measures of structure and functionality of ecological networks are compared, interpreted and characterised with regards to which aspects of organisation they capture. While traditional ecosystem theory usually focusses on measuring either aspects of ecosystem structure or ecosystem functionality, an emphasis is laid on measures of information content, which are able to capture both aspects at the same time. The degree of ecosystem organisation in terms of stored information is assessed over successional and evolutionary time and in different types of ecological communities.

2. *How does order in ecological systems arise, develop and evolve?*

The interplay of mutation, selection and drift is generally considered responsible for the species diversity and their functional interplay we see in

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nature. Classically, fitness or reproductive potential is understood as an intrinsic property of an organism, depending on its adaptation to the abiotic environment. Shifting to a complex systems understanding of ecology emphasises the importance of the biotic environment perceived by the interactions with other species as a determinant for individual fitness. Looking at trends of self-organisation on a macroscopic, systemic level allows for yet another understanding of fitness: fitness becomes then a duality of how well an organism fits into the system (perceived fitness) and how well an organism contributes to overall systemic fitness or organisation (contributed fitness). While selection is generally considered to act on individual entities, those individuals can only persist, if their surrounding ecosystem is able to sustain them - hence evolution has to affect both on individuals and ecosystems. Feedbacks and information transfer between the microscopic and the macroscopic level are assessed to analyse the role of bottom-up and top-down control in developing ecosystems.

3. *Which role do complex dynamics and coadaptation play for ecological communities undergoing habitat loss?*

While both single species traits such as dispersal or competitive ability, and characteristics of the landscape are well-studied when aiming to understand what determines a community's success in fragmented landscapes, little is known about the role that community integrity plays for abundance and persistence of communities undergoing habitat loss. The applied complex systems approach allows for studying whole community characteristics, to quantify the role of coadaptation as well as other traits for species persistence and to assess landscape quality from the perspective of the community rather than the abstract configuration of the landscape itself.

4. *What epistemological value does macroecological research have in general?*

The aim of science is to generate knowledge, and different disciplines apply different techniques. As a conclusion of a series of chapters of applying macroecological research techniques, the question is discussed, in how far these methods can actually help gaining insights about patterns and principles in the real world around us.

1.3 Thesis outline

While *chapter 1* gives a broad introduction and motivation of the thesis context, the following three chapters provide an overview over the necessary methodological background. *Chapter 2* reviews aspects of ecosystem ecology and in *chapter 3*, concepts from information theory to quantify ecosystem organisation and information transfer are introduced. *Chapter 4* follows with background on modelling complex ecosystems and an overview over the applied models.

The following five chapters constitute different case studies on assessing self-organisation in complex ecosystems. *Chapter 5* explores the information content stored in ecosystems (how much information is necessary to describe the macroscopic state of a system, Fig. 1.1 (A)) as well as the information that system contains about itself (how much information do the microscopic entities contain about the future development of the system, Fig. 1.1 (B)). *Chapter 6* looks at the information transfer between the micro- and the macrolevel (Fig. 1.1 (C)).

The following *chapter 7* focusses specifically on food web structure and self-organisation - again measuring the information stored in the macroscopic state of the food web (Fig. 1.1 (A)).

The case studies are rounded off by two spatial examples. *Chapter 8* looks at the role of coadaptation and system functionality for communities undergoing habitat loss, and *chapter 9* assesses the perceived landscape quality from the perspective of the remaining community.

Finding common patterns in natural complexity, building models for their occurrence and formulating theories which explain their emergence is based on fundamental assumptions about our ability to perceive and represent the world, which are debatable from an epistemological context. These difficulties are discussed in *chapter 10* from the perspective of epistemology and the philosophy of science. *Chapter 11* concludes the thesis.

Parts of the introductory chapters 2 to 3 build on pieces from my masters thesis (Brinck, 2014). Chapter 7 is based on a publication in the Journal of Theoretical Biology (Brinck and Jensen, 2017). Chapters 6, 8 and 10 are in the process of submission.

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us."

Charles Darwin
On the Origin of Species (1859)

2

Background: ecosystems and their complexity and organisation

2.1 Context: an intuition of ecosystem organisation

The idea of regarding and understanding ecosystems as complex systems triggers the assumption that changes in the state of the system can be captured by measuring its complexity. Complexity however is an abstract concept, which has to be translated into quantifiable measures. Generally, the macroscopic characteristic "complexity" is envisioned as a function of the regularity of a system, which peaks at intermediate levels, right between entire order and complete disorder. Complexity can thereby have temporal, spatial and structural aspects and is generally seen to be increasing over time due to self-organisational processes (Parrott, 2010). Ecosystem health, function or activity, ecosystem organisation and ecosystem resilience should all play a role when quantifying ecosystem complexity (Mageau et al., 1995), but broad consensus about measures of ecosystem complexity are still missing.

While ecosystem health is usually regarded as a multi-dimensional but short-to intermediate term measure (Costanza, 1992), ecosystem organisation or in-

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egrity is meant to focus on a longer-term and more comprehensive perspective (Ulanowicz, 1995). Before conceptualising a measure of ecosystem organisation, it is useful to formalise our intuitive understanding of growth and development in ecosystems. Naturally, ecosystems change due to the immigration and emigration of species (ecological succession) and due to evolutionary changes within species. During ecological succession, hence when ecosystems develop from early-successional systems like open grasslands to late-successional systems like old-growth forests, we would expect for ecosystem organisation to start at an intermediate degree and increase over time (Fig. 2.1a). Anthropogenic disturbances should have an even stronger negative effect on ecosystem organisation than natural disturbances (like forest fires) do, as they affect ecosystem integrity in a more severe way (Fig. 2.1b).

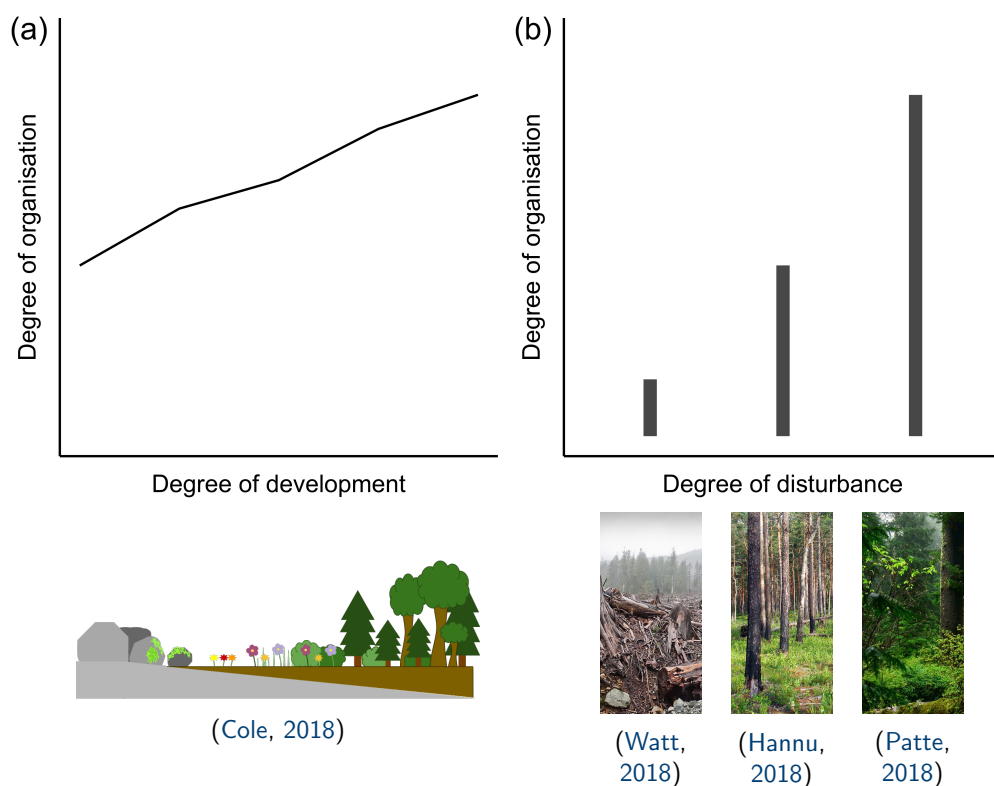


Figure 2.1: An intuition of ecosystem organisation as a function of the degree of development (a) and disturbance (b).

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Why does this intuition of ecosystem organisation make sense? Ecosystems function well if their parts, hence the interacting species and individuals, function well together; if species characteristics allow for interactions which permit growth and coexistence, if matter and energy is efficiently processed throughout the network and if hence both ecosystem structure and flows through the network demonstrate ecosystem integrity.

2.2 Ecosystem formation, evolution and development: the search for a macroscopic optimisation criterion

The search for law-like behaviour and fundamental selection principles behind the self-organisation of living systems has fascinated ecologists as well as physicists and engineers entering the field of ecology for decades and has inspired a variety of abstract concepts and more concrete hypotheses over the years.

The theoretical study of formation, evolution and development of ecosystems is generally approached in one of two different ways. The reductionist starts at the level of individuals and predicts an interaction network from traits and processes within single organisms, constructing ecosystems using a bottom-up approach. Systems ecologists on the other hand tackle ecological systems as a whole, starting from visible large scale patterns and trying to explain ecosystem development from a top-down perspective.

2.2.1 The reductionist perspective

The dynamics and organisation of ecological systems take place at a range of different scales. The biosphere can be divided into different ecosystems, which are built up of interacting populations, forming communities. The organisms of a single species however are the product of processes acting on the organic, tissue and cell level - which in turn are governed by the biochemistry of molecules. Which scale is the best to address depends very much on the specific question. Few reductionist ecologists would argue that the cell level is the right starting point for the study of ecosystem formation, but if the scale of reference should be evolving individuals or fixed species is already ambiguous. Nevertheless, from

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a reductionist's perspective, ecosystems are merely the product of the characteristics and dynamics of organisms, forming networks of influence, interaction and feedback.

2.2.2 System's ecology and phenomenology

Just as the macroecologist starts with descriptive statistical patterns of abundance, distribution and diversity of species and individuals and aims to infer causal mechanisms resulting in these observed patterns ([Brown and Maurer, 1989](#)), the systems ecologist studies the phenomenology of whole ecological systems and tries to therefrom deduce fundamental principles behind ecosystem formation and development.

The comprehensive phenomenology of ecosystem succession has at first been characterised by [Odum \(1969\)](#). He defines ecological succession as an orderly, directional and therefore predictable process, resulting from community-control, mediated and constrained by the physical environment, and culminating in a stabilised ecosystem. Characteristic differences between early- and late-successional ecosystem stages can be found in the species attributes (shift towards larger, less fast and stably growing organisms with more complex life cycles and higher degrees of specialisation), community structure (shifting from low diversity and strong dependence on extrabiotic nutrients to high species, biogeochemical and spatial heterogeneity, storing a large amount of organic matter and nutrients) and community energetics (shift from high rates of production compared to the standing biomass to a high biomass/energy flow ratio along with a balance between production and respiration), which all result in a trend towards more stable, self-sustaining and organised systems with developed cycling and feedback. ([Odum, 1969](#))

2.2.3 Maximum power and empower

Hypotheses about how and why species assemble into complex ecological networks can be traced as far back as to Darwin's *Origin of the Species*, in which he in the very last paragraph "contemplate[s] a tangled bank, clothed with many

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plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us" (Darwin, 1859). Natural selection and fitness differences are influenced by the complex ecological community forming the environment of an organism, while at the same time these interdependences are responsible for the formation of ecological networks of interactions and exchange. In the search of natural laws of patterns in ecosystem formation, Lotka was the first to propose a "physical principle" (Lotka, 1922) behind the development of ecological networks: the maximization of the power for useful purposes, hence the total energy flux through the system, would act as a selection principle on ecosystem evolution and development (see also Lotka, 1925). Lotka's understanding of this characterisation of the behaviour of living systems *far* from equilibrium as a necessary extension to the first and second law of thermodynamics, has in the 70s been taken up and reformulated by H.T. Odum as the "maximum power principle", stating it as "systems prevail that develop designs that maximize the flow of useful energy" (Odum, 1994). Later, Odum (1995) refined his ideas in the Maximum Empower Principle, taking into account the qualitative differences between types of energy when they are transformed during their way through the (eco-)system, and defined as the amount of a certain type of energy necessary to generate a flow or storage (Odum, 1968); empower is emergy over time. In the competition of self-organising processes, networks are stated to be selected for maximum empower.

2.2.4 Thermodynamics and biology

While both Lotka and Odum claim to have identified possible natural laws as extensions of the three laws of thermodynamics, which describe the behaviour of thermodynamic systems in or close to thermodynamic equilibrium, there are also more abstract hypotheses for the behaviour of systems far from thermodynamic equilibrium, based on the concept of entropy production. Entropy is the core concept of modern thermodynamics and statistical physics, and the trend of isolated systems to reach the state of maximum entropy is stated by the

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second law of thermodynamics. However, for the behaviour of thermodynamic systems far from the thermodynamic equilibrium, such axiomatic laws are missing. Developing physical systems produce entropy during irreversible processes, and the notion of entropy production has always interested scientists (like e.g. Clausius, Boltzmann and Gibbs), which has led to various physical and ideological discussions and, among other theories, the formulation of the principle of Maximum Entropy Production (MEP). It states for non-equilibrium systems to evolve in such a way that entropy production is maximised, and thereby offers a very general optimisation principle, which can determine the development of any kind of system in our known universe. Entropy production in the thermodynamic sense can therefore be interpreted as the heat loss organisms experience to maintain their basal metabolic function and their structured body (their state of order) which is measured in units of calories or energy. The counterpart to the principle of Maximum Entropy Production is Prigogine's Principle, which claims minimum entropy production. Those two principles however may not be regarded as contradictory or complementary; they are rather two different concepts acting in different frameworks and boundary conditions and have to be evaluated separately. ([Martyushev and Seleznev, 2006](#))

Both maximal and minimal entropy production can be useful ideas when applying thermodynamics to biology. On the one hand, ecosystems are non-isolated systems in the thermodynamic sense, receiving energy from the sun and dispensing energy back to the universe via heat. Thus if the principle of Maximum Entropy Production is valid for the universe, ecosystems which are closed, meaning that they don't exchange matter with their surrounding, but non-isolated (as they exchange energy over their borders) should maximise entropy production, thus dispense entropy with the highest possible rate constrained by the rates of energy in- and outflow. On the other hand, individual organisms or processes are superior if they produce minimal entropy and can use most of the energy for growth, storage and reproduction. Natural selection should therefore promote minimal entropy production. At the same time, systems of living beings are of course much further constrained than for example ideal gases, which consist of a number of particles. The evolution of living beings is constrained by evolutionary pathways, by the limits of random mutations and properties of life inherited from

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ancient generations, which is why there is a fair chance that any assembly of life, which optimises whatever kind of principle, just by pure chance will never have emerged.

Nevertheless, the relation of thermodynamics and living systems has occupied biologists and ecologists at the latest since Schrödinger's question of life (1944). The foundation for the application of entropy production to evolution and ecology has however been laid already earlier by Lotka (1922; 1925) with the proposition of the maximization of the total energy flux through an ecosystem as a selection principle during evolution, which, as he postulates, is to be understood as a necessary extension of the first and second law of thermodynamics for the explanation of the course of processes in ecological systems. This idea can be linked to both maximum and minimum entropy production. At first, compare two ecosystems with access to the same energetic resource, of which one does absorb the energy Q and the other doesn't. The first system will have more energy available than the second ($Q - Q_{diss}$, the dissipated energy which contributes to entropy production respectively) and therefore predominate due to the imposed selection principle. Now to maximise the total energy flux through the system, individuals who absorb most energy will dominate, thereby increasing Q and inevitably also Q_{diss} . Entropy production is thus maximised in the ecosystem. As soon as species have become that abundant that all the available energy is absorbed, evolution will proceed towards more effective energy use, decreasing Q_{diss} and thereby implementing the principle of minimum entropy production. (Martyushev and Seleznev, 2006)

Quantifying entropy production is highly non-trivial, which is why few practical attempts to evaluate the principles of maximum or minimum entropy production have been made. Prominent is the work of Dewar et al. (2006), in which he shows that the functional design of the molecular motor ATP synthase has evolved to a state which is consistent with selection for maximum entropy production - while still being highly efficient. The concept of minimum entropy production has also been applied to developmental biology by Prigogine and Wiame (Zotin and Zotin, 1997) with both interesting and controversial results Stoward (1962). The main conclusion of the studies is that heat production does decrease at separate stages of the ontogenesis, but much stronger increases

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during biological evolution ([Martyushev and Seleznev, 2006](#)). But not only the phylogeny, also the appearance of life has been explained as a consequence of the principle of Maximum Entropy Production: [Ulanowicz and Hannon \(1987\)](#) found support for Schrödinger's hypothesis ([1944](#)) that entropy production is larger in the presence of biota than in the absence of life. The same results derived from a different perspective provided [Swenson \(1997\)](#) by interpreting thermodynamic entropy as disorder. If a system as a whole (like the universe) proceeds to the state of maximum disorder with maximum speed, a subsystem (as an ecosystem) proceeds to ordered states (which is what we can see), as by doing so, it can produce disorder respectively entropy at a higher rate. A more applied entropy production theory for aquatic ecosystems, combining both notions of minimum and maximum entropy production, has been presented by [Johnson \(1990, 1992\)](#). Just recently, the arising flow configuration due to thermodynamic principles has been proposed as the constructal law, on the base of which the generation and evolution of design in nature, from the origin of life to human culture, is claimed to be explained ([Bejan, 2007](#); [Bejan and Lorente, 2011](#)).

Many more considerations about entropy production in biology and other scientific disciplines can be found in ([Martyushev and Seleznev, 2006](#)) along with additional references (see also e.g. [Nielsen and Ulanowicz 2000](#); [Smith 2008a,b,c](#)). Empirical data for concrete tests or even support of the proposed theories is scarce (though available, [Jaffé and Fonck 1994](#); [Holdaway et al. 2010](#)), but so is counter-evidence - the question about what is life is still troubling ecologists ([Meysman and Bruers, 2010](#)).

2.2.5 Self-organisation

Even though the perspective of the systems ecologist is from a top-down perspective, observing the macroscopic development of an ecological community, the goal is still to find (most simple) rules acting on the microscopic level, which can give rise to the system's behaviour. The spontaneous appearance of macroscopic structure or pattern without any external force, resulting, but being a priori not predictable from the stochastic interactions on the microscale of a complex system, is referred to as emergence. Emergent phenomena and complex systems are

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2.3. *A short overview over complexity measures applied in ecology*

thus two sides of the same coin: while complex systems are defined by appearance of emergent phenomena, emergent phenomena are just those phenomena, which spontaneously arise from complex interactions.

Ecosystems can be regarded as open complex systems far from equilibrium, which are stabilised by "self-organising autocatalytic structures, that serve as pathways for the dissipation of unusable energy" (Weber et al., 1989). Autocatalytic feedbacks within a system are responsible agencies for the selection for growth enhancing systemic configurations and act as a self-organising driver in ecosystem formation, evolution and development (Ulanowicz, 1979). Other examples of emergence and self-organisation in biology are swarm dynamics of birds and fish, which arise from simple interaction rules between individuals, the mind as being emergent from brain physiology and processes, life itself as being emergent from thermodynamic principles, the complexity of organisms emerging from selection and evolution, as well as the assembly of ecosystems, culminating in the Gaia hypothesis of a complex, self-regulating earth system (Lovelock, 1972; Ryan, 2007).

2.3 A short overview over complexity measures applied in ecology

The first approach to the complexity of an ecosystem is usually via the study of the structural properties of a food web, hence the trophic interactions between species and the therefrom resulting network. Measures and concepts from graph theory and network analysis allow for the quantification and analysis of the structure and dynamics of food webs. Questions of interest are common patterns in the topology of different food webs and the relationship between structure, dynamics and stability of ecological networks. (Dunne, 2009)

2.3.1 Structural complexity

The two fundamental state variables of the network topology are the number of species S and the number of interaction links L . The connectance $C = \frac{L}{S^2}$ is defined as the fraction of realised interactions given the potential number of interactions. Other summary measures of food web characteristics are the frac-

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tion of primary producers and top consumers, the maximum and average trophic level across taxa, number and length of food chains, measures of clustering and functional similarity between species, degrees of specialisation and generality and many more (compare [Dunne, 2009](#)). Apart from summary measures of the network as a whole, special attention is paid to the degree distribution across the network, which is the distribution of the number of interaction links over the species nodes.

Many real-world networks like social, technological, economic and biological networks have a "small-world" network topology, characterised by high clustering and small characteristic path lengths compared to random networks. Food webs have shown to be more highly connected and much smaller than other empirical networks studied and generally don't exhibit small-world properties. ([Dunne et al., 2002](#))

While in random networks, the degree distribution follows a Poisson distribution, many real-world networks show a power law distribution, where most nodes have few links and few nodes have many links. Most empirical food webs exhibit exponential or even uniform distributions do therefore not fall in the category of scale-free networks. These distribution are for example created from models in which allow for random immigration to local webs from a randomly linked meta-community combined with random extinctions in the local web. Networks with highly skewed distributions like a power law distribution are sensitive to the targeted loss of highly-connected nodes and comparably robust to random loss of (with high likelihood weakly connected) nodes. ([Dunne, 2009](#))

Another network property of interest is the degree of nestedness or assortedness. Assortative mixing refers to the tendency of nodes with similar degrees to be linked together. It has been shown that plant-animal mutualistic networks tend to be highly nested, highlighting asymmetric interactions, which points towards a way of ecosystem organisation to be situated between highly specialised pairwise coevolution leading to compartmentalisation and highly diffuse random coevolution ([Bascompte et al., 2003](#)). Disassortative mixing is assigned to stabilising effects of the interaction of specialists with generalists and vice versa ([Dunne, 2009](#)).

2.3.2 Ecosystem complexity

The idea that ecological complexity is not only a function of the structural, but also the functional properties of ecological systems, can be traced back to [Odum \(1962\)](#). He criticised the original definition of ecology as the relation between organisms and environment as too vague and broad, and called for the reformulation of ecology to be defined as the relationship between structure (such as community composition, the distribution of abiotic resources as well as the environmental conditions), representing the conditions of existence, and function, including eco-energetics, eco-cycling and eco-regulation on the scale of populations, communities and ecosystems. (see also [Odum, 1968](#)) Understanding ecosystem complexity hence requires taking into account both the structure of ecological networks and the flow through the system. Based on the energy flow through food webs, summary statistics of ecological networks incorporating structure and function such as the total system throughput or the average weighted path length have been derived and analysed across ecological networks ([Finn, 1976](#)). One question in ecosystem ecology is the quantification of ecosystem health and maturity, which has been suggested to be captured by energy recycling in the system (i.e. the fraction of flow devoted to cycling) ([Finn, 1976](#)). This Finn cycling index FCI has later been refined as the comprehensive cycling index CCI by [Allesina and Ulanowicz \(2004\)](#) to account for all flows engaged in energy re-usage.

Energy recycling is certainly one measure of ecosystem health, which incorporates both aspects of structure and functionality, but obviously also the flows related to recycling or non-recycling can be distributed in different ways and contribute to ecosystem complexity and maturity, as suggested by [Odum \(1969\)](#). To capture the flow patterns across ecosystems in a more comprehensive way, different information theoretical measures have been suggested over time. The first to notice a potential relation between ecosystem stability and the uncertainty of the flow links arbitrarily small units of energy take during their way through the food web, was [MacArthur \(1955\)](#). By realising that food webs can be regarded as energy transformers represented as a Markov chain and relating community stability to the amount of choice which energy has in following pathways through the network, he proposed the average entropy of the exiting flow distributions

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at each node as a measure of ecosystem stability. Focussing less on stability but on ecosystem resilience (hence "the ability of an ecosystem to resist changes in the presence of perturbations"), [Rutledge et al. \(1976\)](#) proposed the conditional entropy, the difference between the entropy of the flows and the average mutual information, which reflects the constraints on the flow pattern imposed by species characteristics and the network structure, as a measure of ecosystem stability: the remaining scope for choice regarding the pathways of energy flows is suggested to mirror ecological stability.

Inspired by [MacArthur \(1955\)](#) and [Rutledge et al. \(1976\)](#), [Ulanowicz \(1986, 2011\)](#) developed the idea of applying information theoretic diversity measures not to stocks but to processes further. Instead of focussing on stability, he aims to quantify ecosystem organisation, to study growth and develop in ecosystems and to assess ecosystem health maturity. His measure of *ascendency* is the product of two factors, which quantify the activity of the system (total energy throughput) and the level of organisation or constraint inherent among the trophic exchanges (average mutual information of the energy flows between pairs of species, see chapter 3) respectively. He proposes a tendency for self-organising ecosystems to develop towards higher values of ascendency in the absence of major perturbations and justifies this principle by linking ascendency to autocatalytic feedback processes in ecological systems ([Ulanowicz, 2002](#)).

2.4 Conclusion

The search for a metaphysical optimisation criterion for ecosystem development, an overarching trend of the living universe has fascinated mankind for a long time. However looking at measures of ecosystem organisation and integrity and hypothesising potential developmental trends does by no means rely on believes in systemic optimisation: the simple fact that any single entity, which is undergoing evolutionary processes, can only become as "fit" as its surrounding system allows, is reductionist motivation enough to seek descriptions of the system's status. Over the course of history, ecologists have proposed and borrowed from other disciplines a range of measures for ecosystem health and complexity, as discussed above, hence this thesis has a broad foundation to build upon. In the next chapter, complexity measures and hypotheses grounded in information theory will be introduced and motivated in more detail.

"Why don't you call it entropy? In the first place, a mathematical development very much like yours already exists in Boltzmann's statistical mechanics, and in the second place, no one understands entropy very well, so in any discussion you will be in a position of advantage."

(To Shannon, who at that time was looking for a good name for 'missing information'.)

John von Neumann (1940/41)



Background: information theory in ecosystems

3.1 Context: information, entropy and life

In the previous chapter, we have looked at the complexity of self-organising systems from a dynamical perspective, focussing on the emergence of macroscopic properties from microscopic interactive behaviour. In this chapter, we want to move our focus on ways of measuring differences in complexity, focussing on the emerging macroscopic state and its characteristics.

So what characterises a macroscopically "complex" state? Intuitively, complexity lies somewhere between order and disorder. More concretely, we regard macroscopically complex systems as those at intermediate zones of regularity - contrary to simple highly ordered and highly disordered systems (following [Parrott, 2010](#), compare Fig. 3.1).

The challenge of measuring complexity can hence be equated with the task of quantifying the degree of orderliness" of a system. And here is, where information and uncertainty enter the game. When looking at the spatial patterns in Fig.

3. Background: information theory in ecosystems

3.1. Context: information, entropy and life

3.1, one can ask oneself, given a two-dimensional coordinate on the grid, which colour the pixel is expected to have. In the most disordered case, basically any of the about a dozen different colours is equally likely. In the most ordered example on the other hand, we have complete certainty about the colour of our pixel: if the x- and the y-coordinate are both odd or both even, the pixel is yellow, and otherwise it is blue. The complex case lies somewhere in between: at the upper-left and lower-right corners of the spatial grid, we expect yellow pixels with high certainty, and in the centre, blue pixels are most likely. We have neither complete information about the configuration of the system (as in the ordered state), nor complete uncertainty (as in the disordered state).

These considerations reveal an important aspect about information in the information theoretic sense. Information doesn't have any direct connection to meaning, insight or understanding - it doesn't necessarily need to be useful for understanding the state or quality of the landscape, which pixel colour distribution it has. It rather is the counterpart to uncertainty. This becomes even more clear, when looking at written messages as an example. If you are to guess a six-letter word and know the places of the most common letters, such as " _ u _ _ l e", many words are possible (e.g. muscle, bubble, jungle) and a lot of uncertainty remains. If you know "p _ z z _ _", uncertainty about the final word is basically reduced to "puzzle" or "pizzas". "p _ z z _ _" hence contains more information in the information theoretic sense than " _ u _ _ l e" - no matter, if the word occurs in "Mowgli walked through the _ _ _ _ _", where " _ u _ _ l e" would reduce quite some uncertainty about the ending of the sentence, whereas "p _ z z _ _" doesn't make sense at

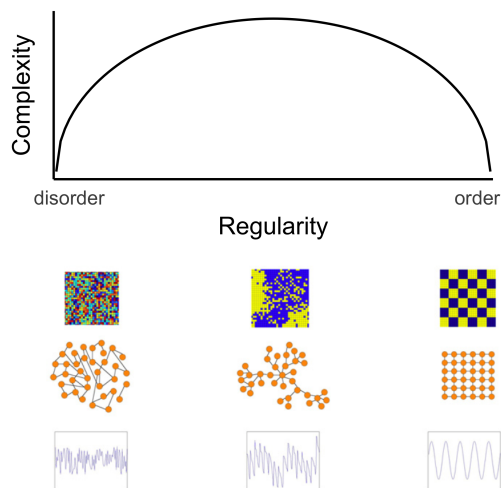


Figure 3.1: Complexity versus regularity, including corresponding examples of spatial, structural and temporal signatures. Both highly ordered and disordered systems are simple, whereas the most complex systems lie in the intermediate zone of regularity. The graphic is adapted from [Parrott \(2010\)](#).

3. Background: information theory in ecosystems

3.2. A short introduction to information entropy

all (example adapted and expanded from [Harte, 2011](#)).

The concept of uncertainty (or *entropy*) will be introduced more formally in the remainder of this chapter. What should be pointed out here is that systems, which differ in their regularity, do so because they differ in their information content, and that complex systems are those with an intermediate degree of determinacy.

It is important to note, as the anecdotal conversation between Shannon and von Neumann at the beginning of this chapter hints at, that while thermodynamic and information theoretic entropy bear the same name and share many characteristics, they are different concepts with different scientific background and applicabilities. Except where explicitly stated, all notions of entropy in this thesis relate to information theoretic entropy and shall not be confused with the thermodynamic correspondent.

3.2 A short introduction to information entropy

The core measure of information theory is information theoretic *entropy*. This measure along with the foundations of information theory has been developed by [Shannon \(1948\)](#), to quantify the uncertainty corresponding to a probability distribution. Intuitively, the less information about the possible outcomes of a stochastic phenomenon there is available, the higher the associated uncertainty. To illustrate this in more detail, we look at two dice (Fig. 3.2). The red die X is fair, meaning each of its six outcomes are equally likely, whereas the blue die is biased towards the six:

$$\begin{aligned} P(X_r = x_r) &= 1/6 \quad \forall x_r \in \{1, \dots, 6\} \\ P(X_b = x_b) &= \begin{cases} 0.05 & x_b \in \{1, \dots, 5\} \\ 0.75 & x_b = 6 \end{cases} \end{aligned} \quad (3.1)$$

For the fair red die, for each next outcome, the uncertainty is fairly high: each of the values occurs with equal probability, and a lot of uncertainty is resolved once

3. Background: information theory in ecosystems

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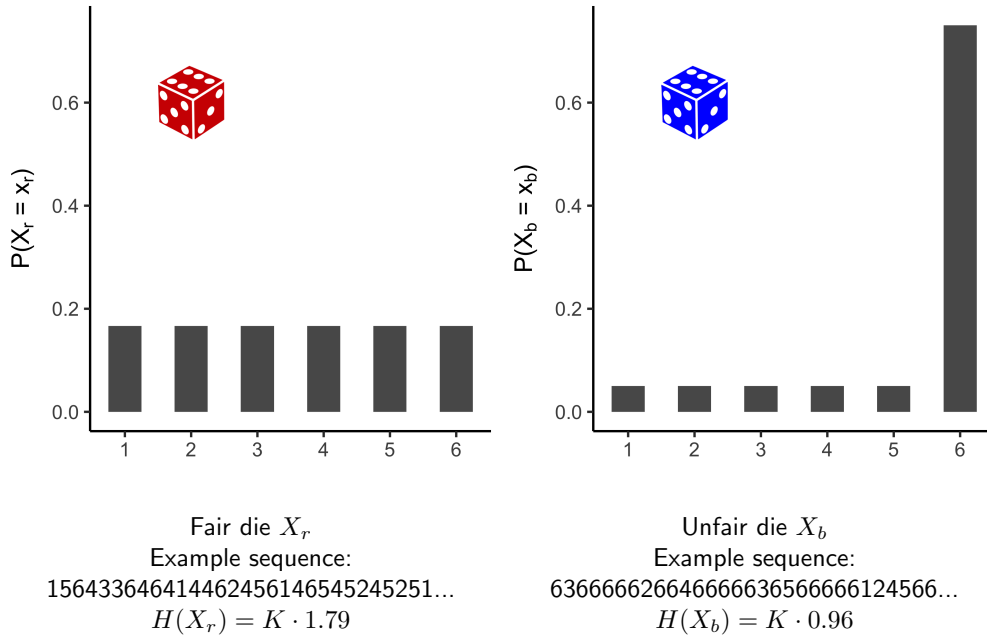


Figure 3.2: Two dice with different probability distributions, given in equ. 3.1

the new outcome is discovered. For the blue die however, there is less uncertainty about the next outcome: a six is always a good guess, and in case a six appears, very little additional information is gained.

This intuition is formalised in the definition of information entropy. The information entropy H of a discrete random variable X with n outcomes of probability $(p_1 := P(X = x_1), \dots, p_n := P(X = x_n))$ is defined as

$$H(X) = -K \sum_{i=1}^n p_i \ln p_i \quad (3.2)$$

where K is a positive constant and $0 \ln 0$ is treated as being equal to 0. It has been shown by [Khinchin \(1957\)](#), that any function $H(p_1, \dots, p_n)$ which is defined for any integer n and all $p_1, \dots, p_n$ such that $p_i \geq 0$ ($i \in 1, \dots, n$), $\sum_{i=1}^n p_i = 1$ and which is continuous for all n with respect to all its arguments, is of the form of equ. 3.2, if it fulfils the following so-called Khinchin axioms:

1. $H(p_1, \dots, p_n)$ takes its maximum, for a given n , when $p_i = 1/n$ for all i .

3. Background: information theory in ecosystems

3.2. A short introduction to information entropy

2. $H(p_1, p_2, \dots, p_n) = H(p_1, p_2, \dots, p_n, 0)$, hence adding any number of impossible events to a random variable doesn't change its entropy.
3. The entropy of the joint distribution of any two random variables X and Y is the sum of the entropy of one variable plus the expected value of the other, given the first: $H(X, Y) = H(X) + \sum_x P(X = x)H(Y|X = x)$.

In the following, K will, without constraints to generality, be set to 1 and left out of the equations for notational convenience.

The Shannon entropy can also be rewritten as $H(X) = \sum_{i=1}^n p_i \ln \frac{1}{p_i}$, which describes the weighted average of all the $\ln \frac{1}{p_i}$. The reciprocal of the probability of an outcome $\frac{1}{p_i}$ can be interpreted as the amount of surprise connected with this event – the smaller the probability of the outcome, the larger the surprise if it occurs anyway. In this way, the term information gets a more clear-cut meaning: a high information entropy of the whole distributions means a large average surprise or average uncertainty, along with a maximum information gain from new information (Harte, 2011).

The conditional entropy of a random variable Y conditioned on X , which has already been mentioned in the 3rd Khinchin axiom, is defined as

$$\begin{aligned}
 H(X|Y) &= \sum_{x \in \mathcal{X}} p(x) H(Y|X = x) = \\
 &= - \sum_{x \in \mathcal{X}} p(x) \sum_{Y \in \mathcal{Y}} p(y|x) \ln p(y|x) = \\
 &= - \sum_{x \in \mathcal{X}, y \in \mathcal{Y}} p(x, y) \ln \frac{p(x, y)}{p(x)},
 \end{aligned} \tag{3.3}$$

where $\mathcal{X}$ is the image of X and $\mathcal{Y}$ the image of Y . Looking at the chain rule for the conditional entropy

$$H(X|Y) = H(X, Y) - H(Y), \tag{3.4}$$

3. Background: information theory in ecosystems

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which can easily be derived from the entropy definitions*, the conditional entropy of X conditioned on Y can be understood as the amount of uncertainty about the joint distribution of X and Y , that remains, once Y is known/the uncertainty of Y is resolved.

The mutual information of two random variables X and Y quantifies how much uncertainty about one variable is reduced by knowing the other. It compares the joint probability distribution to the product of the marginal distributions,

$$MI(X, Y) = \sum_{x \in \mathcal{X}, y \in \mathcal{Y}} p(x, y) \ln \frac{p(x, y)}{p(x)p(y)}, \quad (3.5)$$

and is zero if and only if X and Y are independent.

Fig. 3.3 visualises how entropy, conditional entropy and mutual information of two random variables relate.

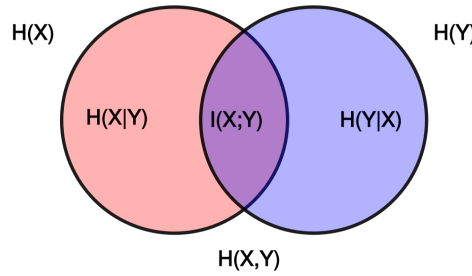


Figure 3.3: The mathematical relation between the entropy, conditional entropy and mutual information of two random variables X and Y

*

$$\begin{aligned} H(X|Y) &\stackrel{\text{Equ. 3.3}}{=} - \sum_{x \in \mathcal{X}, y \in \mathcal{Y}} p(x, y) \ln \frac{p(x, y)}{p(x)} = \\ &= - \sum_{x \in \mathcal{X}, y \in \mathcal{Y}} p(x, y) \ln p(x, y) + \sum_{x \in \mathcal{X}, y \in \mathcal{Y}} p(x, y) \ln p(x) = \\ &= H(X, Y) + \sum_{x \in \mathcal{X}} p(x) \ln p(x) = \\ &= H(X, Y) - H(X) \end{aligned}$$

3.3 Entropy and (mutual) information in quantitative networks

The above discussed measures of entropy can be used to assess the uncertainty or amount of information stored in any kind of probability or frequency distribution. One of the most commonly referred to distributions in a network is the so called degree distribution. The degree of a node is the number of links it has to other nodes.

In a weighted network, the links represent some sort of flow or flow capacity through the network. In the case of a food web, the flow represents matter, nutrients or kilocalories. In an interaction network, the weights could quantify more indirect flows such as general "effects" of species on each other. In any case, a quantified flow network allows the definition of probability distributions, related to the likelihood of finding a small unit of the flowing entity anywhere in the network.

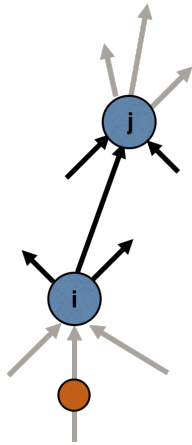


Figure 3.4: Conceptualisation of flow in a quantitative network - see text for details.

Imagine a flow quantum, an infinitesimally small unit of flow, as visualised in Fig. 3.4, and let the amount of flow along the link from node i to node j be denoted by T_{ij} . For notational simplicity, we furthermore define

$$\begin{aligned} T_{i.} &:= \sum_j T_{ij} \\ T_{.j} &:= \sum_i T_{ij} \\ T_{..} &:= \sum_{i,j} T_{ij}. \end{aligned} \tag{3.6}$$

The probability of finding the flow particle on the link between node i and j is given by $\frac{T_{ij}}{T_{..}}$. The entropy of the distribution of flow or flow particles across the network is hence given by

$$H_N = - \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{T_{ij}}{T_{..}}. \tag{3.7}$$

3. Background: information theory in ecosystems

3.3. Entropy and (mutual) information in quantitative networks

Another interesting property of the quantified network is the relation of in- and outflow distributions. In the example in Fig. 3.4, any flow particle has three different options for leaving node i , and three options for entering node j , hence there is a distribution of flow or flow particles across in- and outflowing links. In general, for any pair of nodes, we can look at two distributions

$$\begin{aligned}\mathcal{I}_{\text{out}} &= \left(\frac{T_{i1}}{T_{i.}}, \frac{T_{i2}}{T_{i.}}, \dots, \frac{T_{in}}{T_{i.}} \right) \\ \mathcal{J}_{\text{in}} &= \left(\frac{T_{1j}}{T_{.j}}, \frac{T_{2j}}{T_{.j}}, \dots, \frac{T_{nj}}{T_{.j}} \right).\end{aligned}\tag{3.8}$$

The average mutual information of $\mathcal{I}_{\text{out}}$ and $\mathcal{J}_{\text{in}}$ across the network is given by

$$\begin{aligned}MI(\mathcal{I}_{\text{out}}, \mathcal{J}_{\text{in}}) &\stackrel{\text{Equ. 3.5}}{=} \sum_{x \in \mathcal{I}_{\text{out}}, y \in \mathcal{J}_{\text{in}}} p(x, y) \ln \frac{p(x, y)}{p(x)p(y)} \\ &= \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{\frac{T_{ij}}{T_{i.}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}} \\ &=: MI_N.\end{aligned}\tag{3.9}$$

It quantifies, on average, how much information about the inflow to a node is resolved by knowing the outflow distribution of another node. In a network with only one single flowpath from source to sink, the outflow "distribution" across the one outflow link fully determines the inflow distribution of the reachable nodes, pushing the mutual information to its maximum. In a fully connected network on the other hand, where any node is equally likely reachable from any other node, the in- and outflow distributions are independent and not constrained by each other at all, which is why uncertainty remains maximal and the mutual information in of the flows is zero.

Two related measures to entropy and mutual information in networks, the capacity C_N and the ascendancy A_N , are defined by multiplying them with the total throughflow, so quantify both flow uncertainty respectively organisation

and network activity in one variable,

$$\begin{aligned} C_N &:= T_{..} \cdot H_N = - \sum_{i,j} T_{ij} \ln \frac{T_{ij}}{T_{..}} \\ A_N &:= T_{..} \cdot MI_N = \sum_{i,j} T_{ij} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}} \end{aligned} \quad (3.10)$$

3.4 Markov chain entropy in stochastic systems

Stochastic processes consist of not only one, but a sequence of random variables. The entropy of a random sequence of length n grows with n . The entropy rate of the stochastic process $\{\mathcal{X}_i\}$ is defined as

$$H(\mathcal{X}) := \lim_{n \rightarrow \infty} \frac{1}{n} H(X_1, X_2, \dots, X_n), \quad (3.11)$$

in case the limit exists. In case the X_i are independent, $H(X_1, X_2, \dots, X_n) = \sum_{i=1}^n H(X_i)$ (Thomas and Thomas, 2006).

In case the random variables of the stochastic process only depend on their predecessors, a so called Markov process or Markov chain is at hand. The entropy rate of a stationary Markov process $\mathcal{Y}$ with a finite number n of states, transition matrix (P_{ij}) and a stationary distribution (μ_i) is defined as

$$H(\mathcal{Y}) = - \sum_{ij} \mu_i P_{ij} \log P_{ij} \quad (3.12)$$

(Thomas and Thomas, 2006). The entropy of the trajectory from i is given by

$$H_i(\mathcal{Y}) = - \sum_j P_{ij} \log P_{ij}. \quad (3.13)$$

It quantifies the amount of information obtained, when the Markov chain moves one step ahead, starting in state i (Khinchin, 1957). The average of the entropy

of the trajectories gives the entropy of the Markov chain.

The higher the transfer entropy, the higher is the uncertainty about the outcome of the next stochastic event. A lower transfer entropy is hence related to increased certainty about the next state. In case these favoured more certain next states are similar to the previous one and don't disrupt the system's trajectory, lower Markov entropy can be related to increased stability in the system.

3.5 Transfer entropy as a measure of selection directionality

Transfer entropy quantifies the information transfer between two stochastic processes. Other than time-delayed mutual information, it is able to distinguish information shared due to common history or input signals from actually exchanged information (Schreiber, 2000).

The transfer entropy from Markov process X to Markov process Y (both of order 1, meaning the future state depends only on the current state and not any further previous states) with time delay 1 is defined as

$$TE_{X \rightarrow Y} := \sum P(Y_{n+1}, Y_n, X_n) \ln \frac{P(Y_{n+1}|Y_n, X_n)}{P(Y_{n+1}|Y_n)}. \quad (3.14)$$

The transfer entropy is non-symmetric and can be extended to Markov chains of higher order and time delays in the information transfer between the two processes. It can serve as an indicator of the direction of causality in stochastic systems.

The transfer entropy can be rewritten as

$$\begin{aligned} TE_{X \rightarrow Y} &\stackrel{\text{Equ. 3.14}}{=} \sum P(Y_{n+1}, Y_n, X_n) \ln \frac{P(Y_{n+1}|Y_n, X_n)}{P(Y_{n+1}|Y_n)} \\ &= E \left[\ln \frac{P(Y_{n+1}|Y_n, X_n)}{P(Y_{n+1}|Y_n)} \right] \\ &= H(Y_{n+1}|Y_n) - H(Y_{n+1}|X_n, Y_n) \end{aligned} \quad (3.15)$$

3. Background: information theory in ecosystems

3.5. *Transfer entropy as a measure of selection directionality*

([Razak, 2013](#)). Expressing the transfer entropy in terms of the conditional entropies of the respective time series as in equ. 3.15 eases its interpretation. The transfer entropy from X to Y can be understood as the amount of uncertainty about the next state of $\mathcal{Y}$, Y_{n+1} given the current state of $\mathcal{Y}$, Y_n , reduced by the uncertainty about the next state of $\mathcal{Y}$ given X_n and Y_n . Hence in case knowing X_n reduces the uncertainty about Y_{n+1} tremendously, the right term in equ. 3.15 is very small and the transfer entropy large. In case knowing X_n doesn't add any certainty about Y_n , $H(Y_{n+1}|Y_n) = H(Y_{n+1}|X_n, Y_n)$ and the transfer entropy is zero.

To calculate transfer entropies of empirical data sets, it is necessary to reconstruct the state space. This can be tricky due to finite sampling effects, unknown underlying probability distributions and the need to discretise potentially continuous distributions. An overview over different non-parametric estimators of population probability distributions in relation to transfer entropy estimates is given by [Razak \(2013\)](#). The simplest technique, which is to be favoured in case no further assumptions can be made, is the state space reconstruction via so called coarse graining or equidistant binning (classical histogram). The convergence of mutual information and transfer entropy estimates to continuous values via this technique has been proven theoretically ([Kaiser and Schreiber, 2002](#)).

3.6 Conclusion

Information is a core building block of life. The DNA contains information about the blueprint of cells, tissues and organs, those organs inform about the species an organism belongs to, and the distribution of species informs about the type of community we expect to be formed. Moreover, information is transferred in living systems - bottom-up from the genetic code to the organism to the ecosystem, top-down from the biotic environment back to a competing individual, and within hierarchical levels between cooperating, competing, mating or otherwise interacting individuals.

This chapter gives an overview, how moreover, information and related measures in their strict information theoretic definitions can give insights about the degree of organisation or complexity of complex systems. On top of their conceptual usefulness, they have the practical advantage of being able to project multidimensional entities such as quantitative networks onto one comprehensive measure. Aspects of their applicability to complexity-assessment in model ecosystems are presented in the case studies this thesis is comprised of.

"Essentially, all models are wrong, but some are useful."

George E. P. Box

Empirical Model-Building and Response Surfaces (1987)

4

Background: modelling complex ecosystem dynamics

4.1 Context: a complexity perspective on ecological modelling

The dynamics and organisation of ecological systems take place at a range of different scales and are in modelling studies generally approached in one of two different ways. The reductionist starts at the level of individuals and predicts an interaction network from traits and processes within single organisms, constructing ecosystems from systems biology applying a bottom-up approach. Macroecologists on the other hand deal with statistical patterns of abundance, distribution and diversity at the level of ecosystems as a whole ([Brown and Maurer, 1989](#)). The gap between reductionist and holistic approaches can be bridged by a complex systems' perspective on ecosystems, which 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.

4. Background: modelling complex ecosystem dynamics

4.2. *Modelling ecosystems: a brief overview*

The Tangled Nature Model of evolutionary ecology is an individual based stochastic model, in which species are emergent structures arising from the interactions between individual organisms. The reproduction rate of an individual is determined by the interaction with the other present genotypes. The coevolution of genotypes leads to intermittent dynamics of the species composition, mirroring quasi-stable periods of species composition, interspersed with mass extinction events, as indicated by the fossil record. The model has been studied extensively from different perspectives over the last years. Despite its simplicity and independence of specific parametrizations, the model is able to generate realistic macroecological properties such as species abundance distributions, species relationships and trophic networks (Christensen et al., 2002; Hall et al., 2002; Anderson et al., 2004; Jensen, 2004; Rikvold, 2007; Laird et al., 2008; Brinck and Jensen, 2017). 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.

For the presented research, different models of complex ecosystem dynamics and evolution are used - all of them based on or inspired by the Tangled Nature Model of evolutionary ecology (Christensen et al., 2002). In this chapter, the original model as well as the different modified versions are introduced and summarized. More detailed descriptions of the respectively applied models can be found in the respective chapters.

4.2 Modelling ecosystems: a brief overview

Ecosystems are generally depicted as networks of interactions between species coexisting within defined boundaries. The two main observables are species or groups of species and the interactions between them, either representing abstract degrees of influence or carrying energy, carbon, nutrient or other matter flow. Also in- and outflows to the environment and external compartments such as detritus can be included. Species sit at different positions in the web, which

4. Background: modelling complex ecosystem dynamics

4.2. *Modelling ecosystems: a brief overview*

in case of food webs are called trophic levels. The bottom trophic level of a food web is comprised of autotrophs, which produce complex organic compounds from an external energy source such as light and simple inorganic molecules such as carbon dioxide. The higher trophic levels of food webs are made up of heterotrophic organisms, which ingest organic carbon for energy production and biosynthesis. Food webs are generally represented in the language of graph theory and conceptualized as networks, where species are represented by vertices or nodes, and the trophic interactions by directed weighted edges or links. This allows to embed the field within in the discipline of complex network analyses, using tools from network theory to quantify, analyse and model the structure and dynamics of food webs. Common described network properties are for example the number of species and links in a web, network connectivity, the number of trophic levels, chains and cycles, clustering coefficients, degree distributions and degrees of nestedness and hierarchy ([Dunne, 2009](#)).

4.2.1 Types of models

The goal of the theoretical study of network formation and development is to find simple and yet fundamental rules which govern the mechanistics of ecological interactions and lead to the overarching network characteristics observed in nature. It is thereby important to distinguish between two different types of generating models in network ecology. In models of network dynamics, species networks are observed and those empirical observations are translated into a predefined species network. Models are then applied to study the population dynamics, dependent on the species interactions, ranging from Lotka-Volterra-models of a predator and a prey species ([Wangersky, 1978](#)) up to whole dynamic food web models. The other type of models are food web assembly models, which attempt to regenerate food web structures from species assembly rules, for example dependent of species sizes or feeding preferences. The aim of these models is to evaluate assumptions about the fundamental drivers behind ecological network formations (by comparing predictions with actual data) and to assess the stability of a food web as well as its reactions to disturbances such as species introduction or removal.

4.2.2 Network assembly models

The latter type of ecosystem model is of main interest for the addressed questions and in the following, different models of ecosystem development and evolution are introduced. The structure of ecological networks, may it be food webs, mutualistic networks or even gene regulatory networks, deviates from randomly assembled networks (May, 2006), hence any kind of network formation algorithm must incorporate some assumptions about rules which govern the development of observed network characteristics. Generally, three key features of biological networks have to be incorporated: biological networks gain and lose nodes (by migration or speciation and extinction), node properties can change (due to external influences or internal changes) and external forces alter the network structure (Proulx et al., 2005).

In the cascade model introduced by Cohen and Newman (1985), species are ordered according to their trophic positions and can only prey on species with a lesser trophic rank. Each species has the fixed probability $P = \frac{2CS}{S-1}$ of feeding on one of the C species with lesser rank than itself. The resulting food webs are therefore hierarchical and acyclic (Dunne, 2006; Solow and Beet, 1998). While early comparisons of the observed and from the cascade model predicted network patterns confirmed the validity of the model and its predictions are still far better than assumptions of random species assembly, more detailed data and analyses revealed later, that basic assumptions such as no looping and missing clustering don't agree with widely found empirical observations. (Dunne, 2009)

The niche model proposed by Williams and Martinez (2000) extends the cascade model by relaxing the strict feeding hierarchy and allows for more flexible and realistic ecological networks. To achieve this, each species is assigned an interval range, from which it is able to consume all species. Centre and width of the prey segment are randomly assigned. Comparisons with data show that the niche model performs much better in predicting network structure properties than the cascade model. Despite the fact that empirical food webs do not truly follow the assumption of "intervality", it has been shown that complex food webs "do exhibit a strong bias toward contiguity of prey, that is, toward intervality", which substantiates the usefulness of the model. (Dunne, 2009)

4.2.3 Complex ecosystem models

Complex systems science studies how the interactions between microscopic entities give rise to collective macroscopic behaviour, which is not intrinsically predictable from the actions on the microscale. The Tangled Nature Model as a complex ecosystem model lies somewhere in between network dynamics and network assembly models, being built on a predefined set of interactions between the overall species community, but allowing ecosystem to emerge from evolutionary dynamics (see below).

4.3 The Tangled Nature Model of evolutionary ecology (TNM)

The fundamental microscopic entity in the Tangled Nature Model is the genotype - an individual belonging to a species, defined by its genotype. No difference is made between genotypes and phenotypes. The genotype space is large (usually at least 1000 species) and can be imagined as the overall possible space of genotypes which could potentially be present in the studied environment. If the genotype space size is set large enough, this could potentially be the whole planet earth, with all imaginable viable biophysiochemical genotype configurations. In reality and at any certain time of the simulation, only a small subset of this overall genotype space will be populated with individuals. Between all pairs of genotypes in the genotype space, interaction strengths are predefined, which remain constant over time. Hence genotype S^α will always have the same effect on genotype S^β - however if S^β evolves into S^γ , interactions can obviously change. The interactions are envisioned to incorporate all types of interactions which can appear between two species - physical, chemical and indirect interactions. Interactions are non-zero for only a fraction of all species-pairs and independent independent for all $J(S^\alpha, S^\beta)$ (and $J(S^\beta, S^\alpha)$).

The initial population is randomly distributed over the genotype space, after which population and evolutionary dynamics go hand in hand. In each time step, individuals are prone to die and can reproduce with certain probabilities. The offspring probability of an individual is thereby solely determined by the strengths of interactions it perceives from all other present genotypes - hence if

4. Background: modelling complex ecosystem dynamics

4.3. *The Tangled Nature Model of evolutionary ecology (TNM)*

it is affected well by the biotic environment, it is more likely to reproduce than in case the net effect of the community on the genotype is strongly negative. Offspring undergo mutations, thereby allowing the species community to explore the genotype space for different viable ensembles. These dynamics give rise to 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 (compare Fig. 4.1).

Examples for model validity

Previous studies have confirmed that despite the simplicity of the Tangled Nature Model, the model is well capable of reproducing complex macroecological patterns found in nature such as the log-normal shaped species-abundance distribution, a power law relation between area and species diversity and exponential degree distributions of the indirect interaction network (Hall et al., 2002; Laird and Jensen, 2006; Laird et al., 2008; Lawson and Jensen, 2006). A most notable feature is the intermittent nature

of macro-evolution, denoted as punctuated equilibrium by Eldredge and Gould (1972), where the quasi-stable communities become more durable and stable over time (Christensen et al., 2002). In the course of co-evolution, the realised indirect interaction strengths tend to become more positive (di Collobiano et al., 2002), allowing for the support of a higher number of total individuals in the system, which is in accordance with previous proposals and findings (compare e.g. Fath and Patten (1998)). Furthermore, the communities become on average more coadapted (Jones et al., 2010), supporting claims made by Ulanowicz (1986) and others. The interactions play an important role for the evolution of species diversity in a system constrained by a single resource (Lawson et al., 2006), which is in line with the competitive exclusion principle (Hardin, 1960).

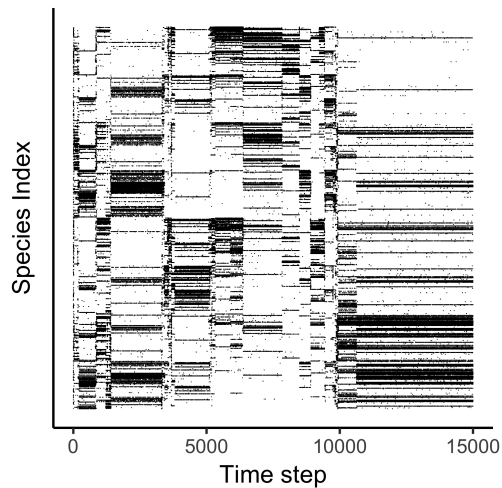


Figure 4.1: Occupation of the genotype space over time. Alternating stable (qESS) periods interrupted by transitions are clearly visible.

4. Background: modelling complex ecosystem dynamics

4.4. *Introducing trait similarity inheritance (CTNM)*

Overall, the Tangled Nature Model has in its 15 year long history shown to be able to reproduce a range of qualitative ecological patterns found in nature, and furthermore proven to be quite flexibly adaptable to the modelling necessities at hand, as will be discussed in the following paragraphs.

4.4 Introducing trait similarity inheritance (CTNM)

In the classical version of the Tangle Nature Model, interaction patterns between genotypes are distributed randomly over the genotype space. Offspring which undergo one or more mutations form a completely new species and don't necessarily inherit interactions strengths from their parents. The classical version of the model can hence be regarded as a model of macroevolution being detached from gradual microevolution - a concept vividly discussed in the literature (see eg. [Eldredge and Gould, 1972](#); [Bokma, 2015](#)). However in reality, single genetic mutations usually relate to phenotypes which are fairly similar to their parents. To account for genotype-phenotype similarity, an extension of the Tangled Nature Model includes correlations in the interaction patterns defined in the genome space, as first suggested and explored by [Laird and Jensen \(2006\)](#). In this thesis, to study the effect of inheritance, the procedure to introduce genotype-phenotype correlations in the interaction-matrix as defined by [Andersen and Sibani \(2016\)](#) is applied. Therefore, couplings (entries to the interaction-matrix) are described by a modified Bessel function of zeroth order (a product of two Gaussian variables), which resembles a Laplace distribution ($e^{-|x|^a}$) for the correlations. The correlation length (the number of gene locations for which the correlation applies) is regulated by the parameter K . The dynamics follow the same routine as in the classical version of the Tangled Nature Model.

4.5 Introducing intrinsic fitness

In the original Tangled Nature Model, the only difference between individuals of different species as well as the only determinant of their reproductive ability is the interspecific interaction pattern. Additionally, genotypes can be ascribed an intrinsic fitness - the fitness of a species in the environment in the absence of any

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4.5. *Modelling food webs (HTNM)*

other types, as first introduced by [Lawson et al. \(2006\)](#). This intrinsic fitness is uniformly distributed, randomly assigned and independent of space and time. The contribution of the intrinsic fitness and the interactions effects of the other genotypes both enter the offspring probability with given weights. The dynamics follow the same routine as in the classical version of the Tangled Nature Model. This version of the Tangled Nature Model is used to study explicitly the selection for intrinsic fitness versus the selection for coadaptation to the community.

4.6 Modelling food webs - a hierarchical version of the Tangled Nature Model (HTNM)

In the classical version of the Tangled Nature Model, the randomly predefined species interaction coefficients determine the offspring probability of a certain genotype dependent on the occupation of the rest of the genome-space, but no actual interactions which influence the abundance of other species take place. In reality, population dynamics are influenced by both direct and indirect effects. While indirect effects can facilitate (e.g. mutualism between bees and flowers) or impede (e.g. any parasite-host relationship) a species' growth, predator-prey-relationships have direct effects on the prey's abundance. Including predator-prey-relationships in the Tangled Nature Model introduces the transfer and circulation of matter and energy within the system and leads to the emergence of a hierarchical structure between species of different trophic layers.

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 Tangled Nature Model and

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has been introduced by [Brinck and Jensen \(2017\)](#).

Starting from the classical Tangled Nature Model, species are additionally classified as primary producers or consumers. Predator-prey relationships are arbitrarily predefined just like the indirect interactions, where each consumer is assigned a list of potential prey species. Indirect interaction strengths as denoted in interaction-matrix 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](#)). Offspring probability is, similar to the classical version of the Tangled Nature Model, given by currently perceived biotic environment of a species as defined in the interaction-matrix. Additionally, the reproduction of consumers is limited by competition for their prey species.

The dynamics occur in 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, the primary producer immediately gets the chance to regrow immediately. 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. $T_{ij}(t)$ stands for the amount of energy/biomass transfer from species i to species j during generation t .

Examples for model validity

The Tangled Nature Model has successfully been used to study predator prey interactions and therefrom resulting (non-quantitative) model food webs before ([Rikvold, 2007](#); [Rikvold and Sevim, 2007](#); [Rikvold, 2010](#)). Furthermore, it could be shown that in the here presented model, average and maximum food chain

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4.6. *Modelling habitat fragmentation (FTNM)*

lengths as well as feeding link degree distributions are well in line with empirical findings (Brinck and Jensen, 2017).

4.7 Modelling habitat fragmentation - complex population dynamics on a spatial landscape (FTNM)

To study population dynamics in fragmented landscape, a complex systems based model of interacting species with individual based stochastic dynamics on a spatial grid. The model is inspired by the Tangled Nature Model, but models population rather than evolutionary dynamics and is thus better understood as a new model of complex community dynamics rather than an extension to the Tangled Nature Model.

In this model, species have three intrinsic properties: maximum dispersal distance (indicating their dispersal ability), an intrinsic fitness term as well as a fitness effect of the community on the individual, both influencing their reproductive and competitive ability. Current reproductive success therefore depends on the current environment, which is determined by the interactions with individuals present in the same patch. Ecological communities are hence emergent structures arising from the interactions between individual organisms.

The initial landscape is comprised of 75 grid cells of equal size, located in a rectangular area with periodic boundaries. Individuals can migrate between patches according to their maximum dispersal distance. At time of fragmentation $\hat{t}$, two thirds of the habitat is removed and the remaining patches become largely isolated from immigration fluxes.

The community dynamics consist of four steps: death, reproduction, migration between patches and immigration from the species pool - a far distant and not explicitly modelled metacommunity on the mainland. A species' dispersal ability influences its migration distance, and both a species' intrinsic fitness and its interactions with community in the same patch determine its offspring probability (similar to Lawson et al., 2006). Emigration is density-dependent, while immigration is constant, but substantially higher before compared to after habitat fragmentation, accounting for the isolation of the landscape.

Examples for model validity

When looking at population dynamics after fragmentation, most of the species go extinct within in a very short timeframe, which matches empirical findings of rapid biodiversity loss due to habitat loss and isolation (see eg. [Wilson et al., 2016](#)). Diversity drops to the lowest values in the most remote patches, which can be attributed to less mixing and is in line with empirical findings (eg. [Economo and Keitt, 2010](#)).

Species life time distributions generally show to be exponentially or power-law distributed ([Stenseth and Smith, 1984](#); [Solé and Bascompte, 1996](#); [Pigoletti et al., 2005](#)), where power-law exponents have been found ranging from $-\frac{3}{2}$ to -2 ([Bak, 1996](#); [Keitt and Stanley, 1998](#); [Newman and Sibani, 1999](#)). The distribution of species life times found in this version of Tangled Nature Model of species life times follow well a power law with roughly similar steepness.

4.8 Conclusion

The Tangled Nature Model has initially been introduced as a genotype-based stochastic model to reproduce and study punctuated equilibria ([Gould and Eldredge, 1977](#)) and the relation between micro- and macroevolution. It's generic structure and complex systems based nature however can be transferred to questions on different spatial scales (landscape dynamics and fragmentation studies), temporal scales (community ecology) and systemic scales (covering studies of genotype, species, food web and whole ecosystem dynamics) and allows for new approaches from a different perspective. While food web studies for example have mainly been addressed from either a mechanistic bottom-up or a macroecological distribution-based perspective, the Tangled Nature Model enables bridging the gap between reductionist and holistic approaches in this field. When it comes to community dynamics, classical models usually focus on a subset of interactions, studying the role of mutualism, competition or hierarchies alone. Due to its abstraction from specific species with concrete real-world equivalents, the Tangled Nature Model in contrary is able to cover all interaction types at once. Its flexible implementation make it a valuable tool to dive into the exploration of self-organisation and coadaptation in ecological communities.

5

Case study: the evolution of information content in complex ecosystems

5.1 Context

This first case study looks at the evolution of the information content stored in complex model ecosystems during the course of evolution. Two types of measures are regarded: the amount of information necessary to describe the system, and the amount of information the system contains about itself.

In this chapter, the behaviour of information theoretic measures in simple evolving interaction networks is explored, before heading on to explore the applicability of information theoretic measures to ecosystem ecology in more complicated settings in the next chapters. The underlying models are very similar to the ones presented by [Christensen et al. \(2002\)](#) and [Andersen and Sibani \(2016\)](#). The dynamics are modified in order to permit the calculation of entropy rates.

5.2 Introduction

Living systems are situated between order and disorder, displaying a high degree of complexity due to their self-organising properties, being open and far-from equilibrium systems (Gatenby and Frieden, 2007; Jorgensen et al., 2007; Parrott, 2010, compare chapter 3, Fig. 3.1). The information content of living systems has been postulated as one of the major tools for understanding organism and ecosystem functioning (Nurse, 2008) and been attempted to be quantified from various sides (Morowitz, 1955; Ulanowicz, 1986). Due to the multidimensionality of ecosystems, the ambiguous definition of the term *complexity* and the context-dependency of information, agreed-upon measures and comprehensive studies about their long-term development in evolving ecosystems are lacking.

This chapter compares the behaviour of several different measures to quantify the information content of complex ecosystems. It is important to distinguish two different types of information in living systems. First, one can analyse how much information is stored within the system, hence how much information is necessary to describe the state of the system. Second, the system contains some information about itself and one can look at how much information the system stores about its own future or developmental path. One would expect, that both types of information content (information within the system, and information the system contains about itself) are larger, the more developed, organised and stable the system is. We therefore compare two scenarios, an early and a late successional stage, to assess the development of information content in complex ecological systems.

5.3 Methods

The models

The modelling study builds on the Tangled Nature Model of evolutionary ecology, as introduced in chapter 4.3 (Christensen et al., 2002), with the only difference being the modelling of offspring creation and mutations (see below), to simplify the calculations. To extend the range of results, not only the original version,

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but also the correlated version (Andersen and Sibani, 2016) are studied (compare chapter 4.4). The later differs from the further in the way the genome space is set up. While in the original TNM, one mutation can transform a species in an offspring with very different interaction characteristics from its parent, in the CTNM, a mutated offspring has a similar interaction pattern to the other species in the ecosystem as its parent. This mirrors the course of evolution more realistically. We therefore assume that evolutionary dynamics happen more quickly in the correlated version and effects are detectable sooner. The dynamics in both models are adapted as follows to simplify the entropy calculations.

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, the following dynamics are executed.

1. Select one individual from whole pool of individuals at random.
2. With P_{off} , the individual reproduces. The parent individual is replaced by two exact copies of the parent.
3. With P_{mut} , in one offspring a single mutation occurs: one gene is chosen at random and its digit is changed from -1 to 1 or vice versa.
4. The same individual that has reproduced (or its offspring with the exact same genotype for that matter) dies with P_{death} .

P_{mut} and P_{death} are constant and equal for all species, while P_{off} is determined by the degree of coadaptation $\tilde{J}(S^\alpha, t)$ with the other currently present individuals,

$$\tilde{J}(S^\alpha, t) := \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t)}{N(t)}, \quad (5.1)$$

where J is a matrix of dimension $(2^L \times 2^L)$ and stores the interaction effects for

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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 (compare chapter 4.3).

Asexual reproduction occurs with probability

$$P_{\text{off}}(S^\alpha, t) = \frac{\exp(\Xi(S^\alpha, t))}{1 + \exp(\Xi(S^\alpha, t))} \in (0, 1), \quad (5.2)$$

where the weight function $\Xi(S^\alpha, t)$ is defined by

$$\Xi(S^\alpha, t) = w \cdot \tilde{J}(S^\alpha, t) - \frac{N(t)}{R}. \quad (5.3)$$

w scales the relative importance of the interaction effects for the offspring probability of a species and R stands for the quality of the habitat and controls the carrying capacity of the community.

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 $N(t)/p_{\text{death}}$ 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, which, within a certain regime of parameters, form 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.

To study the difference between early and late successional communities, two different scenarios are compared. In the *late successional* scenario, quasi-stable communities emerge from the interactions (see Results). In the *early successional* scenario, species enter and exit the community fairly rapidly and no coadapted communities become dominant yet. The parameter values for the scenarios are specified in Table 5.1.

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5.3. Methods

	TNM		CTNM	
Successional stage:	late	early	late	early
L	10	10	16	16
K	-	-	4	4
θ_{int}	0.8	0.8	0.8	0.8
N_{init}	500	500	5000	5000
w	50	11	60	75
P_{death}	0.02	0.02	0.4	0.4
P_{mut}	0.5	0.8	0.7	1.0
R	100	100	4	4

Table 5.1: Choice of parameters for the two models and two scenarios. (L = genome length, K = correlation parameter, θ_{int} = probability of interaction, N_{init} = initial number of individuals, w = strength of interaction effect, P_{death} = probability of death, P_{mut} = mutation probability, R = carrying capacity parameter)

Information content within the system

Different entropic measures, which describe the information content of macroscopic properties of the system are analysed.

The Shannon entropy of the species abundance distribution (Shannon index) is given by

$$H_{\text{Shannon}}(t) = - \sum_{S^\alpha \in \{1, \dots, 2^L\}} \frac{n_{S^\alpha}(t)}{N(t)} \ln \frac{n_{S^\alpha}(t)}{N(t)} \quad (5.4)$$

and measures the diversity of the species in the community, taking into account the evenness of the species abundances. The more species there are and the more even the individuals are distributed over the species, the higher the uncertainty about the species affiliation of a randomly chosen individual.

Degree distributions in ecological networks play a central role in the description and interpretation of complex networks (Williams, 2010). The entropy of the degree distribution is calculated as

$$H_{\text{deg.dist.}}(t) = - \sum_i \frac{d_i}{D} \ln \frac{d_i}{D} \quad (5.5)$$

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where d_i is the number of species with degree i and D the current species diversity.

Furthermore, the distribution of interaction strengths is analysed. The effect of any species S^i on species S^j is given by the product of the interaction effect between two individuals, the number of individuals in the one species and the number of individuals in the other species,

$$T_{ij}(t) := \underbrace{|J(S^j, S^i)|}_{\substack{\text{effect of an individual of species } S^i \\ \text{on an individual of species } S^j}} \cdot n_{S^i} \cdot n_{S^j}. \quad (5.6)$$

We look at the net (absolute) effect between species, to quantify the distribution of interaction strengths and to avoid cancelling out interactions which are strong but of different sign. We assess two entropic measures with regards to the interaction network, the entropy H_{int} and the average mutual information MI_{int} ,

$$H_{\text{int}} = - \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{T_{ij}}{T_{..}} \quad (5.7)$$

$$MI_{\text{int}} = \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}}. \quad (5.8)$$

Information the system contains about itself: entropy rates

Entropy rates describe the amount of information related to the transition between different states of a system. In order to calculate these, we regard the Tangled Nature Model as a Markov process.

The state of the system $Q(t)$ can be described by the distribution of individuals over species $Q(t) = (n_1(t), \dots, n_{2L}(t))$. As the future state $Q(t+1)$ solely depends on $Q(t)$ (P_{mut} and P_{kill} are time-independent, and P_{off} only depends on $Q(t)$, compare equ. 5.2), the evolution of the model ecosystems is a Markov process. For any given state $Q(t)$, only a small number of states $Q(t+1)$ can be reached with non-zero probability, as summarized in Table 5.2.

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Current state	$Q(t) = (n_1(t), \dots, n_{S^\alpha}(t), \dots, n_{2^L}(t))$
Transition 1	
Future state:	$Q(t+1) = (n_1(t), \dots, n_{S^\alpha}(t), \dots, n_{2^L}(t))$
Transition type:	$n_i \rightarrow n_i \quad \forall i \quad (1 \text{ future state})$
Dynamics:	No reproduction, no death OR reproduction, no mutation, death
Transition probability:	$P(n_i \rightarrow n_i \quad \forall i) = \sum_{S^\alpha \in \{1, \dots, 2^L\}} \frac{n_{S^\alpha}(t)}{N(t)} (1 - P_{\text{off}}(S^\alpha, t))(1 - P_{\text{death}}) +$ $+ \sum_{S^\alpha \in \{1, \dots, 2^L\}} \frac{n_{S^\alpha}(t)}{N(t)} P_{\text{off}}(S^\alpha, t)(1 - P_{\text{mut}})P_{\text{death}}$
Transition 2	
Future state:	$Q(t+1) = (n_1(t), \dots, n_{S^\alpha}(t) - 1, \dots, n_{2^L}(t))$
Transition type:	$n_{S^\alpha} \rightarrow n_{S^\alpha} - 1 \quad (2^L \text{ future states})$
Dynamics:	No reproduction, death in S^α
Transition probability:	$P(n_{S^\alpha} \rightarrow n_{S^\alpha} - 1) = \frac{n_{S^\alpha}(t)}{N(t)} (1 - P_{\text{off}}(S^\alpha, t))P_{\text{death}}$
Transition 3	
Future state:	$Q(t+1) = (n_1(t), \dots, n_{S^\alpha}(t) + 1, \dots, n_{2^L}(t))$
Transition type:	$n_{S^\alpha} \rightarrow n_{S^\alpha} + 1 \quad (2^L \text{ future states})$
Dynamics:	Reproduction in S^α , no mutation, no death OR reproduction within species close to S^α (distance = 1 gene), mutation to S^α , no death
Transition probability:	$P(n_{S^\alpha} \rightarrow n_{S^\alpha} + 1) = \frac{n_{S^\alpha}(t)}{N(t)} P_{\text{off}}(S^\alpha, t)(1 - P_{\text{mut}})(1 - P_{\text{death}}) +$ $+ \sum_{\{S_\beta \in \{1, \dots, 2^L\} : \text{gen. diff.}(S_\alpha - S_\beta) = 1\}} \frac{n_{S_\beta}(t)}{N(t)} P_{\text{off}}(S_\beta, t)P_{\text{mut}} \frac{1}{L}(1 - P_{\text{death}})$
Transition 4	
Future state:	$Q(t+1) = (n_1(t), \dots, n_{S^\alpha}(t) - 1, \dots, n_{S^\beta}(t) + 1, \dots, n_{2^L}(t))$
Transition type:	$n_{S^\alpha} \rightarrow n_{S^\alpha} - 1 \ \& \ n_{S^\beta} \rightarrow n_{S^\beta} + 1 \quad (2^L \cdot L \text{ future states})$
Dynamics:	Reproduction of S^α , mutation to close species S^β , death of S^α
Transition probability:	$P(n_{S^\alpha} \rightarrow n_{S^\alpha} - 1 \ \& \ n_{S^\beta} \rightarrow n_{S^\beta} + 1) = \frac{n_{S^\alpha}(t)}{N(t)} P_{\text{off}}(S^\alpha, t)P_{\text{mut}} \frac{1}{L} P_{\text{death}}$

Table 5.2: Possible state transitions in the Tangled Nature Model

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5.4. Results

As discussed in chapter 3.4, the entropy of a trajectory of a Markov process $\mathcal{Y}$ with a finite number n of states and transition matrix (P_{ij}) , starting in state i , is defined as

$$H_i(\mathcal{Y}) = - \sum_j P_{ij} \ln P_{ij}. \quad (5.9)$$

As mentioned before, from any current state $Q(t) = (n_1(t), \dots, n_{2L}(t))$, only the few future states enlisted in Table 5.2 are reachable, and all other transition probabilities are zero. The entropy of the trajectory of the Tangled Nature Model simulation at any given state $Q(t)$ is therefore given by

$$\begin{aligned} H_Q(t) &= - \sum_j p_{Q(t)Q_j} \ln p_{Q(t)Q_j} \stackrel{f(x) := -x \ln x}{=} \\ &= \sum_j f(p_{Q(t)Q_j}) = \\ &= f(P(n_i \rightarrow n_i \quad \forall i)) + \\ &\quad + \sum_{S^\alpha \in \{1, \dots, 2^L\}} f(P(n_{S^\alpha} \rightarrow n_{S^\alpha} - 1)) + \\ &\quad + \sum_{S^\alpha \in \{1, \dots, 2^L\}} f(P(n_{S^\alpha} \rightarrow n_{S^\alpha} + 1)) + \\ &\quad + \sum_{S^\alpha \in \{1, \dots, 2^L\}} L * f(P(n_{S^\alpha} \rightarrow n_{S^\alpha} - 1 \ \& \ n_{S^\beta} \rightarrow n_{S^\beta} + 1)). \end{aligned} \quad (5.10)$$

5.4 Results

Dynamics

The adaptations to the dynamics of the Tangled Nature Model don't change the macroscopic intermittent behaviour of the species community. Alternating quasi stable periods are interrupted by transitions as shown in Fig. 5.1b and 5.1d. In the early-successional stages, the whole species space is explored and no stable communities have formed yet (Fig. 5.1a and 5.1c).

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5.4. Results

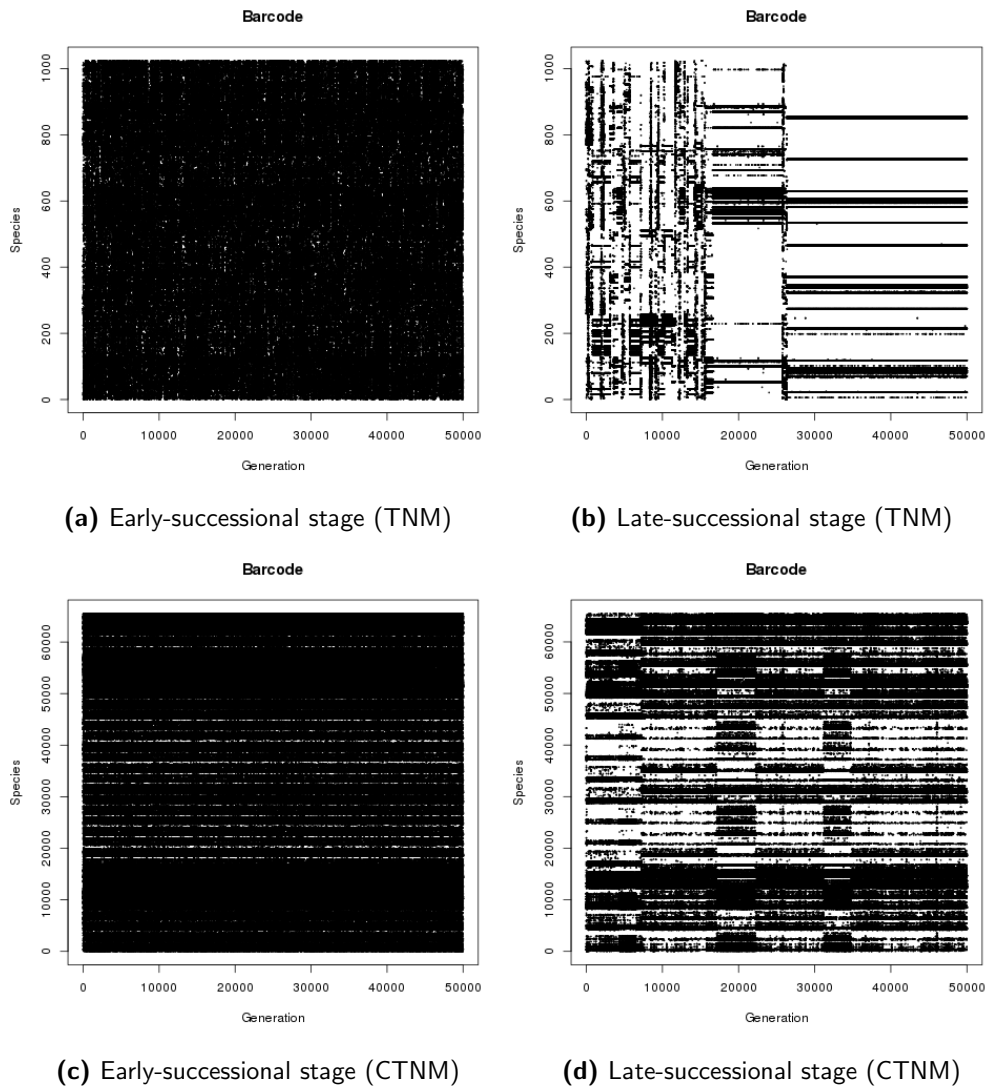


Figure 5.1: Occupation of the genotype space over time (parameters in Table 5.1)

The higher degrees of coadaptation in the late-successional quasi stable communities allow for a higher number of individuals (Fig. 5.2a), while the subset of present species becomes smaller (Fig. 5.2b).

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5.4. Results

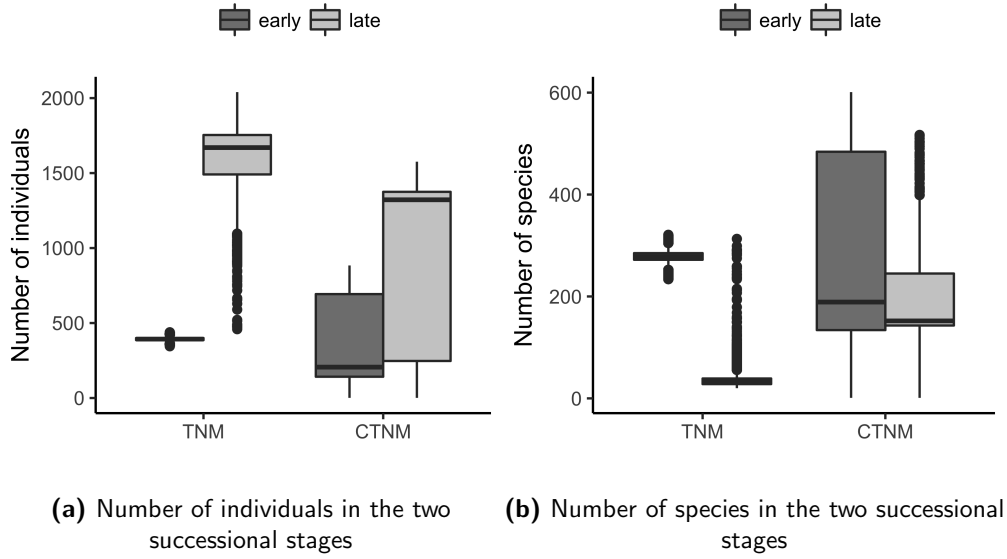


Figure 5.2: Box-Whisker-Plots of the number of individuals and species in an early and late successional stage for the uncorrelated and the correlated version of the model. The boxes show the median (solid line in the middle of the box), the lower and upper quartile ($Q1$ and $Q3$, boundaries of the 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). Data stems from $2*10$ simulation runs covering 50000 generations each.

Information content within the system

We hypothesised that the information content within the system increases the further developed an ecosystem is. This hypothesis is confirmed by the discovered decrease in entropy (or uncertainty) of the distribution of individuals over species (Shannon entropy, Fig. 5.3a), the degree distribution (Fig. 5.3b) and the distribution of interaction strengths between species (Fig. 5.3c). The decreased entropy implies that more bits of information are necessary to describe the state of the system and hence denotes a higher information content within the system. These findings are independent of the underlying genotype space as they hold for both studied models.

5. Case study: the evolution of information content in complex ecosystems

5.4. Results

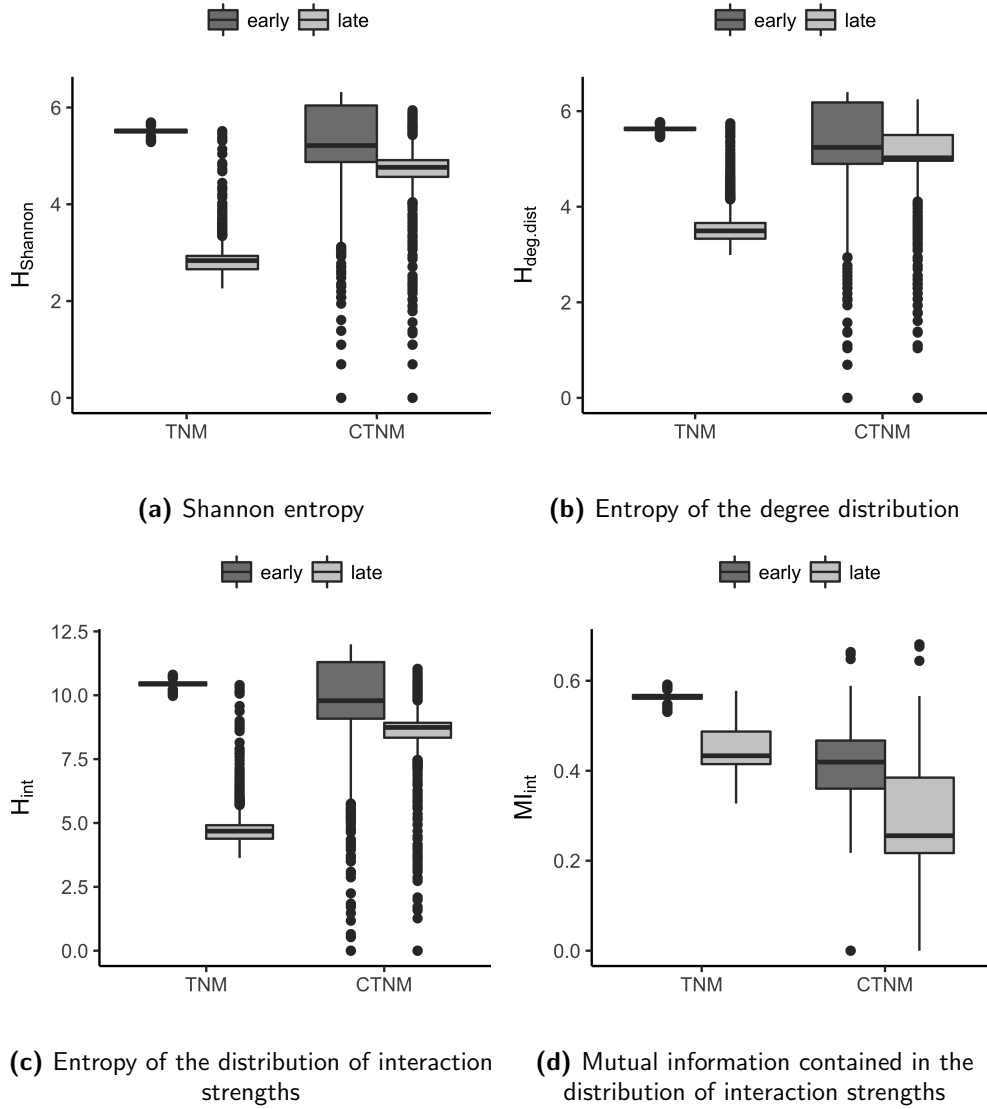


Figure 5.3: Box-Whisker-Plots of the information content within the model ecosystems in an early and and late successional stage for the uncorrelated and the correlated version of the model. The boxes show the median (solid line in the middle of the box), the lower and upper quartile ($Q1$ and $Q3$, 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). Data stems from $2*10$ simulation runs covering 50000 generations each.

The entropy of the distribution of interaction strengths is partly explained by the mutual information contained in the in- and outflow distributions (compare equ.

5. Case study: the evolution of information content in complex ecosystems

5.4. Results

5.8). Fig. 5.3d shows, that the relative amount of mutual information drops in the late successional stage. This means, that progress in the successional development of the model ecosystem goes along with reduced uncertainty about the distribution of interaction strengths, but is not explained by increased correlation of interactions in the network.

Information the system contains about itself

When it comes to the amount of information the system contains about itself, there are differences between the two models. While in the classical version of the Tangled Nature model, the entropy rate decreases hence the information content becomes higher in later successional stages, the opposite is true in case the underlying genotype space is correlated (Fig. 5.4a). The decrease in the entropy rate in the classical version of the model can be explained by the strong stabilisation of the system. As the probability of the system transitioning to the exactly same state it currently resides in (transition 1 in Table 5.2) approaches 1 (Fig. 5.4b), the transition probabilities become very unevenly distributed and hence the entropy rate, defined as the entropy of the distribution of transition probabilities (equ. 5.10), decreases. The increase in the probability of no state change is also visible in the correlated version of the model, however the absolute probabilities reside much lower around 0.4. It must be therefore, that the increased probability of no state change doesn't make the distribution of transition probabilities much more even and hence doesn't resolve but actually increase uncertainty and hence the entropy rate.

5. Case study: the evolution of information content in complex ecosystems

5.5. Discussion

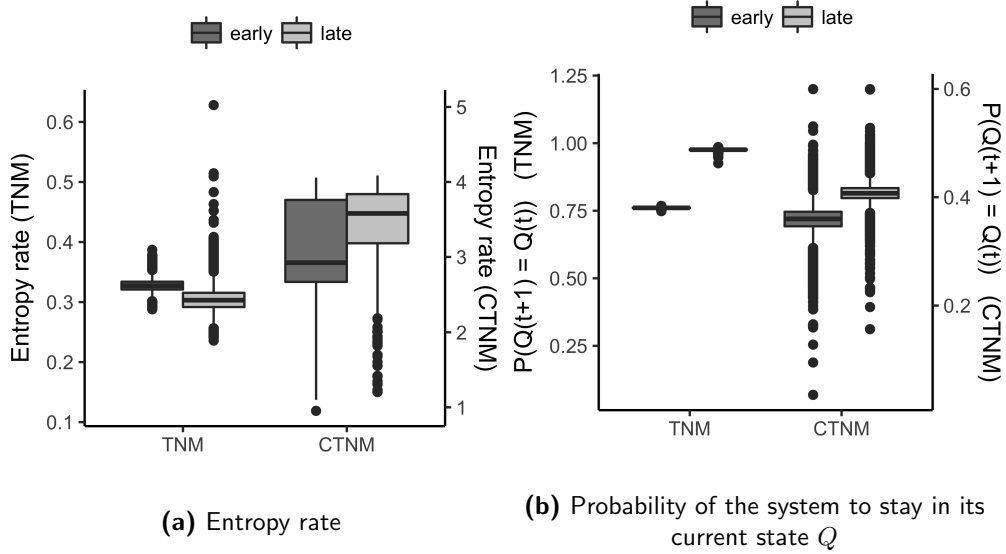


Figure 5.4: Box-Whisker-Plots of the entropy rate within the model ecosystems as well as the probability that the system stays in its current state in an early and and late successional stage for the uncorrelated and the correlated version of the model. The boxes show the median (solid line in the middle 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). Data stems from $2*10$ simulation runs covering 50000 generations each.

5.5 Discussion

As hypothesised, the information content within the system increases when the model ecosystem progresses further in successional development, for a variety of macroscopic distributions. The distribution of individuals over species 5.3a, of interactions across species 5.3b and of interaction strengths across interactions 5.3c becomes more constrained and uneven as the system coadapts and develops. These findings are in line with hypotheses of living systems being information processing entities (Morowitz, 1955; Nurse, 2008) and with previous findings of increased information storage in model ecosystems over evolutionary time scales (Jones et al., 2010).

The information the system contains about itself only increases in situations, where the system becomes extremely stable and the probability of transitions to

the current state lie close to 1 (Fig. 5.4).

The advantage of model studies is, that a range of different measures can easily be compared due to complete data availability. The results show, that the information content within ecosystem increases during the course of succession for all the assessed macroscopic distributions. Hence the development of the information content in the species abundance distribution - a distribution, for which data is available in many cases - can give insights about the developmental state of the system, without the necessity to also collect interaction network degree distributions.

5.6 Conclusion

The results of this first chapter show, that there is a relation between developmental stage and information content of ecological systems, and that simple information theoretic measures of species interaction networks can reveal properties of the underlying ecosystems. We hence move on to explore more complex and specific measures in less general settings in the next chapters.

6

Case study: selection transfer in complex ecosystems

6.1 Context

This case study continues the exploration of ecological communities emerging from species interactions, but rather than assessing the information content *within* or about the system, it looks at the information *transfer* giving rise to the system. As discussed in the introduction, ecological systems are usually regarded from a reductionist perspective, where natural selection on the individuals and species determines the ecosystem. This reductionist perspective can be contrasted with the view that as species have to fit in the surrounding system, the system exerts selection pressure on the evolutionary pathways of the species themselves. In this chapter, a mathematical framework to quantifying the relative weight of bottom-up control through natural selection and bottom-down control through coadaptation grounded in information theory is presented and assessed in complex model ecosystems.

The used model is the original version of the Tangled Nature Model as presented by [Christensen et al. \(2002\)](#).

6.2 Introduction

Ecosystems are emergent features of ecological and adaptive dynamics of a community of interacting species. By natural selection through the abiotic environment and by co-adaptation within the community, species evolve, thereby giving rise to the ecological networks we regard as ecosystems. From this classical reductionist perspective depicted in Fig. 6.1, ecosystems are simply the sum of those communities, populations and organisms, which have shown to be "fittest" in the course of adaptation and selection.

At the same time, as discussed in detail in chapter 2, ecosystems form coadapted entangled networks, where species are dependent on each other in complex manners. For a species to do well within its ecological community, it doesn't only need to win natural selection for intrinsic fitness and adaptation to the environment - it also has to fit in its ecological community; being benefited by the current system and at the same time being beneficial for the persistence of the system. Not even taking into account any metaphysical considerations, it becomes clear that the system exerts selection pressure on the evolutionary pathways of the species themselves.

This interplay of bottom-up and top-down control in the development and growth of ecological systems has long been discussed, however empirical ecosystem data is scarce and a comprehensive mathematical framework is lacking. We present a way of quantifying the relative weight of natural selection and coadaptation grounded in information theory, to assess the relative role of bottom-up and top-down control in the evolution of ecological systems. We use an individual based stochastic model of coevolution inspired by the Tangled Nature Model of evolutionary ecology to assess the measures over the course of ecosystem development.

The aim of this study is to assess transfer entropy as a potential mathematical framework for quantifying selection transfer in terms of bottom-up and top-down control in ecosystems. In case the technique works, we expect to see differences in the relative role of bottom-up and top-down control in different successional stages. Furthermore, those species which are strongly coadapted to the current community are expected to be the ones mainly influenced by top-down control,

and those species with a high contribution to the system's overall degree of coadaptation should be the main drivers of bottom-up control.

6.3 Methods

The model

The modelling study uses on the Tangled Nature Model of evolutionary ecology, as introduced in chapter 4.3. The following description closely follows the one given by [Christensen et al. \(2002\)](#).

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, the following dynamics are executed.

1. Select one individual from the pool of individuals at random and remove it from the community with probability P_{death} .
2. Select one individual from the pool of individuals at random and let it reproduce with probability P_{off} . Reproduction happens asex-

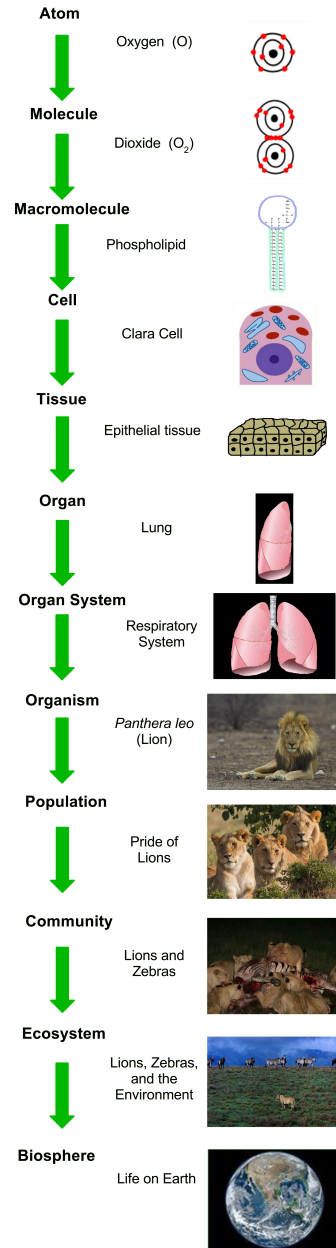


Figure 6.1: Levels of biological organisation - a reductionist perspective ([Mikala, 2013](#))

6. Case study: selection transfer in complex ecosystems
6.3. Methods

ually and the parent individual is replaced by two offspring being exact copies of the parent.

3. Each of the both offspring undergoes mutation in each of its genes with probability P_{mut} . Mutations means that the gene value is changed from -1 to 1 or vice versa.

P_{mut} and P_{death} are constant and equal for all species, while P_{off} is determined by the degree of coadaptation $\tilde{J}(S^\alpha, t)$ with the other currently present individuals,

$$\tilde{J}(S^\alpha, t) := \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t)}{N(t)}, \quad (6.1)$$

where 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 $J(S^\beta, S^\alpha)$). $\tilde{J}(S^\alpha, t)$ can be understood as the average interaction effect of all individuals S in the genotype space $\mathcal{S}$ on genotype S^α (compare chapter 4.3).

Asexual reproduction occurs with probability

$$P_{\text{off}}(S^\alpha, t) = \frac{\exp(\Xi(S^\alpha, t))}{1 + \exp(\Xi(S^\alpha, t))} \in (0, 1), \quad (6.2)$$

where the weight function $\Xi(S^\alpha, t)$ is defined by

$$\Xi(S^\alpha, t) = w \cdot \tilde{J}(S^\alpha, t) - \frac{N(t)}{R}. \quad (6.3)$$

w scales the relative importance of the interaction effects for the offspring probability of a species and R stands for the quality of the habitat and controls the carrying capacity of the community.

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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 $N(t)/p_{\text{death}}$ time steps, which corresponds to the average time taken to kill all living individuals. The model is run for a total of NG generations. Evolutionary dynamics acting on the individual genotypes give rise to species, which, within a certain regime of parameters, form 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.

To study the difference between early and late-successional communities, three different scenarios are compared. The first scenario represents the early stages of succession, an only recently disturbed system, which has to rearrange and no stable communities have formed yet. In the intermediate scenario, quasi-stable communities emerge from the interactions (see Results). In the third scenario, a late-successional enduring community is modelled. The scenarios can be imagined to lie on the left, in the middle and on the right of the developmental trajectory depicted in Fig. 6.2. The parameter values for the scenarios are specified in Table 6.1.

Successional stage:	early	medium	late
L	10	10	10
θ_{int}	0.25	0.25	0.25
N_{init}	100	100	100
w	33	33	33
P_{death}	0.2	0.2	0.2
P_{mut}	0.1	0.01	0.001
R	143	143	143

Table 6.1: Choice of parameters for the three scenarios. (L = genome length, θ_{int} = probability of interaction, N_{init} = initial number of individuals, w = strength of interaction effect, P_{death} = probability of death, P_{mut} = gene-wise mutation probability, R = carrying capacity parameter)

Quantifying information transfer

As discussed in chapter 3.5, transfer entropy quantifies the information transfer between two stochastic processes and is defined as

6. Case study: selection transfer in complex ecosystems
6.3. Methods

$$TE_{X \rightarrow Y} := \sum P(Y_{n+1}, Y_n, X_n) \ln \frac{P(Y_{n+1}|Y_n, X_n)}{P(Y_{n+1}|Y_n)}. \quad (6.4)$$

where X and Y are Markov processes of order 1.

To quantify the information transfer from the micro- to the macrolevel and vice versa, we need to pick two time series, representing micro- and macrodynamics. The concrete choice of time series is somewhat arbitrary, which is why we use the most straight forward choice, namely the number of individuals in a species respectively the system:

$$\begin{aligned} m_{S^\alpha}(t) &= n(S^\alpha, t) \\ M_{S^\alpha}(t) &= N(t) - n(S^\alpha, t). \end{aligned} \quad (6.5)$$

The reason we chose to look at the difference between the total number of individuals in the system and the number of individuals within a certain species as macroscopic time series $M(t)$ is the exclusion of autocorrelation as far as possible. We use these two time series to calculate the transfer entropy from the micro- to the macrolevel $TE_{m \rightarrow M}$ and vice versa $TE_{M \rightarrow m}$. The state space is reconstructed by coarse graining of the measurements in 15 equidistant histogram bins.

Species traits

To assess, which species are the main drivers of bottom-up control and which are those, which are most influenced by top-down control, a couple of species traits are regarded.

The average current degree of coadaptation of a species to the community is the time-average of $\tilde{J}(S^\alpha, t)$

$$\overline{J_{\text{in}}(S^\alpha)} := \frac{1}{NG} \cdot \sum_{t=1}^{NG} \tilde{J}(S^\alpha, t), \quad (6.6)$$

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as $\tilde{J}(S^\alpha, t)$ denotes the effect of all individuals in the community on an individual of species S^α (compare equ. 6.1).

The average current degree of contribution to the coadaptation of the community is defined as the sum of all effects an individual of species S^α has on the individuals of the community

$$\begin{aligned}\overline{J_{\text{out}}(S^\alpha)} &:= \frac{1}{NG} \cdot \sum_{t=1}^{NG} J_{\text{out}}(S^\alpha, t) \\ J_{\text{out}}(S^\alpha, t) &:= \frac{\sum_{S \in \mathcal{S}} J(S, S^\alpha) n(S, t)}{N(t)}.\end{aligned}\tag{6.7}$$

As a third possible explanatory for driving bottom-up or top-down control, we look at the average number of individuals in a species

$$\overline{n(S^\alpha)} := \frac{1}{NG} \cdot \sum_{t=1}^{NG} n(S^\alpha, t).\tag{6.8}$$

Statistical methods

To assess, if the direction of information transfer differs between the successional stages, the statistical method of effect sizes is applied. It describes the strength or relative magnitude of a phenomenon and quantifies, whether an effect "matters". Contrary to statistical significance, where with large sample sizes, very small effects can stand out as significant, the method of effect sizes reduces false positives. Cohen's d for one sample is used to assess whether the transfer entropies are effectively larger than zero, and effect sizes for multiple groups are analysed to assess the effect of the successional stage on the information transfer (Cohen, 1988; Lenhard and Lenhard, 2016).

To analyse which species are the main drivers of bottom-up selection and are most affected by top-down selection, a linear model based on species abundance $\overline{n(S^\alpha)}$, species coadaptation $\overline{J_{\text{in}}(S^\alpha)}$ and species contribution to the system's coadaptation $\overline{J_{\text{out}}(S^\alpha)}$ is created (Crawley, 2005).

6.4 Results

Dynamics

The model behaviour for the three different scenarios is visualised in Fig. 6.2. In the early successional stages of the system, no stable communities could yet have been formed, which is why many different species enter and exit the community, giving rise to hectic dynamics (Fig. 6.2a). The more coadapted the system becomes, the longer quasi-stable communities persist (Fig. 6.2b), until a fairly stable and persistent late successional community is formed (Fig. 6.2c).

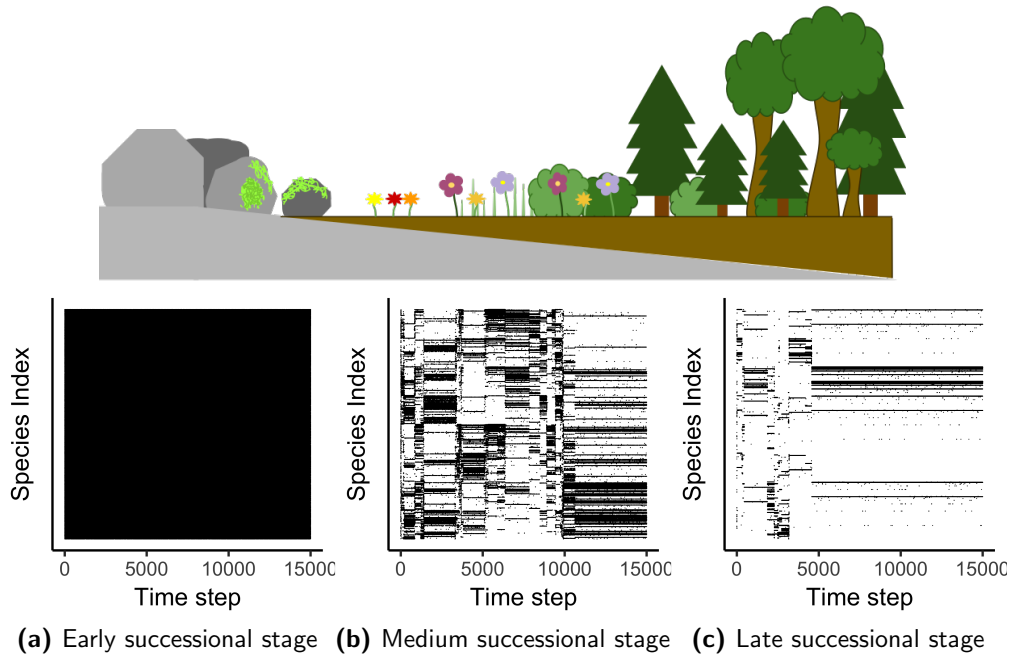


Figure 6.2: Three model scenarios, representing early (a), medium (b) and late successional (c) stages. The scenarios are parametrised according to Table 6.1.

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The behaviour of transfer entropy in the different successional stages

The information transfer between the microscopic and the macroscopic time series are small, but detectably larger than zero, for all successional stages and both directions (Table 6.2b). Bottom-up control is highest in the early successional stage and decreases over the course of ecosystem development (Fig. 6.3a to c). The opposite is true for top-down control: here information transfer increases on average, the more stable the system becomes. Overall, the successional stage has a strong effect on bottom-up and a small effect on top-down information transfer (Table 6.2c). These results support H1 and reveal a trend towards weaker bottom-up and stronger top-down control over the course of ecological succession. The differences in transfer entropy comparing bottom-up and top-down information transfer as well as the differences comparing the successional stages are both significant (ANOVA, $p < 2e^{-16}$, $n = 1024 \times 6$).

	$TE_{m \rightarrow M}$	$TE_{M \rightarrow m}$	Δ
(a) Means $\pm$ Standard Deviation			
Early	0.0115 ± 0.0009	0.0053 ± 0.0007	0.0062 ± 0.0010
Medium	0.0052 ± 0.0066	0.0057 ± 0.0060	-0.0006 ± 0.0069
Late	0.0025 ± 0.0041	0.0085 ± 0.0216	-0.0060 ± 0.0200
(b) Effect size compared to $TE = 0$			Effect size of Δ
Early	12.886 (***)	8.009 (***)	7.690 (***)
Medium	0.781 (**)	0.954 (***)	-0.079
Late	0.609 (**)	0.394 (*)	-0.386 (*)
(c) Effect size of the successional stage on the TE			
	1.536 (***)	0.313 (*)	

Table 6.2: Mean and standard deviation of the selection transfer entropies in the different scenarios as well as effect sizes. $\Delta := TE_{m \rightarrow M} - TE_{M \rightarrow m}$, (*): small effect, (**): intermediate effect, (***): large effect (according to [Cohen, 1988](#))

6. Case study: selection transfer in complex ecosystems

6.4. Results

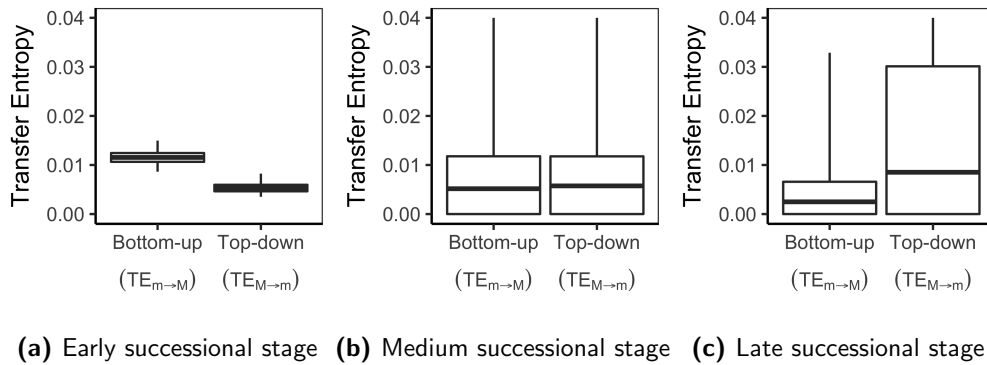


Figure 6.3: Distribution of selection transfer from the micro- to the macrolevel (bottom-up control, $TE_{m \rightarrow M}$) and vice versa (top-down control, $TE_{M \rightarrow m}$) over the set of species in the community, measured in terms of transfer entropy for the different successional stages. The boxes show the mean (solid line in the middle of the box) $\pm$ the standard deviation (boundaries of the box) as well as the minimum and maximum value (end of the solid dash). Note that the y-axis is capped; the maximum transfer entropy in the medium successional stage is 0.07, and in the late successional stage it is 0.11.

Which species drive bottom-up respectively top-down control?

Fig. 6.3 also gives an indication about the spread of the influences different species have on the bottom-up and top-down information transfer. While in the early successional stage, most species are lowly populated, barely coadapted and hence have similar influence on the information transfer, in the medium and especially late successional stage, a few species lie far higher than the median and have a comparably large effect on bottom-up control respectively are strongly affected by top-down control.

Fig. 6.4 shows, how the traits of species, which have a particularly high or low bottom-up or top-down control, compare to the overall distribution of species traits in the community (compare equ. 6.8, 6.6 and 6.7). It can be seen, that the high control-species are generally more abundant (upper row), better coadapted (middle row) and have a stronger influence on community adaptation (lower row). However significant deviations from the overall species pool mean only appear in the medium successional stage, and for abundance also in the early-successional stage.

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6.4. Results

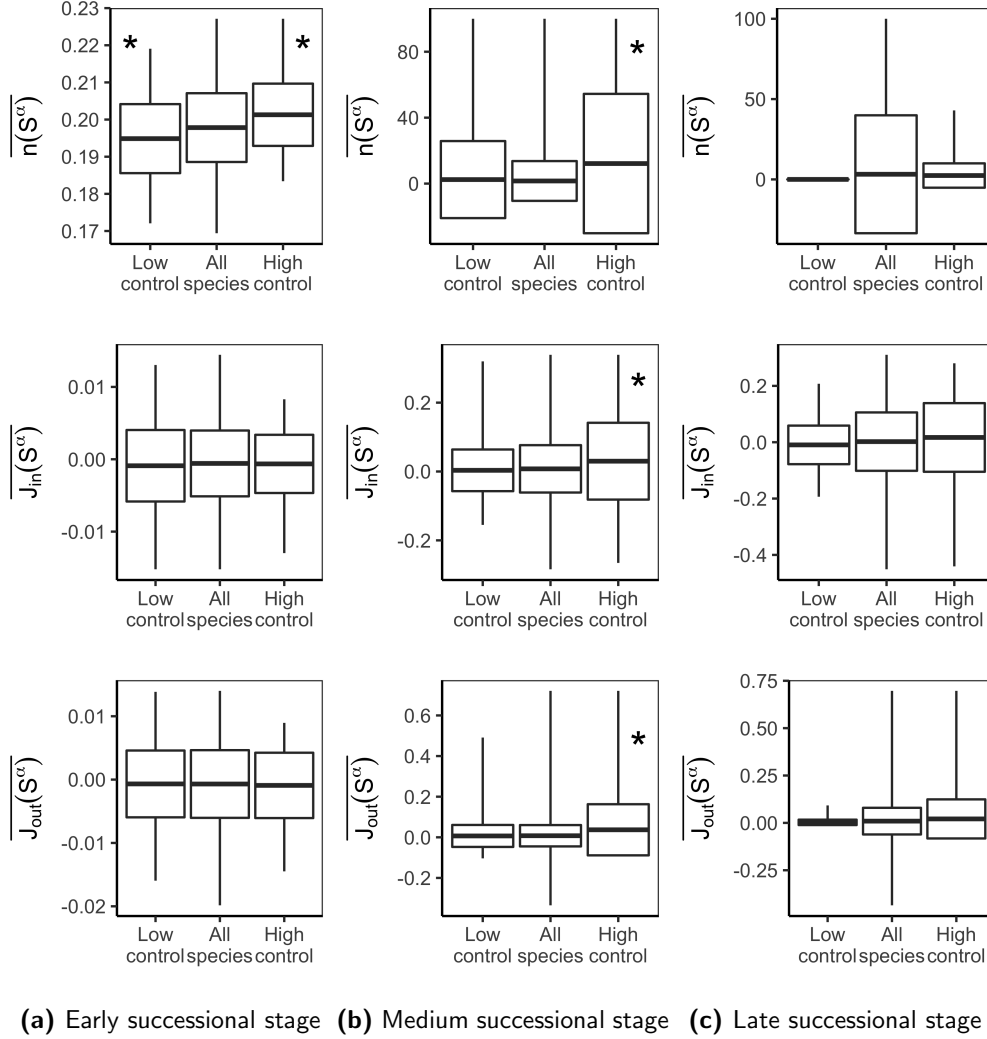


Figure 6.4: Trait distribution of species with low and high bottom-up and top-down control compared to the overall set of species in the community. Regarded traits are abundance $\overline{n(S^\alpha)}$, species coadaptation $\overline{J_{in}(S^\alpha)}$ and species contribution to the system's coadaptation $\overline{J_{out}(S^\alpha)}$. The boxes show the mean (solid line in the middle of the box) $\pm$ the standard deviation (boundaries of the box) as well as the minimum and maximum value (end of the solid dash). A species is defined as having a "high control" / "low control" effect, if its respective transfer entropy is in the upper/lower 5% percentile of the respective transfer entropies in the population. Significant deviations from the overall species community means are marked with an asterisk.

To analyse, which species traits explain best how much a species contributes to the transfer entropies, a linear model with the average number of individuals in

6. Case study: selection transfer in complex ecosystems

6.5. Discussion

the species, the average degree of coadaptation and the average contribution of the community's coadaptation is constructed (Table 6.3). Different than expected, there is no clear distinction between which species traits explain high bottom-up and which strong top-down control. In the early successional stage, the abundance and degree of coadaptation of a species determine its effect on bottom-up and top-down control. In the medium successional stage, the coadaptation effect of and on a species significantly influence top-down control, whereas in late successional stages, the same is true for bottom-up control.

Scenario		$\overline{n(S^\alpha)}$	$\overline{J_{in}(S^\alpha)}$	$\overline{J_{out}(S^\alpha)}$	R^2
early	$TE_{m \rightarrow M}$	$\uparrow (p < 0.001)$	$\uparrow (p < 0.05)$		5.3%
	$TE_{M \rightarrow m}$	$\uparrow (p < 0.001)$	$\uparrow (p < 0.05)$		4.0%
medium	$TE_{m \rightarrow M}$	$\uparrow (p < 0.001)$			22.6%
	$TE_{M \rightarrow m}$	$\uparrow (p < 0.001)$	$\uparrow (p < 0.05)$	$\uparrow (p < 0.01)$	1.8%
late	$TE_{m \rightarrow M}$		$\uparrow (p < 0.01)$	$\uparrow (p < 0.001)$	7.9%
	$TE_{M \rightarrow m}$				0.2%

Table 6.3: Results of a linear model to explain which species play the largest role for bottom-up and top-down information transfer in ecological communities. $\overline{n(S^\alpha)}$, $\overline{J_{in}(S^\alpha)}$ and $\overline{J_{out}(S^\alpha)}$ and R^2 are the independent variables; R^2 describes the amount of variance explained by those independent variables.

6.5 Discussion

Fitness is a multidimensional measure and can be regarded from two sides - how well does a species do in the current context, and how much does a species contribute to sustain the current environment. The information theoretic concept of transfer entropy can serve as a mathematical framework to capture these aspects of top-down and bottom-up selection in ecosystems.

The results in this chapter show, that bottom-up and top-down control are of different importance over the course of ecosystem succession. While early successional stages are dominated by bottom-up control, late successional systems are more strongly influenced by top-down control (Fig. 6.3). This makes sense as in early successional communities, no coadapted subset of species has become dominant yet, most species have similar influence on the community and the

6. Case study: selection transfer in complex ecosystems

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system can basically be regarded as the sum of its parts. Over the course of succession, the ecological communities become more coadapted, which is why top-down selection or how well a species fits into the community plays a larger role for its survival.

With progressing developmental stage, the variance in contribution to information transfer across species increases (Fig. 6.3). While in the early successional stage, the number of individuals and the amount of benefit a species perceives *from* the community ($J_{\text{in}}(S^\alpha)$) predominantly explains a species' contribution to information transfer, in medium and late successional stages also the contribution *to* the community ($J_{\text{out}}(S^\alpha)$) becomes a significant explanatory variable for effect on information transfer.

These findings imply, that more developed ecological systems do indeed exert selection pressure on the present species - without the need for any metaphysical macroscopic optimisation criteria, group selection hypotheses or anything related, but only via information transferring feedbacks within the system.

This study however has to be understood as a first exploration of the concept of transfer entropy to explore bottom-up and top-down control in ecological communities. Further research on different models and ideally also empirical data has to show if the concept can serve as a basis for a rigid mathematical framework to quantify the roles of bottom-up and top-down control in evolving ecosystems. If so, it can shed light on general selection principles and eventually help to forecast and potentially prevent periods rapid change accompanied by mass extinctions in real-world ecosystems.

6.6 Conclusion

This chapter has shown, that information theoretic measures can not only quantify information stored within system (chapter 5), but also information that is transferred through the system and shapes its state and developmental path. The applicability of transfer entropy to quantify bottom-up and top-down control in ecological communities needs further evaluation, but has so far been shown to be a promising tool.

After having looked at general ecological communities forming interaction networks, we will now switch the focus to the complexity and organisation of food webs.

7

Case study: a focus on food webs - the evolution of ecosystem ascendancy

7.1 Context

The idea that ecological complexity is not only a function of the structural, but also the functional properties of ecological systems, can be traced back to [Odum \(1962\)](#). He criticised the original definition of ecology as the relation between organisms and environment as too vague and broad, and called for the reformulation of ecology to be defined as the relationship between structure (such as community composition, the distribution of abiotic resources as well as the environmental conditions), representing the conditions of existence, and function, including eco-energetics, eco-cycling and eco-regulation on the scale of populations, communities and ecosystems. (see also [Odum, 1968](#)) Understanding ecosystem complexity hence requires taking into account both the structure of ecological networks and the flow through the system. Based on the energy flow through food webs, summary statistics of ecological networks incorporating structure and function such as the total system throughput or the average weighted path length have been derived and analysed across ecological networks ([Finn,](#)

7. Case study: a focus on food webs - the evolution of ecosystem ascendancy

7.1. Context

1976). One question in ecosystem ecology is the quantification of ecosystem health and maturity, which has been suggested to be captured by energy recycling in the system (i.e. the fraction of flow devoted to cycling) (Finn, 1976). This Finn cycling index *FCI* has later been refined as the comprehensive cycling index *CCI* by Allesina and Ulanowicz (2004) to account for all flows engaged in energy re-usage.

Energy recycling is certainly one measure of ecosystem health, which incorporates both aspects of structure and functionality, but obviously also the flows related to recycling or non-recycling can be distributed in different ways and contribute to ecosystem complexity and maturity, as suggested by Odum (1969). To capture the flow patterns across ecosystems in a more comprehensive way, different information theoretical measures have been suggested over time. The first to notice a potential relation between ecosystem stability and the uncertainty of the flow links arbitrarily small units of energy take during their way through the food web, was MacArthur (1955). By realising that food webs can be regarded as energy transformers represented as a Markov chain and relating community stability to the amount of choice which energy has in following pathways through the network, he proposed the average entropy of the exiting flow distributions at each node as a measure of ecosystem stability. Focussing less on stability but on ecosystem resilience (hence "the ability of an ecosystem to resist changes in the presence of perturbations"), Rutledge et al. (1976) proposed the conditional entropy, the difference between the entropy of the flows and the average mutual information, which reflects the constraints on the flow pattern imposed by species characteristics and the network structure, as a measure of ecosystem stability: the remaining scope for choice regarding the pathways of energy flows is suggested to mirror ecological stability.

Inspired by MacArthur (1955) and Rutledge et al. (1976), Ulanowicz (1986, 2011) developed the idea of applying information theoretic diversity measures not to stocks but to processes further. Instead of focussing on stability, he aims to quantify ecosystem organisation, to study growth and develop in ecosystems and to assess ecosystem health maturity. His measure of *ascendancy* is the product of two factors, which quantify the activity of the system (total energy throughput) and the level of organisation or constraint inherent among the trophic exchanges

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7.1. Context

(average mutual information of the energy flows between pairs of species) respectively. He proposes a tendency for self-organising ecosystems to develop towards higher values of ascendancy in the absence of major perturbations and justifies this principle by linking ascendancy to autocatalytic feedback processes in ecological systems ([Ulanowicz, 2002](#)).

There are three major challenges to quantifying the evolution of food web integrity with any hypothesized measure of organisation. First, ecological systems are open systems, receiving energy input from the sun and exchanging nutrients, kilocalories, liquids and matter with their biotic and abiotic surrounding, and drawing boundaries of subsystems generally remains arbitrary at least to a certain extent. Second, measuring biomass stocks for all involved species is an ambitious task, but quantifying energy or matter transfer *between* all involved species is even more challenging. This task involves looking at each pair of predator and prey species and measuring how much matter they exchange within a certain time frame - which must be large enough to form meaningful averages which are independent of seasonal fluctuations. Usually, common knowledge about species' dietary preferences, reported results from the literature, educated guesses based on morphology, visual empirical observations as well as gut content analyses together build the foundation of quantified food webs, with large uncertainties involved. And third, even if quantified food webs with well-defined boundaries could be observed over consecutive years, the studied time frames are usually too short for effects of evolutionary dynamics to become visible. When [Ulanowicz \(1986\)](#) proposed his measure of Ascendancy, he provided two quantified versions of the food web in the Chesapeake Bay, showing that ecosystem ascendancy is higher in summer, when the system has an overall higher level of activity, but mutual information or organisation of the system peaks in winter, when the system needs to be more efficient on less energy and resources. While these results give an initial hint on the usefulness of the proposed measure of organisation, much more empirical data and larger time scales would be needed to draw conclusions about the evolutionary long-term behaviour of ecosystem integrity.

The Tangled Nature model solves all three challenges at least in the context of an ecosystem model. As ecological communities are modelled as emergent from

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7.2. Introduction

a very large genotype space, they can be regarded as "full" communities, making the drawing of artificial boundaries obsolete. Matter transfer between species can simply be tracked over time steps of whole generations - and all is embedded in an evolutionary scenario, allowing to study ecosystem ascendancy over long time scales. The following results can thus be understood as a proof of the concept of ecosystem ascendancy as a measure of ecosystem integrity and organisation.

7.2 Introduction

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 depend 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 \(1969\)](#) 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.

7.3 Methods

A hierarchical version of the Tangled Nature Model

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 Tangled Nature Model. Different interpretations of the networks arising in the Tangled Nature Model have been studied by Rikvold et al. (Rikvold, 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 degree of coadaptation of a species

$$\tilde{J}(S^\alpha, t) := \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n(S, t)}{N(t)} \quad (7.1)$$

enters the weight functions

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7.3. Methods

$$\begin{aligned}\Xi_{PP}(S^\alpha, t) &= w \cdot \tilde{J}(S^\alpha, t) - \frac{N_{PP}(t)}{R} \\ \Xi_C(S^\alpha, t) &= w \cdot \tilde{J}(S^\alpha, t) - \frac{n(S^\alpha, t)}{c \cdot N_{\text{prey}}^\alpha(t)}\end{aligned}\tag{7.2}$$

which determines offspring probability, defined as

$$P_{\text{off}}(S^\alpha, t) = \frac{\exp(\Xi(S^\alpha, t))}{1 + \exp(\Xi(S^\alpha, t))}\tag{7.3}$$

for primary producers and consumers respectively. Here, $N_P(t)$ denotes the current number of primary producers, N_{prey}^α the number of prey individuals of consumer α , R represents the carrying capacity for primary producers and 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 $P_{\text{off}}(S^\alpha, t)$. 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. $T_{ij}(t)$ stands for the amount of energy/biomass transfer from species i to species j during generation t . To enhance readability, the dependence on t is disregarded in the rest of the paper.

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7.3. Methods

Measuring ecosystem organisation

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

Following Ulanowicz's work (compare e.g. [Ulanowicz \(2011\)](#)), the capacity C_N of the network is defined in terms of the entropy H_N of the distribution flows across the network

$$H_N = - \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{T_{ij}}{T_{..}} \quad (7.4)$$

times the total throughflow $T_{..}$

$$C_N = - \sum_{i,j} T_{ij} \ln \frac{T_{ij}}{T_{..}} \quad (7.5)$$

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

$$\begin{aligned} T_{i.} &= \sum_k T_{ik} \\ T_{.i} &= \sum_l T_{li} \\ T_{..} &= \sum_{ij} T_{ij} \quad . \end{aligned} \quad (7.6)$$

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

The average mutual information in a network is defined as

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$$MI_N = \sum_{i,j} \frac{T_{ij}}{T_{..}} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}} . \quad (7.7)$$

While MacArthur (1955) hypothesises that the average entropy H_N increases in ecosystems over time, Rutledge et al. (1976) argue that due to stability aspects,

$$R = H - MI \quad (7.8)$$

should increase during the development of ecological networks. Ulanowicz synthesises characteristics of ecosystem maturity laid out by Odum (1968) and ideas about autocatalysis and intrasystemic feedbacks in the measure of ascendancy A_N as the product of the mutual information MI_N and the total throughflow $T_{..}$.

$$A_N = \sum_{i,j} T_{ij} \ln \frac{\frac{T_{ij}}{T_{..}}}{\frac{T_{i.}}{T_{..}} \frac{T_{.j}}{T_{..}}} . \quad (7.9)$$

Capacity minus ascendancy is called overhead OH_N

$$OH_N = C_N - A_N. \quad (7.10)$$

While Ulanowicz originally hypothesised ecosystems to evolve to ever higher values of ascendancy, more recent considerations and empirical findings led to the proposition of adaptive evolutionary systems to balance between their degree of organisation $\frac{MI_N}{H_N}$ (constraints ensuring function and integrity of the system) and their degree of disorganisation $-\ln \frac{MI_N}{H_N}$ (scope for adaptation and flexibility in face of disturbances) and therefore cluster around maximal "fitness"

$$F_N = -e^{\frac{MI_N}{H_N}} \ln \frac{MI_N}{H_N} \quad (7.11)$$

where they are "best poised for further evolution" (Ulanowicz, 2014). $e = \exp(1)$ scales F_N to the range between 0 and 1.

All measures are compared according to their evolution through the adaptive dynamics of the Tangle Nature Model.

7.4 Results

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. 7.1). Unless otherwise stated, the parameters were chosen as follows: $\theta_{\text{int}} = 0.8$, $\theta_{\text{feed}} = 0.5$, $\theta_{PP} = 0.5$, $L = 10$, $N_{\text{init}} = 500$, $c = 0.012$, $\mu = 0.01$, $\mu_C = 20$, $P_{\text{kill}} = 0.02$, $P_{\text{mut}} = 0.0002$. 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 (see below for a more detailed discussion).

Species diversity remains about constant, both if considering only species with an abundance above a threshold value (hence neglecting mutants who appear and go extinct immediately again) and if considering all present species (Fig. 7.2a). The average number of individuals increases over time (Fig. 7.2b), reflecting the fact that the system during the course of evolution optimises the interactions between species and hence can sustain more biomass.

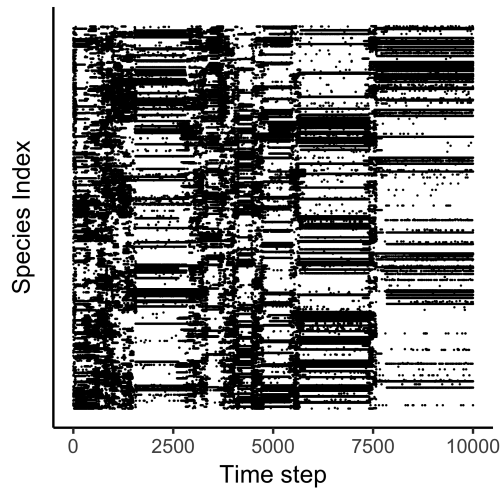


Figure 7.1: Occupation of the genotype space over time. Alternating stable (qESS) periods interrupted by transitions are clearly visible.

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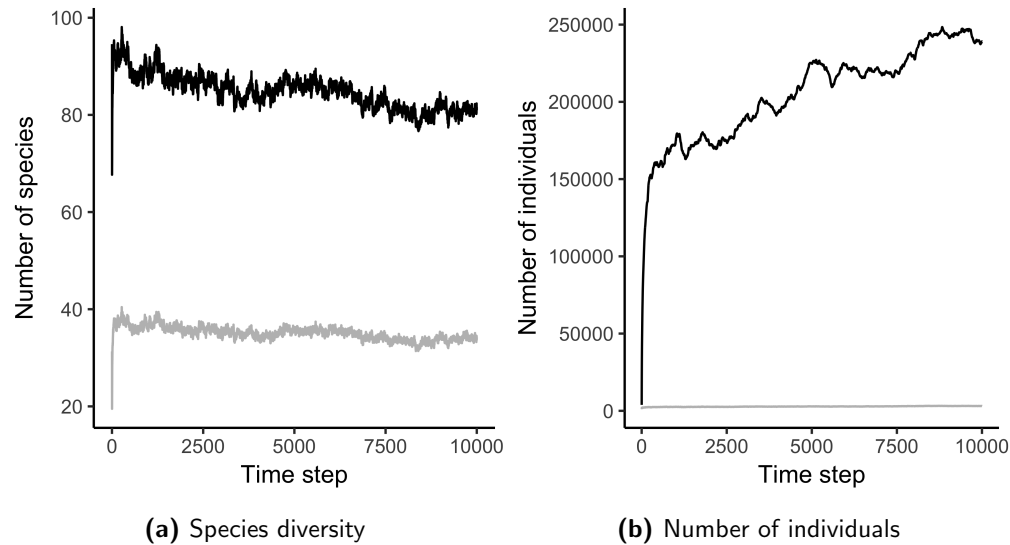


Figure 7.2: Development of the number of individuals and species over time, averaged over 100 runs. Black: all species, grey: only primary producers.

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 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. 7.3) The choice of those parameters which influence the trophic network, biomass exchange and chain length (θ_{feed} , θ_{PP}) is generic.

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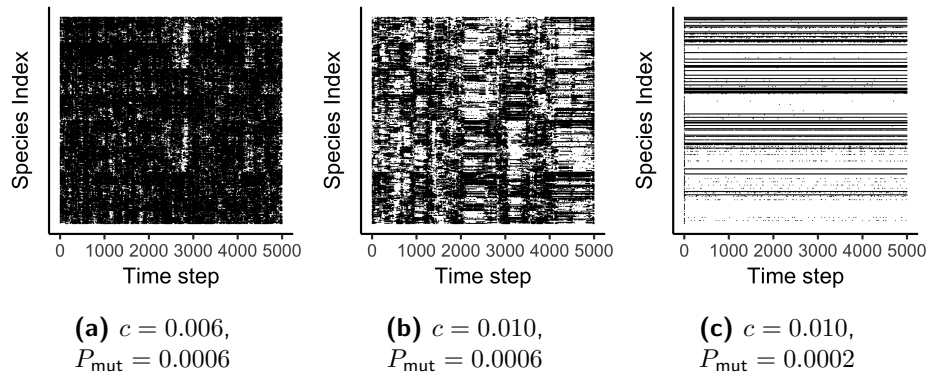


Figure 7.3: Different scenarios of genotype space occupation over time.

Ecosystemic properties

Based on the interaction network and the trophic links, ecological networks emerge (Fig. 7.4). As energy cycling isn't restricted, no clear tree-shaped layout is visible.

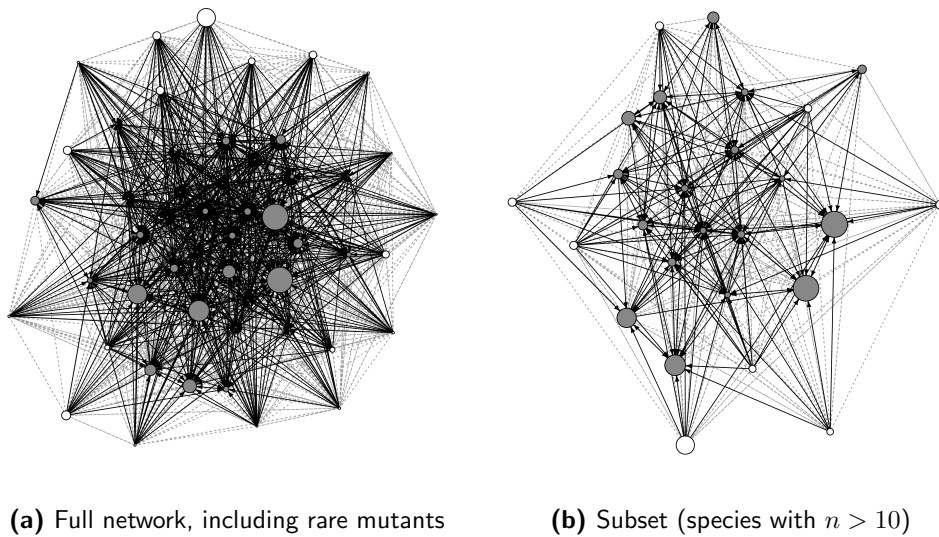


Figure 7.4: Species network after 10000 generations in an equilibrium state. Vertex colour denotes if the species is a primary producer (white) or a consumer (grey); vertex size equal the log of the number of individuals. Dotted grey lines represent J-interactions (both positive and negative), solid black lines are trophic interactions (the arrows point in the direction of energy transfer).

To compare and characterise ecosystem topologies, one often makes use of the

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number of trophic levels and by the degree distribution.

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. 7.5).

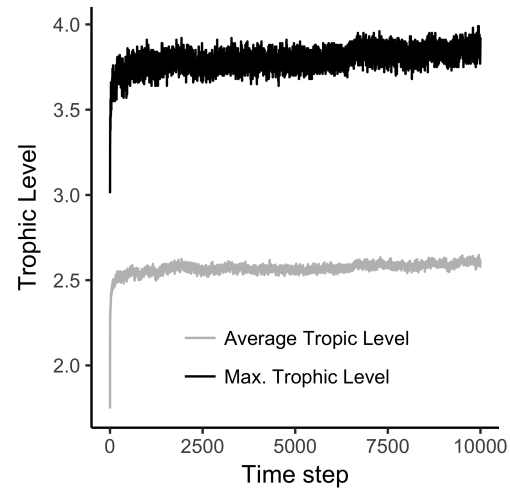


Figure 7.5: Development of the trophic level (TL) of the top consumers (maximum trophic position, black) and the average trophic level (grey) over time, averaged over 100 runs

The degree distribution across the nodes of the trophic ecological network in a mature quasi stable period is visualised in Fig. 7.6.

Ecosystem connectivity, the fraction of present links relative to the potential

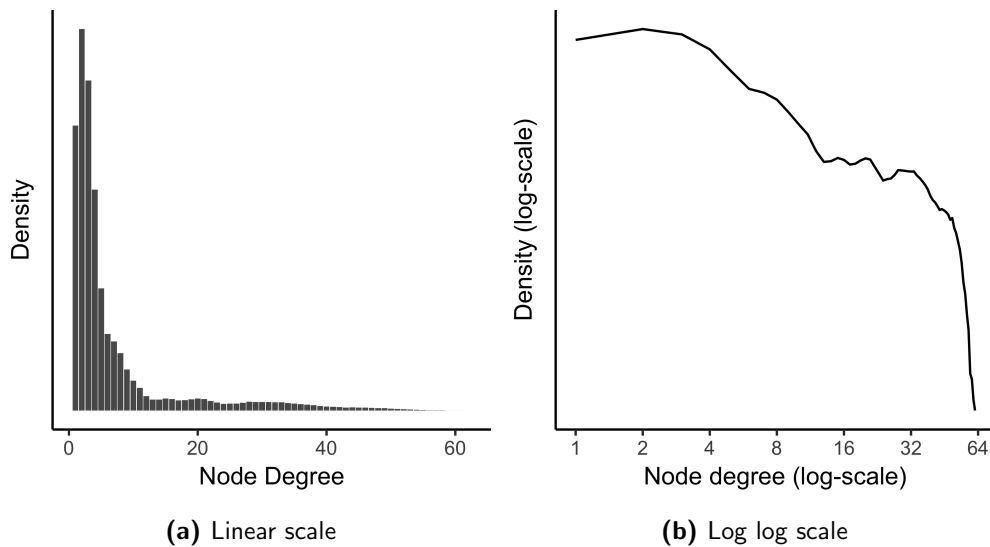


Figure 7.6: Degree distribution of the trophic interactions across generations in qESS

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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. 7.7).

Much debate has been around the relationship between the size of an ecosystem and its connectivity (Dunne, 2009). While early results suggested scale invariance (hence approximately constant L/S) or constant connectivity (constant $C = L/S^2$), later studies report power law relationships in the form of $L = \alpha S^\beta$ with different exponents β . (Dunne et al., 2002; Dunne, 2009). While during stable periods, a clear power law relationship between L and S (exponent = 1.25) can be detected, unstable systems show more scatter (Fig. 7.8a). The corresponding relationship between connectivity and diversity (Fig. 7.8b) mirrors previous findings on the characteristics of the interaction network in the Tangled Nature Model (Laird and Jensen, 2006).

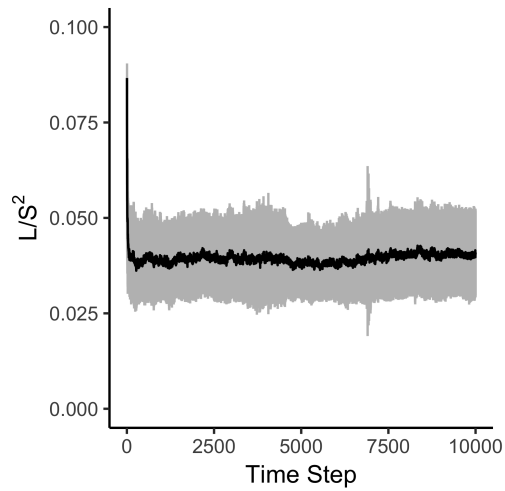


Figure 7.7: Average connectivity over time (black: mean, grey: standard deviation, $n = 100$)

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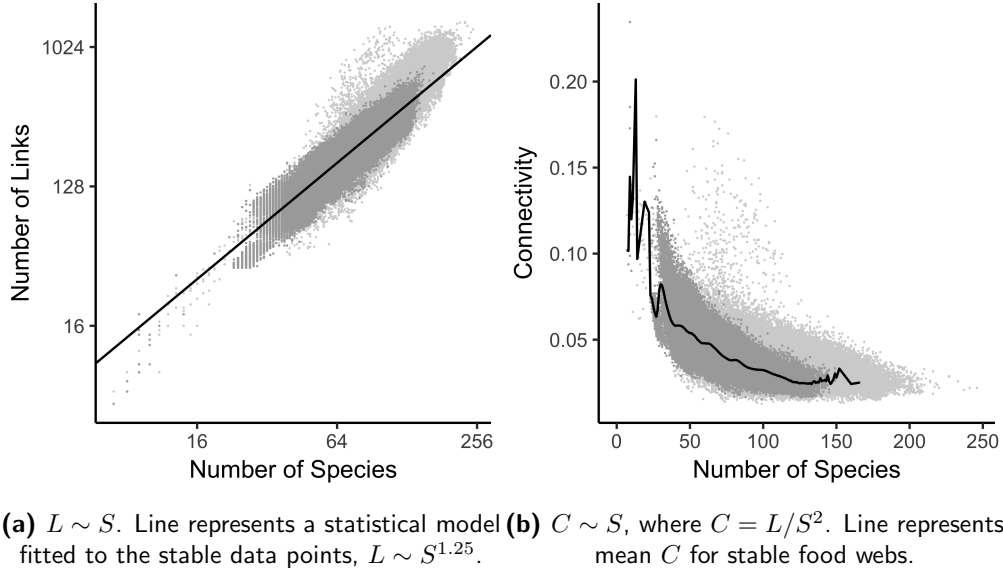


Figure 7.8: Relationship between the number of trophic interaction links and the number of species. Black: (a) linear model, (b) mean, dark grey: stable food webs, light grey: unstable food webs

Ecosystem organisation

Measures of ecosystem capacity and ascendancy show a slight increase over time, whereas the overhead remains constant on average. (Fig. 7.9a).

The relative mutual information $\frac{MI_N}{H_N}$, representing the organisation of the system, increases slightly over time to values around 0.4, while a version of its inverse, $-\ln \frac{MI_N}{H_N}$, a potential measure for disorganisation, decreases on average (Fig. 7.9b). The product $F_N = -\frac{MI_N}{H_N} \ln \frac{MI_N}{H_N}$, which has been suggested to describe the system's fitness (Ulanowicz, 2014), remains more or less constant.

Comparing the distribution of ascendancy values between hectic and stable periods shows a clear shift towards higher ascendancy during qESS periods Fig. 7.10a, with a mean ascendancy A_N 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_N (mean stable periods: 1.07 ($SD = 0.31$), mean hectic periods: 0.99 ($SD = 0.33$), Fig. 7.10b), 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. 7.10c).

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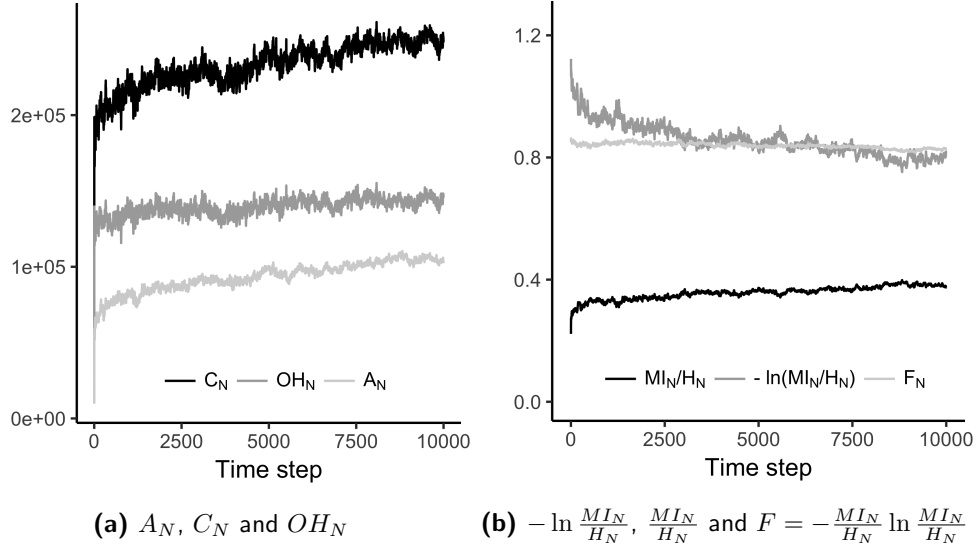


Figure 7.9: Ecosystem organisation: development of ascendancy A_N , capacity C_N and overhead OH_N (left) and relative mutual information $\frac{MI_N}{H_N}$, its inverse $-\ln \frac{MI_N}{H_N}$ and the scaled product $F_N = -e^{\frac{MI_N}{H_N}} \ln \frac{MI_N}{H_N}$ (right) over time, averaged over 100 runs

The difference of MI_N , $T_{..}$ and A_N comparing hectic and stable periods is highly significant ($p < 2.2 \cdot 10^{16}$ for all three measures).

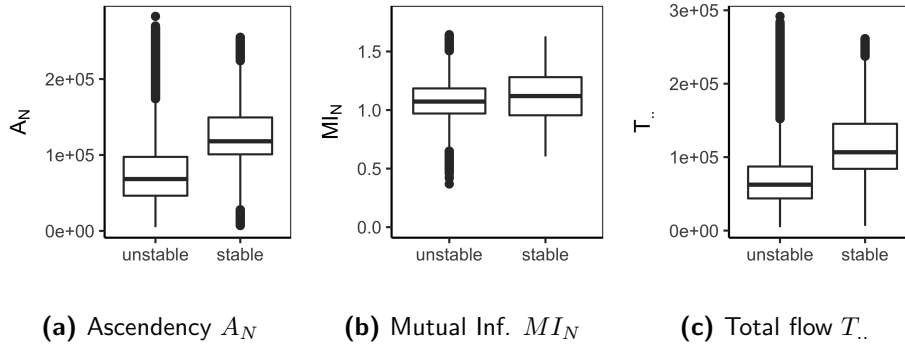


Figure 7.10: Box-Whisker-Plots of ascendancy A_N , mutual information MI_N and total flow $T_{..}$ during hectic and stable periods (50 runs, 352057 stable data points, 147943 hectic data points). The boxes show the median (solid line in the middle of the box), the lower and upper quartile ($Q1$ and $Q3$, 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 ($p < 2.2 \cdot 10^{16}$).

7.5 Discussion

Previous studies have confirmed that despite the simplicity of the Tangled Nature Model, the model is well capable of reproducing complex macroecological patterns found in nature such as the log-normal shaped species-abundance distribution, a power law relation between area and species diversity and exponential degree distributions of the indirect interaction network (Hall et al., 2002; Laird and Jensen, 2006; Laird et al., 2008; Lawson and Jensen, 2006). A most notable feature is the intermittent nature of macro-evolution, denoted as punctuated equilibrium by Eldredge and Gould (1972), which, as shown here, can also be reproduced in the hierarchical version of the model. In the course of co-evolution, the realised indirect interaction strengths tend to become more positive (di Collobiano et al., 2002), allowing for the support of a higher number of total individuals in the system (compare equ. 7.2 and Fig. 7.2b), which is in accordance with previous proposals and findings (compare e.g. Fath and Patten (1998)). The Tangled Nature Model has also been used to study predator prey interactions and therefrom resulting (non-quantitative) model food webs (Rikvold, 2010). The presented results from the quantitative hierarchical Tangled Nature Model additionally reveal an average food chain length of 2.6 (Fig. 7.5), agreeing well with empirical observations of average chain lengths mainly lying between 2 and 3 (Briand and Cohen, 1987). Maximum chain lengths can in reality reach up to 10 species or more, but in the majority of the cases don't exceed 4 (Briand and Cohen, 1987), which is in agreement with the presented findings. Much debate has been around the relationship between complexity and stability of ecological networks. From May's model studies suggesting larger food webs to be less connected in order to be stable May (1973) over suggested "link-species scaling laws" ($L/S \approx 2$, Cohen and Newman (1985)), more comprehensive recent data with higher resolution indicate power law scaling ($L = \alpha S^\beta$) across a wide range of food web types (Dunne et al., 2002; Dunne, 2009).

Stable food webs produced by the Tangled Nature Model exhibit a clear power law relationship with an exponent of 1.25 ($R^2 = 0.82$, Fig. 7.8a), which is in line with most recent findings of real world food web topologies. The Tangled Nature Model hence has shown to be well suitable for reproducing structural properties

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of real-world ecological networks and can therefore be analysed with regard to ecosystem organisation and integrity.

Quantifying ecosystem integrity, growth and development is a controversial undertaking and depends substantially on the assumptions made as well as the properties of the specific system. Ideally one would like to measure ecosystem structure and flow in a real world ecosystem, tracing all species interactions as well the transfers and losses of nutrients and energy between them, relate these properties to observations of functionality, stability and resilience and assess which measures might function best in capturing all these characteristics. As such comprehensive knowledge is unattainable in reality, generic models of evolutionary ecology can help to illuminate these practical questions even within a theoretical setting. The presented results show, that ecosystem ascendancy as a measure of growth and development indeed increases over evolutionary time scales, as the overall capacity for the flow pattern increases (Fig. 7.10a). Ecosystems therefore apparently tend to extend their scope for organisation or integrity, as well as the actual realised 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 $C_N/T_{..}$) 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. 7.10a). This is both accounted for by significantly higher mutual information and significantly higher overall flow rates during stable compared to hectic periods (Fig. 7.10b and 7.10c). 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 as-

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cendency as they grow and develop, more recent findings showed that real world ecosystems tend to cluster around relative values of ascendancy $\frac{A_N}{C_N} = \frac{MI_N}{H_N}$ of 0.4 (Ulanowicz, 2014). This value of ascendancy maximises the function $F_N(\frac{MI_N}{H_N}) = -\frac{MI_N}{H_N} \ln \frac{MI_N}{H_N}$ 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_N is somewhat arbitrary, also the Tangled Nature Model model ecosystems evolve to values of $\frac{MI_N}{H_N}$ around 0.4 (Fig. 7.9b). The relative contribution of mutual information F_N depends both on topology and dynamics on the network and is therefore much more than a mathematical artefact. Reasons and implications for why F_N clusters around 0.4 both real world and in model ecosystems should be the result of future work.

7.6 Conclusion

The Tangled Nature Model of evolutionary ecology has been shown to be both well adaptable to include trophic interactions and to suitable to study the behaviour of ecosystem ascendancy, organisation and integrity.

It allowed to confirm the previous hypotheses of a balance between mutual information and entropy in developing food webs and an increase in ascendancy over evolutionary time scales. Interestingly, also the hypothesised optimisation of network "fitness" F_N clusters around 0.4 just as in real-world ecosystems - despite the fact, that the Tangled Nature Model is set up to study qualitative behaviour, but hasn't been calibrated for quantitative comparisons to real-world data. This suggests, that the clustering around 0.4 could either be a mathematical artefact of the theory, being produced by most networks with certain loose and easily satisfiable constraints, or it could point towards the underlying complex and non-mechanistic behaviour, which is driving the dynamics in the Tangled Nature Model and certainly play a large role in ecosystems.

8

Case study: the crucial role of coadaptation for species persistence - a complex systems approach to habitat fragmentation

8.1 Context

The focus of this thesis lies on the *evolution* of ecosystem organisation and integrity. Selection through the inner and outer biotic and abiotic environment however also occurs on shorter time scales and influences species reproduction rates, their abundances and ultimately the overall community dynamics. These effects could potentially first become visible in systems which undergo stress or disturbances - where system health and coadaptation of the system feedback on species abundances and eventually persistence with potentially critical outcomes. The following chapter about the role of coadaptation for species and community dynamics in fragmented landscapes can hence be understood as a modelling study of community integrity and it's top-down control on the species it is comprised

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8.2. Introduction

of - and at the same time, it is one of the first approaches to model different types of interactions between species simultaneously and quantifying their effect on community and biodiversity dynamics in fragmented landscapes.

8.2 Introduction

The stability, functionality and resilience of ecological communities are strongly dependent on how species interact with each other ([Brown et al., 2001](#); [Cardinale et al., 2002](#); [Fischer et al., 2006](#); [Bailey et al., 2016](#)). Negative and positive interactions between individuals shape the degree of coadaptation of an ecological community, which is crucial for its persistence over time and in the face of habitat disturbances ([Costanza and Mageau, 1999](#); [Stachowicz, 2001](#); [Bruno et al., 2003](#); [Wilson et al., 2016](#)). While the role of single species traits in conferring sensitivity to disturbance have been widely assessed in the ecological literature ([MacArthur and Wilson, 1963](#); [Losos and Ricklefs, 2010](#)), it is yet unknown the extent to which coadaptation among species can affect their vulnerability to habitat changes. Here, we apply a complex systems' modelling approach to quantify the role of coadaptation for species persistence and survival before, during and after habitat fragmentation.

Rapid biodiversity loss due to habitat loss and fragmentation is widely observed ([Wilson et al., 2016](#)), but which mechanisms determine species persistence after fragmentation has been a long-standing debate. While it is certain that small populations are especially more vulnerable ([Richter-Dyn and Goel, 1972](#); [Wilcox and Murphy, 1985](#); [Lienert, 2004](#); [Tylianakis and Morris, 2017](#)), both reproductive and dispersal ability affect species persistence. Due to trade-off between those two traits (compare e.g. [Strauss et al. 2002](#) for herbivores, [Hughes et al. 2003](#) for butterflies, [Togashi and Hoshino 2003](#) for nematodes, [Rodriguez et al. 2007](#) for passerines, [Guerra 2011](#) for wing-dimorphic insects, [Nadell and Bassler 2011](#) for bacteria and [Duthie et al. 2015](#) for fig wasps), even the most abundant species can be among the first to go extinct ([Tilman et al., 1997](#)). Furthermore, cascade effects - due to the complex interactions between the remaining species and the landscape in tightly coupled systems - can lead to non-predicted extinctions ([Wilcox and Murphy, 1985](#); [Pace et al., 1999](#)). Effects dependent on network

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structure (Dunne et al., 2002; Ebenman et al., 2004; Dunne, 2009; Stouffer and Bascompte, 2010) as well as interaction patterns and dynamics (Ives and Cardinale, 2004; Williams, 2008).

The question which species properties determine species abundance before and after habitat fragmentation has been widely discussed in the literature (MacArthur and Wilson, 1963; Losos and Ricklefs, 2010). While dispersal ability is regarded as a main alleviating factor in the face of habitat loss and isolation (Reed, 2004) and during range expansion, reproductive and competitive ability have been found being selected for at the core of spatial landscapes independent of fragmentation (Burton et al., 2010). At the same time, the importance of the entanglement and coadaptation of ecosystems when it comes to understanding and ultimately explaining their development and reaction to external stressors is well known (Odum, 1969; Ulanowicz, 1986; McCann, 2000; Jorgensen et al., 2007). The degree of coadaptation of a species to its community should hence affect species persistence as well, but is difficult to study empirically.

We focus on two main open questions in fragmentation ecology: what determines species persistence after habitat loss, and which species traits explain species abundance both before and after habitat fragmentation, especially focusing on the three discussed traits reproductive ability, dispersal ability and coadaptation to the community. As these traits and their development undergoing fragmentation are difficult to measure in the field, comprehensive studies are missing. We choose a complexity-based model, in which ecological communities emerge from the species' interactions (Christensen et al., 2002). This approach allows to include both facilitating and competitive interactions between species which have been shown to be crucial drivers for community dynamics in nature (Bertness and Callaway, 1994; Callaway and Walker, 1997; Bruno et al., 2003) but which usually are not feasible to assess simultaneously, both in empirical and modelling studies. Furthermore, there have been found trade-offs between interaction patterns (esp. competitive ability) and species traits such as dispersal distance and intrinsic fitness (eg. Strauss et al., 2002; Burton et al., 2010), which are rarely included in modelling studies at the same time due to their complexity. The Tangled Nature Model allows to assess the abundance and persistence of species based on their dispersal ability, their intrinsic fitness and their degree of coadaptation to the

evolving community, undergoing habitat loss and fragmentation.

We hypothesize that the degree of coadaptation of a species to the community is a significant explanatory factor for species persistence, next to intrinsic fitness, dispersal ability and abundance at time of fragmentation, as well as patch centrality for local persistence. We hypothesize further that before fragmentation, selection predominantly acts on intrinsic fitness (representing competitive ability) and the degree of coadaptation, while after fragmentation, selection also favours dispersal ability. Last, we hypothesize, that selection pressure for all three species traits becomes more pronounced after fragmentation.

8.3 Methods

The Tangled Nature Model incorporates a complex systems perspective on ecological communities, where macroscopic properties of the community emerge from the interactions of the individuals. Dynamics are individual-based and stochastic. Species interactions can be both positive and negative and encapsulate all direct and indirect effects, which in reality are almost impossible to measure, but which give rise to the ecological networks in the living world. Despite its simplicity and independence of specific parametrizations, the model has shown to be able to regenerate realistic macroecological properties such as species abundance distributions, species are relationships and trophic networks (Christensen et al., 2002; Hall et al., 2002; Anderson et al., 2004; Jensen, 2004; Rikvold, 2007; Laird et al., 2008; Brinck and Jensen, 2017).

Species traits

Modelled species differ in three traits: their dispersal ability, their intrinsic fitness and their interaction pattern with the current community. Intrinsic fitness and interactions with the community together determine the reproductive ability of an individual.

Dispersal ability $P_{\text{disp}}(S^\alpha)$ of an individual of species S^α is defined by the maximum dispersal distance $d_{\text{max}}(S^\alpha) \in [0, 10]$. This maximum dispersal distance is species-specific, fixed over time and randomly assigned in the beginning of the simulation.

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The intrinsic fitness $E(S^\alpha)$ is uniformly distributed between 0 and 1, randomly assigned and independent of space and time.

The interaction effects for each pair of species is stored in a matrix J of dimension $M \times M$, where M is the total number of species in the species pool. An interaction link $J(S^\alpha, S^\beta)$ exists with probability θ_{int} . Intraspecific competition is equal across species ($J(S^\alpha, S^\alpha) = 0$). The non-zero entries of J are uniformly distributed random numbers between -1 and 1 and independent for all $J(S^\alpha, S^\beta)$ (and $J(S^\beta, S^\alpha)$). The current degree of coadaptation is given by

$$\tilde{J}_f(S^\alpha, t) := \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n_f(S, t)}{N_f(t)} \quad (8.1)$$

where $n_f(S, t)$ is the current number of individuals of species S in patch f and $N_f(t)$ is the current total number of individuals in patch f . The average degree of coadaptation to an evenly distributed fully occupied community $J_{\text{sum}}(S^\alpha) := \sum_{S \in \mathcal{S}} J(S^\alpha, S)$ is called the baseline degree of coadaptation.

The landscape

The initial landscape is comprised of 75 grid cells (representing habitat patches) of equal size R_f , located in a rectangular area with periodic boundaries. Individuals can migrate between patches according to their maximum dispersal distance, where the right border of the landscape is connected to the left and the top to the bottom, simulating an initial well-connected large landscape. At time of fragmentation $\hat{t}$, two thirds of the habitat are removed and only the 25 coloured patches are left (see Fig. 8.1). The boundaries become non-periodic, reflecting the isolation resulting from habitat destruction. All remaining patch cells are of equal size and only differ in terms of their position and centrality in the graph. Closeness centrality C of patch x is defined as the inverse of the average distance to all other patches ($C(x) = \frac{F_{\text{tot}}}{\sum_y d(x, y)}$, [Bavelas 1950](#)), where F_{tot} is the number of patches and $d(x, y)$ the distance between patch x and patch y . The maximum distance between two patches in the fragmented landscape is 14.6.

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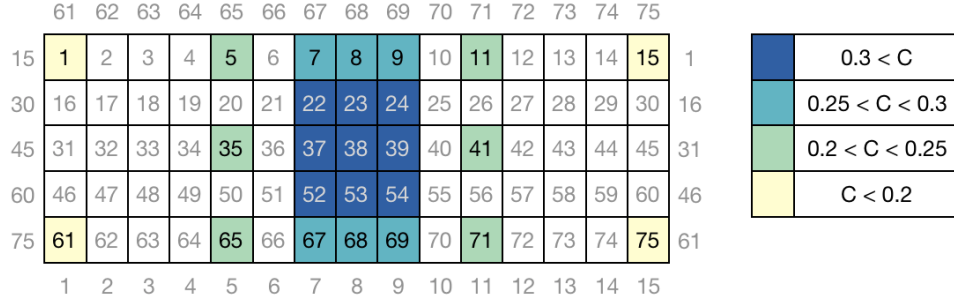


Figure 8.1: The landscape, comprised of 75 patches before and 25 patches after isolation (coloured). The colour indicates the closeness centrality C of the remaining patches (see text for details).

Species dynamics

Population dynamics are modelled based on death, reproduction, migration between patches and immigration from the mainland. The following processes are executed for each patch one after the other. One time step consists of 50 repetitions of the processes. At $t = \hat{t}$, the landscape is fragmented and isolated.

Death: One individual S^α in the patch f is selected at random and removed from the community with probability P_{death} (independent of species).

Reproduction: One individual S^α in the patch f is selected at random and reproduces with probability

$$P_{\text{off}}(S^\alpha, t, f) = \frac{\exp(\Xi(S^\alpha, t, f))}{1 + \exp(\Xi(S^\alpha, t, f))} \in (0, 1) \quad (8.2)$$

where the reproductive capability Ξ is given by

$$\Xi(S^\alpha, t, f) = w_E \cdot E(S^\alpha) + w_J \cdot \tilde{J}_f(S^\alpha, t) - \frac{N_f(t)}{R_f} \quad (8.3)$$

and w_E and w_J define the relative weight of the contributions of intrinsic fitness and interaction effects on the reproductive ability.

Migration: One individual S^α in the patch f is selected at random and migrates

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with probability P_{mig} . P_{mig} is density dependent, based on the population in the source patch. For low numbers of individuals, there is no migration pressure through the population size and a baseline emigration rate represents random exploratory migration. Once the number of individuals exceeds a threshold, which is arbitrarily chosen at $3/4 * N/N^*$, density dependent migration kicks in. A monotonically increasing sigmoid functional form is assumed for the density dependent migration

$$P_{\text{mig}} = \begin{cases} P_{\text{mig.base}} = \text{const.} & \left(\frac{N}{N^*} \leq 3/4\right) \\ P_{\text{mig.dd}}\left(\frac{N}{N^*}\right) = \frac{1}{1+\exp(-s(N/N^*-o))} & \left(\frac{N}{N^*} > 3/4\right) \end{cases} \quad (8.4)$$

where s represents the steepness of the density dependent rate and o the offset, which are solved from smoothness conditions (see below).

Immigration from the mainland: Before fragmentation, one individual of a random species from the overall species pool is introduced into patch f with P_{imm} , to account for the fact that only a small subset of the whole large initial landscape is represented in the model. After fragmentation at $\hat{t}$, immigration rate is lowered to $P_{\text{imm.frag}}$, representing rare immigration events from a far distant mainland.

Derivation of the density dependent migration rate

Intuitively, individuals should be more prone to migrate, the higher the number of individuals is compared to the carrying capacity N^* in the respective patch. Hence, the migration rate is assumed to be density dependent, with a baseline constant migration rate for low population sizes and sigmoidal increase once population sizes approach the carrying capacity (see equ. 8.4). The threshold of $N/N^* = 3/4$ is chosen arbitrarily and small changes don't affect the qualitative behaviour of the model.

The equation for the density dependent migration is solved with respect to s and o with the help of the following two conditions

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$$\begin{aligned} P_{\text{mig.dd}}\left(\frac{3}{4}\right) &= P_{\text{mig.base}} \\ P_{\text{mig.dd}}(1) &= \frac{1}{2}(1 + P_{\text{mig.base}}) \end{aligned} \quad (8.5)$$

to ensure smoothness at the transition. This means, that if the population exceeds 3/4 of the equilibrium population, density dependent migration rates start exceeding a predefined baseline migration rate. If the population is at equilibrium density, migration rates are in the middle between the baseline rate and 1.

Solving equ. 8.4 with the help of equ. 8.5 gives the following expression for $P_{\text{mig.dd}}$:

$$\begin{aligned} P_{\text{mig.dd}}\left(x := \frac{N}{N^*}\right) &= \\ &= \left(1 + \frac{(1 - P_{\text{mig.base}})(1 + P_{\text{mig.base}})^3}{P_{\text{mig.base}}^4} \left(\frac{P_{\text{mig.base}}}{1 + P_{\text{mig.base}}}\right)^{4x}\right)^{-1} \end{aligned} \quad (8.6)$$

Derivation of the carrying capacity N^*

Generally, the carrying capacity of a species is the maximum number of individuals which can be sustained in a given environment. Birth and/or death rates are hence density dependent and equal out at the carrying capacity N^* :

$$P_{\text{off}}|_{N^*} = P_{\text{death}}|_{N^*} \quad (8.7)$$

In the current model, only P_{off} is density dependent.

Inserting equ. 8.2 in equ. 8.7 and substituting

$$\mathcal{F} := \Xi(S^\alpha, t, f) + N_f/R_f = w_E \cdot E(S^\alpha) + w_J \cdot \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n_f(S, t)}{N_f(t)} \quad (8.8)$$

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(compare equ. 8.3) allows for solving equ. 8.7 with regards to N^* :

$$N^* = \mathcal{F}R + R \log \left(\frac{1 - P_{\text{death}}}{P_{\text{death}}} \right). \quad (8.9)$$

The carrying capacity hence depends on the patch's average fitness and degree of coadaptation captured in $\mathcal{F}$. Defining a carrying capacity independent of the current species composition requires an assumption for the long term average of $\mathcal{F}$. The value $F_{\text{ave}} = 13$ used in this simulation is derived from measured long-term averages in the undisturbed landscape.

Parameters

Unless stated otherwise, the parameters are chosen as follows: $M = 800$, $N_{\text{init}} = 100$, $G = 4000$, $\hat{t} = 1000$, $w_J = 10$, $w_E = 2$, $\theta_{\text{int}} = 0.5$, $P_{\text{death}} = 0.15$, $P_{\text{mig.base}} = 0.2$, $P_{\text{imm}} = 0.1$ and $P_{\text{imm.frag}} = 0.001$. This is a generic set of parameters which was found by [Lawson et al. \(2006\)](#) to reproduce evolutionary sensible observations. We have tested the effect of small parameter changes and found them to not affect the qualitative behaviour of the model. We analyse results from 15 simulation run replicates.

Statistical methods

To study which factors explain species life times in the presented fragmentation model, a linear statistical model based on the number of individuals at time of fragmentation $n(S^\alpha)$, dispersal distance $d_{\text{max}}(S^\alpha)$, intrinsic fitness $E(S^\alpha)$, average degree of coadaptation to the species pool $J_{\text{sum}}(S^\alpha)$ and degree of coadaptation to the current community at time of fragmentation $\tilde{J}_f(S^\alpha, \hat{t})$ of a species is created ([Crawley, 2005](#)). Global species life times are defined as the number of time steps until a species goes extinct globally for the first time after fragmentation. Local species life times are defined as the number of time steps until the last local extinction before the first global extinction of a species. This means that recolonization from another patch prolongs local species life times in a patch. This choice is made to make the results better comparable to empirical findings, where brief periods of local extinctions before recolonization from other patches might not be observed.

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8.4. Results

To assess trait selection before and after selection, we use the statistical method of effect sizes, which describe the strength or relative magnitude of a phenomenon. We chose to look at effect sizes rather than statistical significance due to the large sample sizes ($n > 15$ Mio.), which can cause very small effects to stand out as significant. We use Cohen's d for comparison of groups with different sample sizes to assess trait selection for and after fragmentation, and effect sizes from multiple groups based on group means to test the impact of fragment centrality on trait selection (Cohen, 1988; Lenhard and Lenhard, 2016).

Box-Whisker plots

Box-Whisker plots can be used to summarize distributions from different categories. 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).

8.4 Results

Population dynamics

Biodiversity loss after fragmentation occurs rapidly, with most species going extinct within the first 75 time steps after fragmentation (Fig. 8.2), which matches empirical findings of rapid biodiversity loss due to habitat and isolation (see eg. Wilson et al., 2016).

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8.4. Results

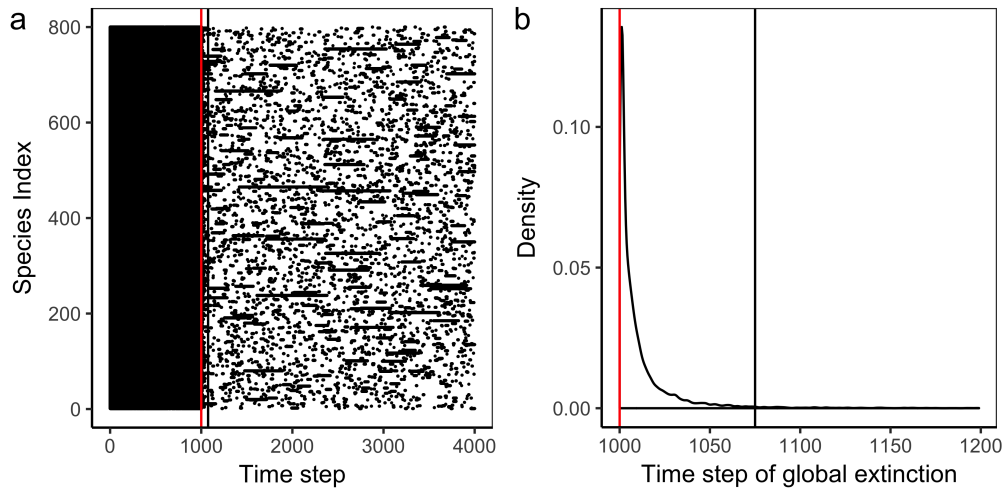


Figure 8.2: Species diversity in the community over time. Isolation occurs at $\hat{t} = 1000$ as indicated by the red line. The transition period lasts from $\hat{t}$ to $\hat{t} + 75$ as indicated by the black line.

Fragmentation has a strong effect both on the number of individuals and on diversity (Table 8.1b). Diversity drops to the lowest values in the most remote patches with a strong effect size (Fig. 8.3b, Table 8.1c) which can be attributed to less mixing and is in line with empirical findings (eg. [Economo and Keitt, 2010](#)). The average number of individuals per patch increases after fragmentation due to increased degrees of coadaptation (see discussion), which is strongest in the most central patches (Fig. 8.3a, Table 8.1b and 8.1c).

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8.4. Results

	N_f	D_f
(a) Means $\pm$ Standard Deviation		
PBF	45.59 ± 8.86	40.31 ± 9.39
PAF	56.71 ± 12.96	5.63 ± 1.83
(b) Effect sizes: change in the population level after versus before fragmentation		
PAF vs. PBF	0.921 (***)	-7.045 (***)
(c) Effect size of fragment centrality on N_f and D_f after fragmentation		
	1.021 (***)	0.987 (***)

Table 8.1: Mean and standard deviation of the number of individuals and species per patch before and after fragmentation, as well as effect sizes. (*): Small effect, (**): intermediate effect, (***) : large effect (according to [Cohen, 1988](#)). SP = species pool, PBF = population before fragmentation, PAF = population after fragmentation.

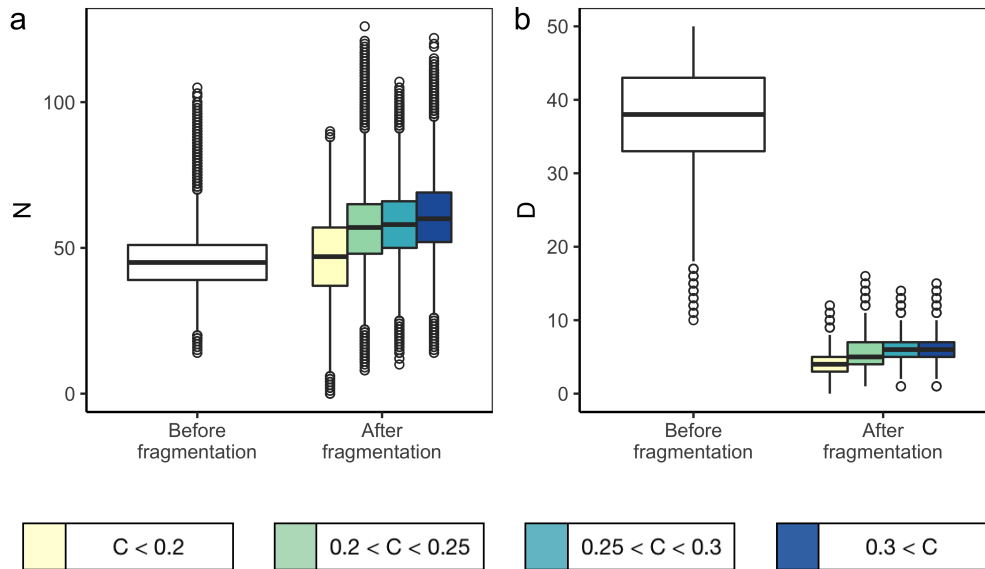


Figure 8.3: Box-Whisker plots of the number of individuals and species before and after fragmentation. Observations from an initial stabilizing period of 250 time steps as well as from a stabilizing period after fragmentation (from $\hat{t}$ to $\hat{t} + 50$) are disregarded. The distributions are obtained from 15 simulation replicates.

A small but non-zero immigration influx from the species pool after fragmentation is crucial to sustain a certain amount of species diversity. If the fragmented

8. Case study: the crucial role of coadaptation for species persistence

8.4. Results

landscape is fully isolated ($P_{\text{imm.frag}} = 0$), the community quickly collapses to only four dominating remaining species, equalling a massive extinction event (Fig. 8.4a). In this case, not even the central patches are able to sustain higher diversities and no centrality effect is obtained (Fig. 8.4b).

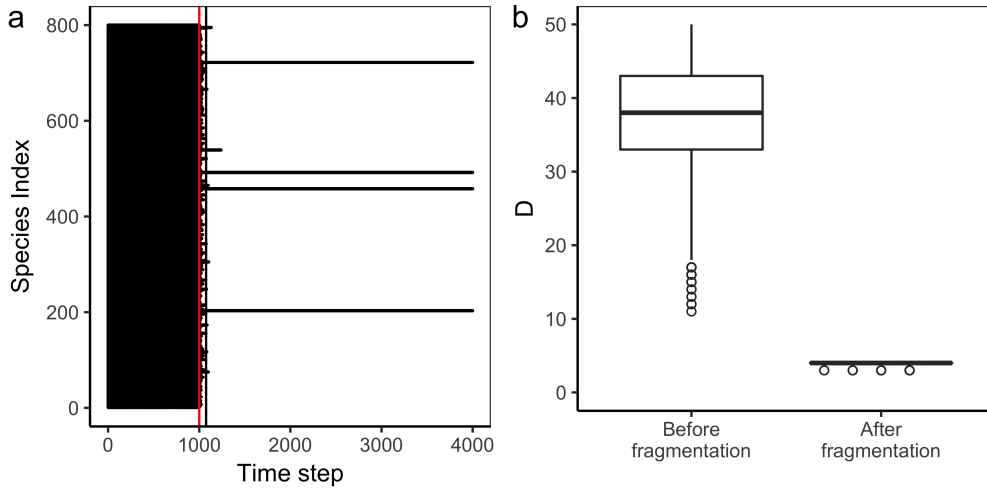


Figure 8.4: Species presence in the community over time and Box-Whisker plot of the distribution of species diversity before and after fragmentation, in a scenario with zero immigration after fragmentation ($P_{\text{imm.frag}} = 0$). Isolation occurs at $\hat{t} = 1000$ as indicated by the red line. The transition period lasts from $\hat{t}$ to $\hat{t} + 75$ as indicated by the black line.

Species persistence

Species life time distributions generally show to be exponentially or power-law distributed (Stenseth and Smith, 1984; Solé and Bascompte, 1996; Pigolotti et al., 2005), where power-law exponents have been found ranging from $-3/2$ to -2 (Bak, 1996; Keitt and Stanley, 1998; Newman and Sibani, 1999).

The distribution of species life times of a total of 15 simulation replicates are displayed in Fig. 8.5. The intermediate part follows well a power law with slightly higher steepness than reported in the literature (-2.30 locally, -2.44 globally).

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8.4. Results

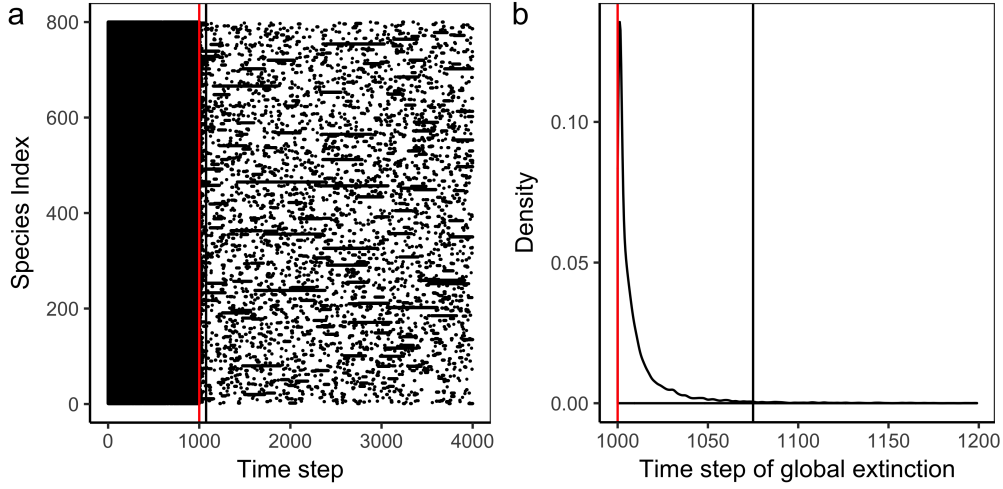


Figure 8.5: Local and global species life time distributions after fragmentation. Data is combined from a total of 15 simulation replicates. The straight red lines indicate the fitted power law. Exponents are -2.30 for the local species life time distribution and -2.44 for the global species life time distribution.

The number of individuals at time of fragmentation $n(S^\alpha)$ as well as the species' traits dispersal ability $d_{\max}(S^\alpha)$, intrinsic fitness $E(S^\alpha)$, baseline degree of coadaptation $J_{\text{sum}}(S^\alpha)$ and degree of coadaptation at the time of fragmentation $\tilde{J}_f(S^\alpha, \hat{t})$ all have a positive effect on species' life times and explain 14.9% the variance in species' global and 11.1% of the variance in local life time distributions (Fig. 8.6). Global life time variance is mainly explained by the number of individuals at the time of fragmentation, followed by the intrinsic fitness, while local life time variance is predominantly explained by the intrinsic fitness, followed by the baseline degree of adaptation and the number of individuals at the time of fragmentation (Fig. 8.6, Table 8.2). Dispersal ability affects *local* species life times but not *global* species persistence in the fragmented landscape. The findings support our hypothesis that species life times are significantly affected by species abundance, intrinsic traits and the degree of coadaptation, even though the traits differ in explanatory power.

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8.4. Results

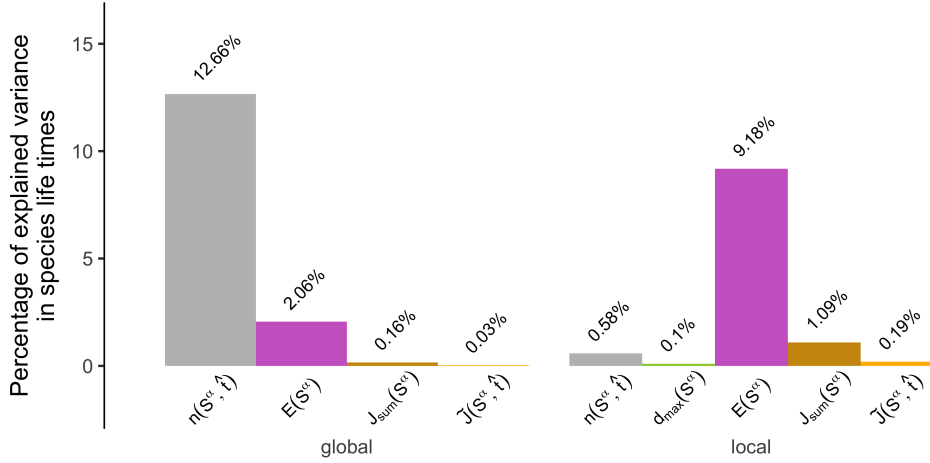


Figure 8.6: Distribution of the explained variance in species global and local life times through the number of individuals at the time of fragmentation ($n(S^\alpha)$), dispersal ability ($d_{\text{max}}(S^\alpha)$), intrinsic fitness ($E(S^\alpha)$), the baseline degree of coadaptation to an evenly distributed fully occupied community ($J_{\text{sum}}(S^\alpha)$) and degree of coadaptation to the community at the time of fragmentation ($\tilde{J}_f(S^\alpha, t)$). All variables positively influence species life times. Only significantly explanatory variables are shown.

Independent variable	Global species life time		Local species life time	
	significance	variance explained	significance	variance explained
$n_f(S^\alpha, t)$	$p < 0.001$	12.7%	$p < 0.001$	0.6%
$d_{\text{max}}(S^\alpha)$	not significant		$p < 0.001$	0.1%
$E(S^\alpha)$	$p < 0.001$	2.1%	$p < 0.001$	9.2%
$J_{\text{sum}}(S^\alpha)$	$p < 0.001$	0.2%	$p < 0.001$	1.1%
$\tilde{J}_f(S^\alpha, t)$	$p < 0.05$	0.03%	$p < 0.001$	0.2%
$C(f)$			not significant	
Total variance explained (R^2)		14.9%		11.1%

Table 8.2: Results of a statistical linear model to explain global and local species life times after habitat fragmentation. All independent variables have a positive effect on species life times.

Trait selection

Before isolation, selection solely acts on intrinsic fitness, while the mean maximum dispersal ability as well as baseline and current coadaptation lie close to

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the expected mean value given the equal distributions preassigned in the model (indicated by the red lines in Fig. 8.7) and hence are not visibly selected for (Table 8.3b). After fragmentation, selection has a notable on all four traits, with the effect on dispersal ability and baseline degree of coadaptation being small and the effect on intrinsic fitness and current degree of coadaptation being large (Table 8.3b). The findings support our hypothesis except for the fact that the selection effect size on the degree of coadaptation is not detectable before fragmentation. After fragmentation, selection pressure on dispersal ability, intrinsic fitness and the degree of coadaptation is increased with a notable effect size, as hypothesized (Table 8.3c).

In addition to looking at effect sizes of the trait average increases after fragmentation, we also tested their significance applying analysis of variance tests. We found the increases of dispersal distance $d_{\max}(S^\alpha)$, intrinsic fitness $E(S^\alpha)$, average degree of coadaptation to the species pool $J_{\text{sum}}(S^\alpha)$ and degree of coadaptation to the current community at time of fragmentation $J_{\text{sum}}(S^\alpha, \hat{t})$ to be strongly significant (two-sample t-test, $p < 2e^{-16}$, $n_1 = 15385385$, $n_2 = 58487305$ for all four species traits).

After fragmentation, habitat patches differ in their centrality in the landscape. The more central a patch, the higher the current degree of coadaptation of a species and the lower its dispersal ability (small effect, Fig. 8.7, Table 8.3d). Selection for intrinsic fitness and baseline coadaptation are not notably affected by patch centrality.

8. Case study: the crucial role of coadaptation for species persistence

8.4. Results

	$d_{\max}(S^\alpha)$	$E(S^\alpha)$	$J_{\text{sum}}(S^\alpha)$	$\tilde{J}_f(S^\alpha, \hat{t})$
(a) Means $\pm$ Standard Deviation				
SP	5 ± 2.88	0.5 ± 0.29	0 ± 11.19	0 ± 11.19
PBF	4.98 ± 2.87	0.57 ± 0.29	0.80 ± 11.76	0.24 ± 3.19
PAF	6.19 ± 2.39	0.70 ± 0.24	2.49 ± 11.95	16.53 ± 11.00
(b) Effect sizes: selection on the populations compared to the species pool				
PBF vs. SP	-0.007	0.231 (*)	0.068	0.075
PAF vs. SP	0.498 (*)	0.832 (***)	0.208 (*)	1.487 (***)
(c) Effect sizes: selection on the population level after vs. before fragmentation				
PAF vs. PBF	0.484 (*)	0.525 (**)	0.141	1.630 (***)
(d) Effect size of fragment centrality on species traits				
	-0.259 (*)	0.009	0.017	0.277 (*)

Table 8.3: Mean and standard deviation of dispersal ability $d_{\max}(S^\alpha)$, intrinsic fitness $E(S^\alpha)$, the baseline degree of coadaptation to an evenly distributed fully occupied community $J_{\text{sum}}(S^\alpha)$ and degree of coadaptation to the community at the time of fragmentation $\tilde{J}_f(S^\alpha, \hat{t})$, as well as effect sizes. (*): Small effect, (**): intermediate effect, (***) : large effect (according to [Cohen, 1988](#)). SP = species pool, PBF = population before fragmentation, PAF = population after fragmentation.

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8.5. Discussion

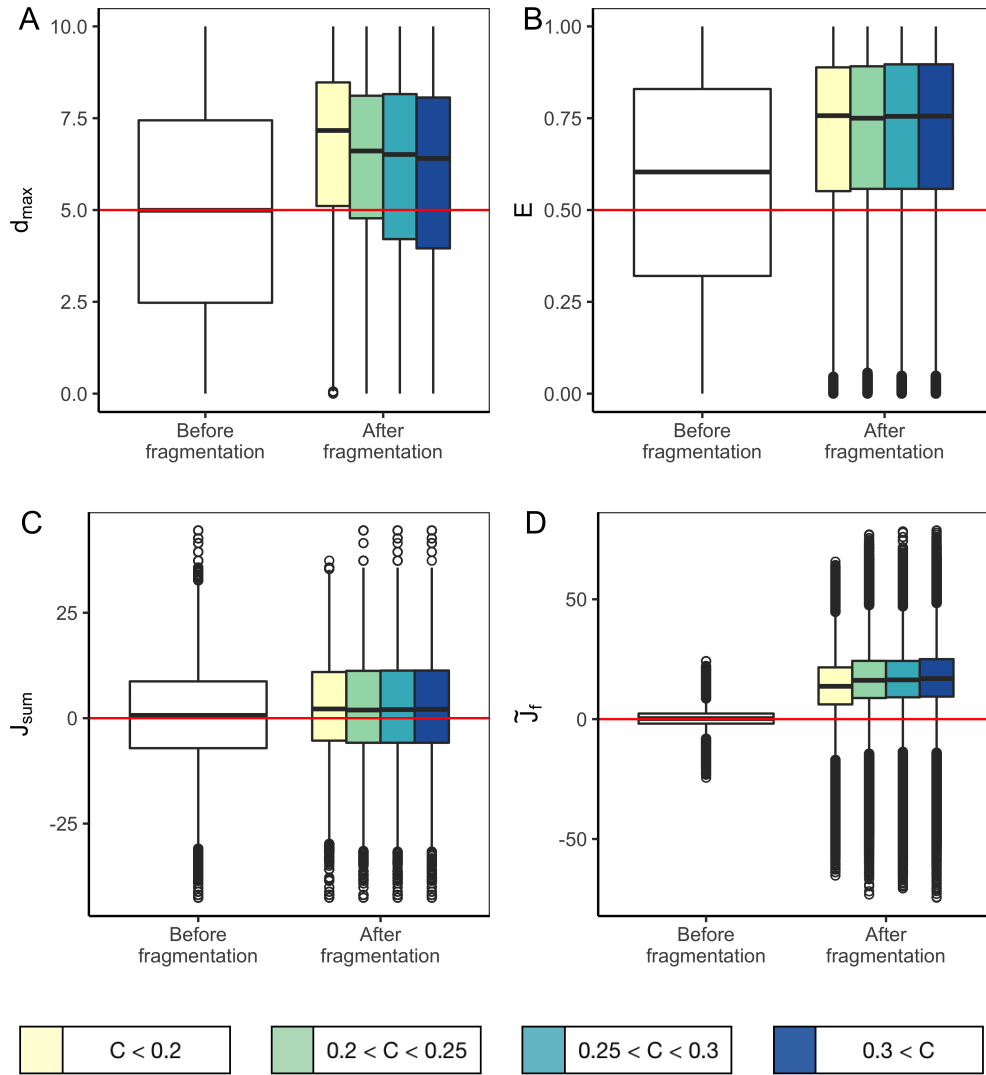


Figure 8.7: Box-Whisker plots of the distribution of dispersal abilities, competitive abilities and degrees of coadaptation of individuals. The red lines represent the respective averages in the species pool. Observations from an initial stabilizing period of 250 time steps as well as from a stabilizing period after fragmentation (from $\hat{t}$ to $\hat{t} + 50$) are disregarded. The distributions are obtained from 15 simulation replicates.

8.5 Discussion

The results strongly indicate, that both individual species traits and the degree of coadaptation of species to the community play a strong role for species' fates

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in the light of disturbances through habitat loss and fragmentation.

When looking at species persistence after fragmentation, population size is the main explanatory factor for longer global life times (Fig. 8.6), which is in line with empirical findings of small populations being especially vulnerable (Richter-Dyn and Goel, 1972; Wilcox and Murphy, 1985; Lienert, 2004; Tylianakis and Morris, 2017). Local life times in the model are mainly explained by the intrinsic fitness of a species, presumably giving it a local competitive advantage - an effect that has been found to evolve in other models as well (Burton et al., 2010). Dispersal ability, which has been regarded as the main alleviating factor for species in highly fragmented landscapes (Reed, 2004), only affects local species life times, as it allows species to repopulate abandoned patches in the exterior of the landscape. On top of these well studied species traits and their relation to species persistence, our results show, that the degree of coadaptation of a species to the community significantly affects both global and local species life times after fragmentation and is the second important factor for local persistence. These findings underline the importance of community coadaptation and the relevance of species coadaptation as a trait when analysing and predicting reactions to habitat fragmentation.

The degree of coadaptation of a species to the community is not only a significant explanatory variable for species persistence, it is also a favoured trait by selection after habitat fragmentation with a large effect (Fig. 8.7). Interestingly, this effect is not only strongly visible when looking at the current degree of coadaptation $\tilde{J}_f(S^\alpha, \hat{t})$. Though minor in effect, also the degree of coadaptation to the overall species $J_{\text{sum}}(S^\alpha)$ is higher on average after fragmentation, compared to before fragmentation and the species pool average. This suggests that while species are mainly benefited if they adapt to their current surrounding community and maximize their perceived interactions with their surroundings $\tilde{J}_f(S^\alpha, \hat{t})$, also some degree of adaptation to the overall species pool $J_{\text{sum}}(S^\alpha)$ pays off potentially to buffer the effects of the rare immigration events of foreign individuals. Our results further show, that selection increases after fragmentation not only on the degree of coadaptation, but also on dispersal and competitive ability (Fig. 8.7), indicating the importance of a diversity of traits in the community for whole-community persistence.

8. Case study: the crucial role of coadaptation for species persistence

8.5. Discussion

Despite the loss of species diversity after habitat fragmentation, selection of species which are well coadapted to the community positively influences community size, through increases in their reproductive success. This can be explained by the fact, that before fragmentation, immigration of individuals from the species pool sustains species diversity independently of the fitness of the species. Once the community becomes more isolated, species, which either show especially high intrinsic fitness or form coadapted assemblages, experience strong growth and outcompete the less well adapted species. Species which experience many negative interaction effects, or are very unfit, go extinct and are only rarely re-introduced into the community.

The reason why coadaptation is not an important factor explaining species persistence before habitat fragmentation (compare Table 8.2) is due to the time scale of model setup. Previous studies based on the Tangled Nature Model have shown that communities undergoing evolutionary dynamics (cross breeding and mutations) do become more coadapted over time, however the process is slow and usually takes tens of thousands of generations ([Christensen et al., 2002](#); [Laird and Jensen, 2006](#)). As the simulations at hand are designed to model ecological processes, the time frame is much shorter. Moreover, the relatively large influx from the species pool counterbalances selective forces.

The importance of dispersal ability and coadaptation were also affected by patch centrality, or connectivity (small effect size, compare Table ??). Species in less central fragments have on average a higher dispersal ability, allowing them to repopulate the fragment and keep migrating despite the remote position and isolation. More central patches are populated by, on average, better coadapted individuals, which also allows for larger population sizes in the landscape core. These findings support the suggestion that dispersal ability is a main alleviating factor in the face of habitat isolation ([Reed, 2004](#)) and corroborate previous results that reproductive and competitive ability is selected for at the core of landscapes ([Burton et al., 2010](#)). External stressors such as habitat loss and fragmentation hence do not only impose critical disturbances on ecological communities they also open up spaces for highly functioning, less diverse, but better coadapted species communities. These positive results however only hold when there is sufficiently large influx of species from the species pool; otherwise, the

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8.5. Discussion

system collapses to only very few remaining species in the whole landscape (instead of around 20), equalling a massive extinction event.

It has long been discussed by ecologists that the entanglement of species within their communities, their interactions and interdependencies are crucial for understanding and ultimately explaining ecosystem development and resilience (Odum, 1969; Ulanowicz, 1986; McCann, 2000; Jorgensen et al., 2007). Overall our findings emphasize the crucial role of community coadaptation and integrity for species abundance and persistence. This has several implications. First, when modelling community dynamics, attention should be paid to include different types of interactions (both positive and negative) between species, as focusing on only one or the other could lead to an insufficient representation of community dynamics and behaviour under stress. Second, when designing empirical research studies, measurements of single species traits could be extended to measurements or estimates of species interactions (of all interaction types) as far as possible. Further method development to pick up species interactions is crucial for better understanding community dynamics in the future. The effects of species coadaptation should be most visible in short-lived species with short generation turn-over times such as invertebrates and microbes. Third, the model results suggest that it is possible for communities to remain viable and even increase in size after major habitat loss and fragmentation and despite the substantial loss of biodiversity if communities are well-adapted or quickly readapt and if a small but sufficiently large influx of species to the fragmented landscape is sustained. This implies that conservation and management efforts should focus on preserving habitat connectivity.

8.6 Conclusion

In this chapter it has been shown, that complex systems modelling can also be a useful tool when studying community dynamics over timescales which are too short for evolution to shape the emergent system, but which are mainly governed by competition and succession. When such communities undergo habitat loss and fragmentation, both individual species traits and community coadaptation significantly influence which species persist and which go extinct. Management efforts thus can't rely on conserving the most abundant or otherwise seemingly dominant species in the community, as those species, which both serve the community best and fit best in the community, might be the ones which in the end ensure diversity and community functionality. Conservation hence has to focus on the self-organizing capacities or resilience of ecological communities, as they might be more important for community persistence than for example key stone species or habitat area thresholds. This could be achieved by conserving biodiversity irrespective of species size or apparent importance in the community before fragmentation and by ensuring sufficient species influx and migration in the landscape.

9

Case study: the complexity of landscape movement patterns

9.1 Context

In the previous chapters, measures to quantify the degree of coadaptation, organisation and integrity in ecosystems have been studied and assessed in complex model ecosystems. The networks of interest have thereby been species interaction networks. In this chapter, the applicability of the same information theoretic measures on spatial networks of landscape graphs and species movement flows are explored. Understanding the degree of organisation of movement patterns and their relation to landscape health and metacommunity functionality can help with conservation and habitat management decisions, which is important under the light of global landscape conversion and habitat loss.

9.2 Introduction

Assessing the quality of fragmented landscapes and the viability of resulting metacommunities remains a crucial task for ecologists in the light of unprecedented

rates of habitat loss (Robinson et al., 1992; Haddad et al., 2015). With rising interest in different ecological indicators for the identification of areas of conservation importance, substantial research effort has been undertaken to evaluate the usefulness of both landscape metrics and species measures for assessing the complexity and functionality of meta-communities in fragmented landscapes (eg. Hargis et al., 1998; Rayfield et al., 2011; Jaeger, 2000; Bunn et al., 2000).

Most of these indicators capture the structural complexity of the landscape, independent of particular species. Others focus on the usability of the landscape for particular key species and therefore depend on picking the most representative species and the context of the question (for further distinction see Banks-Leite et al., 2011). However both types of measures fail to take into account the dynamics of the complexity and functionality of the whole community and its realised fluxes within the landscape.

Envisioning the landscape as a network which is traversed by species allows for applying the measures based on information theory from the food web literature. The effects of different strategies of landscape fragmentation, patch and edge removal on the degree of organisation of the landscape from a species flow perspective can give new and more comprehensive insights on the viability of fragmented landscapes.

This chapter focusses on two questions, namely how well are information theoretic measures able to capture the structural integrity of a landscape, and how do the realised movement patterns change under different scenarios of habitat fragmentation. For the first question, we use the graph theoretic approach of looking at fragmented landscapes from Urban and Keitt (2001) and assess the *potential* flux between habitat patches with classical and information theoretic measures. For the second part, we use a spatial version of the Tangled Nature Model on different landscapes to study the *realised* remaining fluxes and thereby quantify the perceived degree of fragmentation for the community.

9.3 Methods

Potential dispersal flux in landscape graphs

9. Case study: the complexity of landscape movement patterns

9.3. Methods

The approach follows closely the setup of [Urban and Keitt \(2001\)](#) to allow for the comparison of the new results with established findings.

An initial landscape of habitat patches in a non-habitat matrix is set up (Fig. 9.1). The 50 patches vary in size between 1 and 30 ha and are distributed on a 10km * 10km area. Initially, only one species is regarded. It's dispersal probability p_{ij} (probability of dispersal from patch i to j) is given by

$$p_{ij}(d_{ij}) = \exp(-\theta * d_{ij}) \quad (9.1)$$

where d_{ij} is the distance between patch i and patch j and θ is a species-specific distance-decay coefficient. For the considered species, θ is chosen such that $p_{ij}(1500\text{m}) = 0.05$.

The dispersal flux is based on dispersal probability P and patch size s , as the latter is a proxy for the source strength of the outflow patch. Expected dispersal flux f_{ij} is defined as

$$f_{ij} = \frac{s_i}{s_{\text{tot}}} * \frac{p_{ij}}{p_i} \quad (9.2)$$

where s_i is the area of patch i , s_{tot} is the total habitat area and $p_i = \sum_j p_{ij}$. $\frac{p_{ij}}{p_i}$ thus stands for the conditional probability of dispersal from i to j , given that only flow resulting from patch i is regarded.

Due to the different patch sizes, the dispersal fluxes are not necessarily symmetric. To obtain a symmetric representation of the dispersal fluxes which has high edge weights for longer distances, additionally an edge weight is calculated as the average of the directed dispersal fluxes and subtracted from 1.

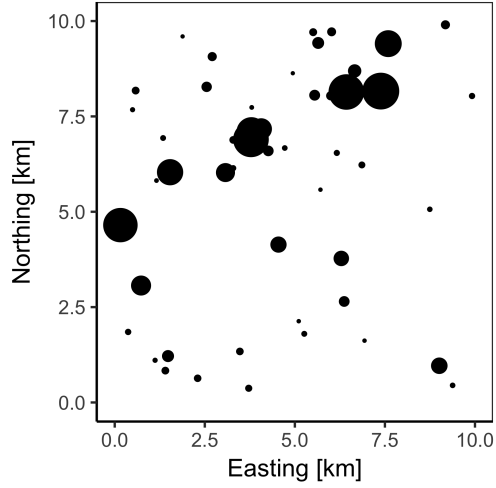


Figure 9.1: Hypothetical landscape of 50 circular patches in a 10km * 10km landscape

$$w_{ij} = w_{ji} = 1 - \frac{f_{ij} + f_{ji}}{2} \quad (9.3)$$

The minimum spanning tree depends on the choice of defining edge weight. As Fig. 9.2 shows, in the minimum spanning tree based on weights (right side), more connections are drawn via larger nodes, reflecting the higher importance of these corridors with regards to actual usage. At the same time, the leaves (end nodes) of the minimum spanning tree based on weights are represented by smaller patches. Larger patches tend to be more central in the graph, reflecting their ecological importance.

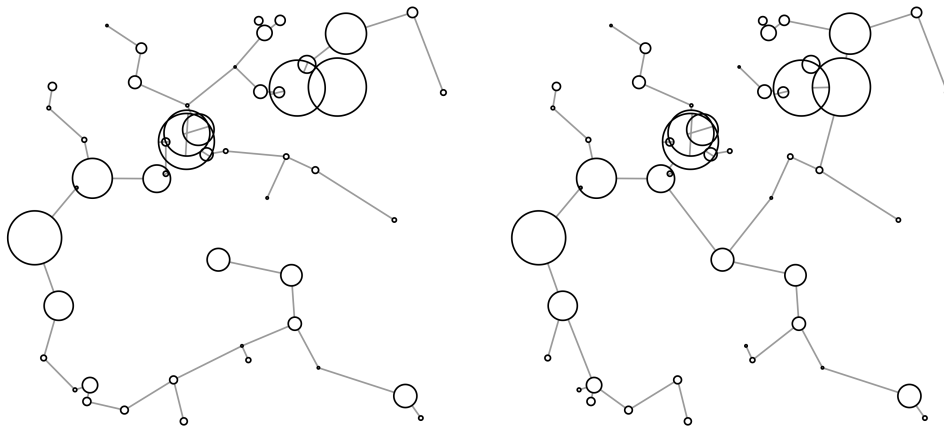


Figure 9.2: Minimum spanning tree based on distance (left) and edge weight (right)

Landscape destruction is modelled according to two different scenarios. The initial landscape graph is defined by the minimum spanning tree of the landscape based on weight. When patches are consecutively removed from the patch, either the patch with minimum area ("Min. area") or the patch with degree 1 of minimum size ("End node") is chosen.

We compare information theoretic measures of flux integrity with established graph theoretic measures, namely recruitment potential, diameter and total flux (Urban and Keitt, 2001).

The recruitment potential is defined as

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$$R = \sum_i s_i * k_i \quad (9.4)$$

where s_i stands for the size of the habitat patch and k_i for its habitat quality. As all k_i are set to 1 for this initial analysis, the recruitment potential simply represents the remaining total habitat area.

The diameter of the largest component is defined as the length of the longest way in the remaining graph and can be understood as a proxy for the traversability of the landscape.

The total dispersal flux is calculated from the edge weights as defined in equ. 9.2.

Furthermore, entropy and mutual information contained in the distribution of movement fluxes across the landscape are assessed,

$$H = - \sum_{i,j} \frac{f_{ij}}{T_{..}} \log \frac{f_{ij}}{f_{.}} \quad (9.5)$$

and

$$MI = \sum_{i,j} \frac{f_{ij}}{f_{..}} \log \frac{\frac{f_{ij}}{f_{..}}}{\frac{f_{i.}}{f_{..}} \cdot \frac{f_{.j}}{f_{..}}} \quad (9.6)$$

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Realised movement flux in model communities undergoing habitat fragmentation

We look at a model community on a spatial grid and compare three different fragmentation scenarios. The initial landscape is comprised of 64 grid cells (so called patches) of equal size R_f , located in a rectangular area with periodic boundaries (Fig. 9.3). Individuals can migrate between patches according to their maximum dispersal distance, where the right border of the landscape is connected to the left and the top to the bottom, simulating an initial well-connected large landscape.

At time of fragmentation $\hat{t}$, 28 habitat patches are removed according to different scenarios, and only the 36 grey patches are left (Fig. 9.4). The boundaries become non-periodic, reflecting the isolation resulting from habitat destruction. All remaining patch cells are of equal size and only differ in terms of their position in the landscape.

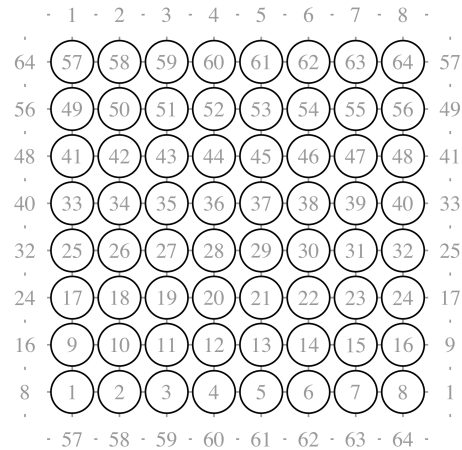
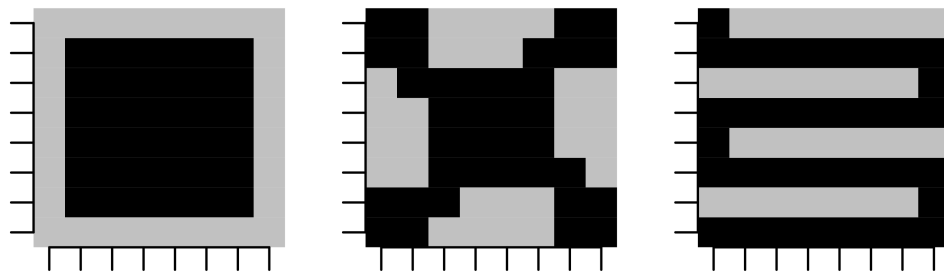


Figure 9.3: The initial landscape with periodic boundaries



(a) Scenario 1 (Average path length: 3.9) **(b)** Scenario 2 (Average path length: 5.5) **(c)** Scenario 3 (Average path length: 12.0)

Figure 9.4: The three landscape fragmentation scenarios. Black denotes habitat, grey denotes uninhabitable matrix. The average path length is defined as the average distance between two patches.

Species differ in two traits: their dispersal ability and their interaction pattern with the current community. The latter determines the reproductive ability of an

individual.

Dispersal ability $P_{\text{disp}}(S^\alpha)$ of an individual of species S^α is defined by the maximum dispersal distance $d_{\text{max}}(S^\alpha) \in [0, 15]$. This maximum dispersal distance is species-specific, fixed over time and randomly assigned in the beginning of the simulation.

The interaction effects for each pair of species is stored in a matrix J of dimension $M \times M$, where M is the total number of species in the species pool. An interaction link $J(S^\alpha, S^\beta)$ exists with probability θ_{int} . Intraspecific competition is equal across species ($J(S^\alpha, S^\alpha) = 0$). The non-zero entries of J are uniformly distributed random numbers between -1 and 1 and independent for all $J(S^\alpha, S^\beta)$ (and $J(S^\beta, S^\alpha)$). The current degree of coadaptation is given by

$$\tilde{J}_f(S^\alpha, t) := \frac{\sum_{S \in \mathcal{S}} J(S^\alpha, S) n_f(S, t)}{N_f(t)} \quad (9.7)$$

where $n_f(S, t)$ is the current number of individuals of species S in patch f and $N_f(t)$ is the current total number of individuals in patch f .

Population dynamics are modelled based on death, reproduction, migration between patches and immigration from the mainland. The following processes are executed for each patch one after the other. One time step consists of 50 repetitions of the processes. At $t = \hat{t}$, the landscape is fragmented and isolated.

Death: One individual S^α in the patch f is selected at random and removed from the community with probability P_{death} (independent of species).

Reproduction: One individual S^α in the patch f is selected at random and reproduces with probability

$$P_{\text{off}}(S^\alpha, t, f) = \frac{\exp(\Xi(S^\alpha, t, f))}{1 + \exp(\Xi(S^\alpha, t, f))} \in (0, 1) \quad (9.8)$$

where the reproductive capability Ξ is given by

$$\Xi(S^\alpha, t, f) = w \cdot \tilde{J}_f(S^\alpha, t) - \frac{N_f(t)}{R_f}. \quad (9.9)$$

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and w defines the weight of the contribution of the interaction effects on the reproductive ability.

Migration: One individual S^α in the patch f is selected at random and migrates with probability P_{mig} . P_{mig} is density dependent, based on the population in the source patch. For low numbers of individuals, there is no migration pressure through the population size and a baseline emigration rate represents random exploratory migration. Once the number of individuals exceeds a threshold, which is arbitrarily chosen at $3/4 * N/N^*$, density dependent migration kicks in. A monotonically increasing sigmoid functional form is assumed for the density dependent migration

$$P_{\text{mig}} = \begin{cases} P_{\text{mig.base}} = \text{const.} & \left(\frac{N}{N^*} \leq 3/4\right) \\ P_{\text{mig.dd}}\left(\frac{N}{N^*}\right) = \frac{1}{1+\exp(-s(N/N^*-o))} & \left(\frac{N}{N^*} > 3/4\right) \end{cases} \quad (9.10)$$

where s represents the steepness of the density dependent rate and o the offset, which are solved from smoothness conditions.

Immigration from the mainland: Before fragmentation, one individual of a random species from the overall species pool is introduced into patch f with P_{imm} , to account for the fact that only a small subset of the whole large initial landscape is represented in the model. After fragmentation at $\hat{t}$, immigration rate is lowered to $P_{\text{imm.frag}}$, representing rare immigration events from a far distant mainland.

Unless stated otherwise, the parameters are chosen as follows: $M = 750$, $N_{\text{init}} = 100$, $G = 1650$, $\hat{t} = 150$, $w = 33.3$, $\theta_{\text{int}} = 0.5$, $P_{\text{death}} = 0.15$, $P_{\text{mig.base}} = 0.2$, $P_{\text{imm}} = 0.1$ and $P_{\text{imm.frag}} = 0.001$. This is a generic set of parameters which was found by [Lawson et al. \(2006\)](#) to reproduce evolutionary sensible observations. We have tested the effect of small parameter changes and found them to not affect the qualitative behaviour of the model.

Statistical methods

To assess trait selection under the different fragmentation scenarios, we use the statistical method of effect sizes, which describe the strength or relative

magnitude of a phenomenon. We chose to look at effect sizes rather than statistical significance due to the large sample sizes, which can cause very small effects to stand out as significant. We use Cohen's effect sizes for multiple groups based on group means to test the impact of fragmentation strategy on trait selection (Cohen, 1988; Lenhard and Lenhard, 2016).

9.4 Results

Potential dispersal flux in landscape graphs

Habitat loss negatively affects the quality of the landscape, and hence recruitment potential, diameter and total potential flux decrease, the more patches are removed from the landscape graph. The strategy of patch removal however affects the speed of landscape degradation with habitat loss (Fig. 9.5). While obviously, remaining area is conserved longest if it is made sure, that always the patch with the least area is removed (Fig. 9.5a), the diameter of the remaining landscape remains longest intact in case the end node is chosen for removal (Fig. 9.5b). Interestingly, the slower degradation of landscape diameter when removing end nodes rather than the node with minimal area (Fig. 9.5b) is not picked up by the total dispersal flux through the landscape (Fig. 9.5c), but both by the entropy of the distribution of fluxes (Fig. 9.5d) and by the mutual information contained in these fluxes (Fig. 9.5e).

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9.4. Results

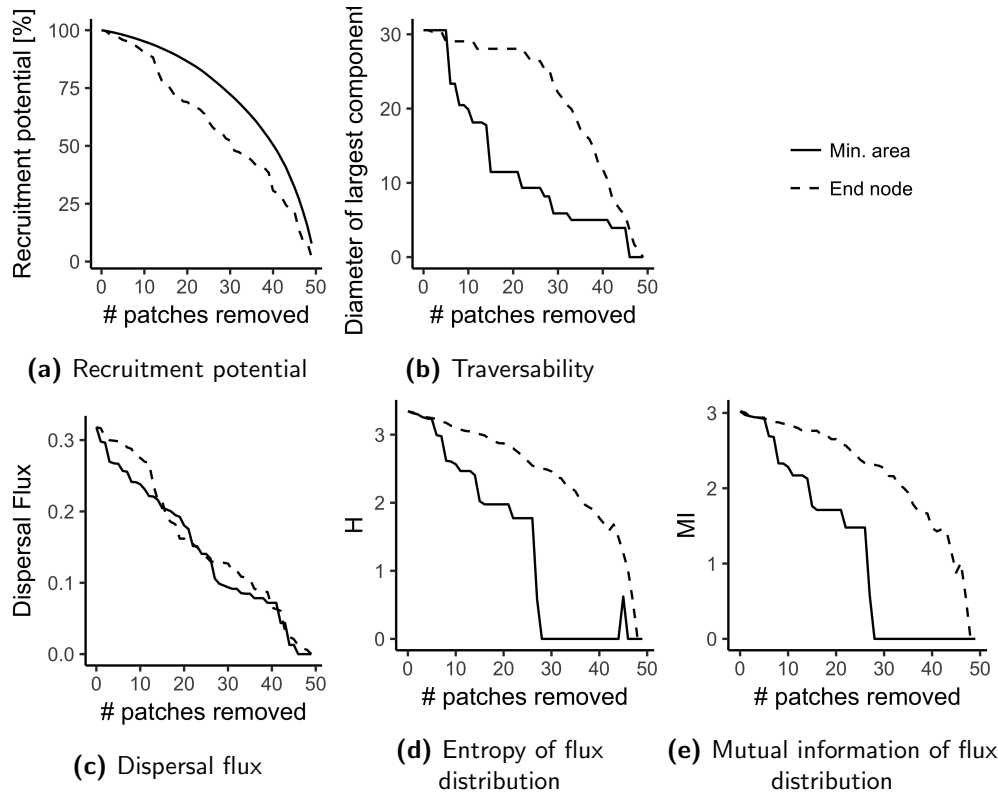


Figure 9.5: Development of landscape quality during habitat destruction under the two patch removal scenarios.

Realised movement flux in model communities undergoing habitat fragmentation

Landscape 3 is much more fragmented than landscape 2 than landscape 1, despite the fact that equivalent amounts of habitat are left (compare Fig. 9.4). The different degrees of fragmentation are also experienced by the species community in the landscape. While in the initial landscape, the average dispersal ability of present individuals lies at 7.5 hence at the exact mean of the species pool, the average dispersal ability rises in the different scenarios (Fig. 9.6a, Table 9.1) - hence the stronger the landscape fragmentation, the stronger the selection pressure for dispersal ability becomes.

However, the selection for dispersal ability isn't very strong and only has an intermediate effect (Table 9.1). When looking at the information contained in the actually realized flux pattern, the selection effects becomes much more apparent

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9.5. Discussion

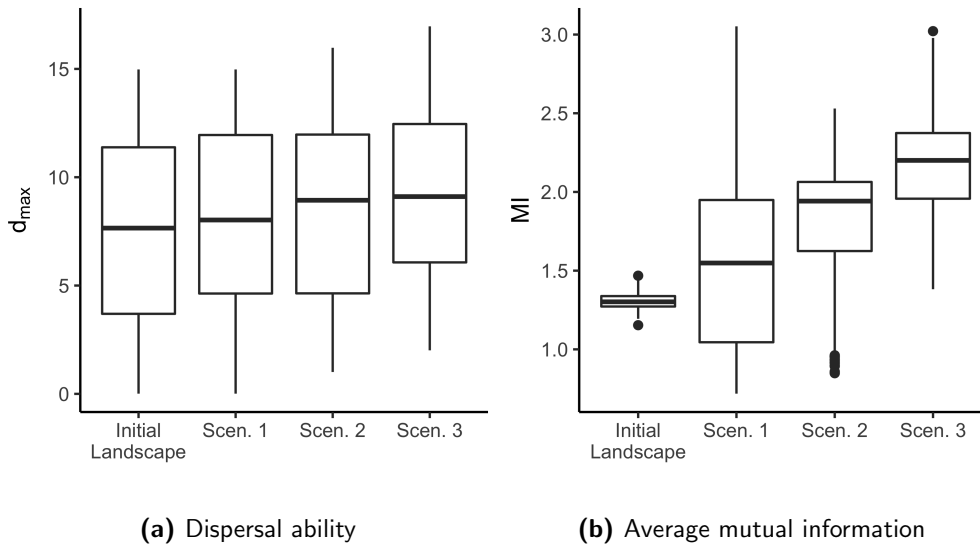


Figure 9.6: Box-Whisker plots of dispersal ability and average mutual information in the three fragmentation scenarios. The boxes show the median (solid line in the middle of the box), the lower and upper quartile ($Q1$ and $Q3$, boundaries of the box), the upper (minimum of $\max(\text{data})$ and $Q3 + 1.5 * (Q3 - Q1)$) and lower (maximum of $\min(\text{data})$ and $Q1 - 1.5 * (Q3 - Q1)$) whisker as well as outliers (circles).

	Initial land- scape	Scenario 1	Scenario 2	Scenario 3	Effect size d
$d_{\max}$	7.5 ± 4.3	8.4 ± 3.7	8.7 ± 4.1	9.5 ± 3.9	0.508**
MI	1.3 ± 0.05	1.5 ± 0.48	1.8 ± 0.34	2.2 ± 0.32	1.817***

Table 9.1: Mean and standard deviation of dispersal ability and mutual information contained in the distribution of fluxes under the different habitat fragmentation scenarios, as well as effect sizes. (*): Small effect, (**): intermediate effect, (***) : large effect (according to [Cohen, 1988](#)).

though (Fig. 9.6a, Table 9.1). Hence in this setting, mutual information serves as an indicator for the perceived landscape integrity by the overall community.

9.5 Discussion

The results show that using information theoretic measures of landscape organisation based on both landscape structure and landscape usage/functionality in terms of the dispersal fluxes can reveal profound differences in landscape quality.

When looking at potential fluxes, the total dispersal flux alone misses important characteristics of landscape quality, which are hidden in the distribution and configuration of the flows (Fig. 9.5c, 9.5d, 9.5e). When studying realised fluxes of whole communities, the distribution of flows picks up landscape quality differences better than other indicators such as the selection pressure on dispersal ability (Fig. 9.6a, Table 9.1). Furthermore, the realised dispersal fluxes will reorganise much quicker than trait selection happens, and hence mutual information could be a more short-term and reliable indicator of perceived landscape quality.

The advantage of looking at dispersal fluxes rather than structural aspects of the landscape lies in that it allows to gain insights about the *perceived* degree of fragmentation for a species or a community rather than the structural, species-independent degree of fragmentation. The results have shown that information theoretic measures of flow organisation are both valuable when looking at single species (potential fluxes) and whole communities (realised fluxes). Mutual information of the distribution of dispersal flows across the landscape picks up degree of fragmentation as measured by the size of the largest remaining component which are hidden when only analysing total flux. Mutual information also emphasizes subtle differences in selection pressure for dispersal ability (a proxy for perceived landscape fragmentation) and can hence possibly serve as a measure of perceived fragmentation. As conservation efforts should focus on species and community conservation rather than on landscape management, the indicators can hence be a useful addition to commonly used indicators when planning and assessing conservation efforts.

9.6 Conclusion

Information theoretic measures are widely applicable in ecology and can serve as a measure of complexity and organisation of not only species interaction networks and food webs, but also movement patterns and landscape quality. Further research should attempt to generalise these findings to other model settings and ideally to empirical data as well as looking at correlations between movement patterns and their integrity and community functionality.

"The eye sees only what the mind is prepared to comprehend."

Robertson Davies
Tempest-Tost (1951)

10

The search for a unified theory: an epistemological look on theoretical macroecology

Or: why grass is not less important than rabbits

10.1 Context

This thesis is situated in the scope of theoretical ecology, which has the goal to understand and explain phenomena of the living world. Based on descriptive observed data in natural ecosystems and empirical studies, theoretical ecologists attempt to find common patterns in natural complexity, build models for their occurrence and formulate theories which explain their emergence. As in any data driven science, this is only possible, if the real-world phenomena we want to gain knowledge about are well representable by measurements and data. In ecology however, there is an additional complication, namely the choice of *species* as the central observable. While taxonomies are getting more and more well resolved, the term species is defined differently for different groups of species (e.g. sexually

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10.2. *Introduction: theoretical ecology*

vs. asexually reproducing species). Furthermore naturally, organisms which are easily observable are described in greater detail and with clearer distinction than less easily observed organisms. This leads to skew and bias in the datasets, from which macroecological distributions are derived and mechanistic explanations are sought (examples will be shown later) - a problem for the search for unifying patterns and mechanisms across scales, e.g. in food webs. Despite this problem, which is confounding theory formation in ecology, ecological models and theories have shown to work well across a range of gradients and scales.

As this thesis strives to assess general patterns behind whole ecosystem measures, it is potentially heavily influenced by the above described complication. This chapter shall hence critically discuss the possible epistemological value of ecosystem models and theoretical macroecology as well as implications for the scientific discipline.

10.2 Introduction: theoretical ecology

The goal of theoretical ecology is to understand and explain organismal diversity and interactions among organisms and their environment (Begon et al., 2005). By combining results from descriptive observations of natural ecosystems and empirical studies both in and outside the lab, theoretical ecologists detect patterns in natural complexity and attempt to build models based on biologically realistic assumptions which reproduce these patterns. These idealised model-representations of ecological systems aim to improve the understanding of the natural world by uncovering fundamental mechanisms behind biological processes.

This process of gathering knowledge is based on two main assumptions. The first assumption deals with the existence of fundamental processes in ecology. Only if there are general underlying mechanisms generating natural complexity across species and ecological environments, theoretical ecology is ever able to detect any of these in observable phenomena. Fundamental research has a long tradition in the classical sciences and in ecology (Scheiner and Willig, 2008; Marquet et al., 2014) and has contributed to deepened understanding of natural phenomena, has led to economic, social and political progress and has served as a source for innovation (Couchamp et al., 2015). Hence this first assumption is widely

acknowledged as acceptable and useful across scientific disciplines.

The second assumption is one which unifies all observation- or data-driven sciences. While the aim of theory-development is to understand and explain natural phenomena, theories in data-driven sciences are based on observations of phenomena recorded as measurements or other data. Thus the value of a theory as a tool for understanding natural phenomena relies on the assumption that there is a detectable relation between the phenomena themselves and the observations of the phenomena on which the theory is grounded - and that the cognitive concepts and conceptual entities, which direct our measurements and observations, correspond to entities present in the real world.

The aim of this chapter is to discuss this second assumption in the scope of ecology, to assess theoretical ecology within a broader context of model-building from the perspective of epistemology and philosophy of science and discuss conclusions and implications for the scientific discipline.

10.3 Complication: the case of theoretical macroecology

The central entity in macroecology is an organism belonging to a certain species. The aim of the scientific subdiscipline is to understand common patterns in the distribution of body masses, organisms and species across space and biodiversity, as well as deriving mechanisms causing these phenomena ([Brown and Maurer, 1989](#)). Macroecologists use statistical techniques to analyse empirically collected large-scale datasets, ideally spanning large geographic scales and covering a large number of different species, to ultimately compare patterns predicted by theory with patterns in nature ([Harte, 2011](#)). The comparison of empirical and predicted distributions leads to refined theories and gives indications for further data collection. The process of hypothesis testing and theory development in macroecology is visualised in Fig. 10.1.

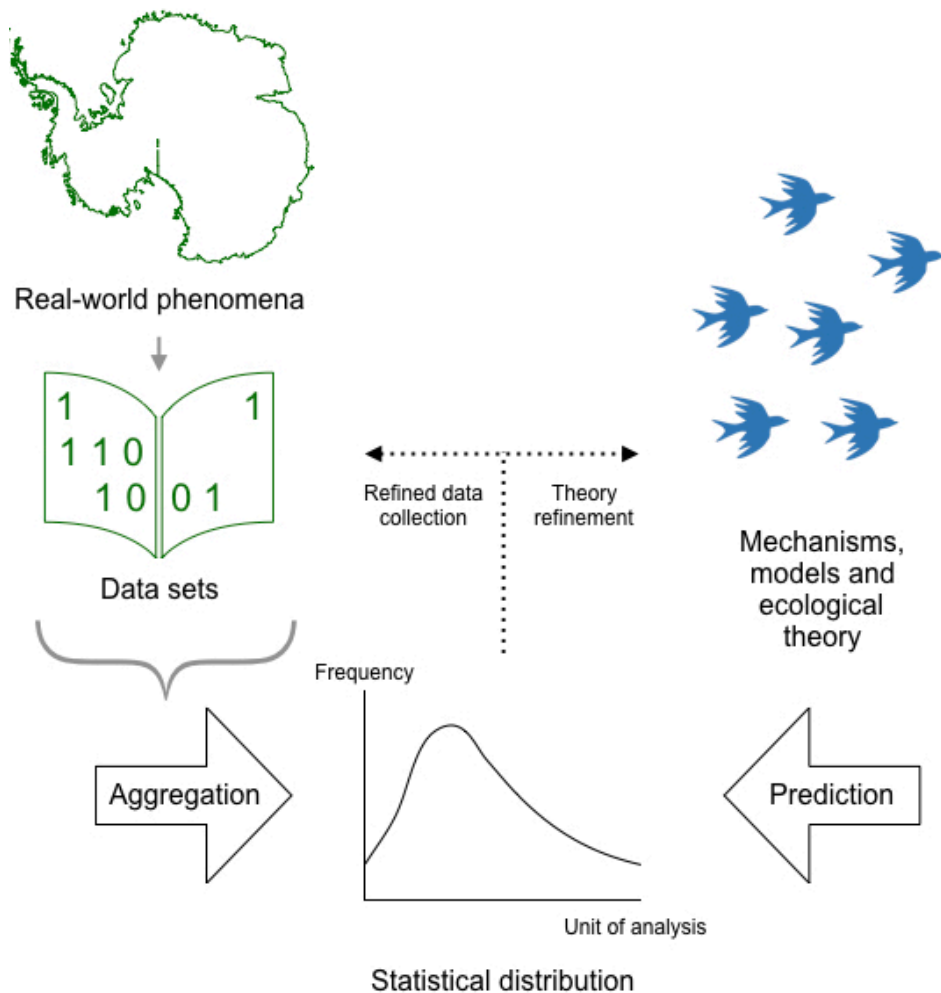


Figure 10.1: A conceptual overview of theory development in macroecology. Macroecological theories as well as underlying mechanisms are hypothesised and used to predict statistical distributions of organisms, species or biomass (right). The predicted theories are validated against aggregated data sets representing real-world phenomena (left). The comparison of aggregated observed and predicted distributions leads to both theory refinement and to the collection of additional empirical data.

Theory development in macroecology hence crucially depends on the quality of the statistical distributions which are aggregated from data sets, and thereby on

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the correct and ideally unbiased translation from real-world phenomena into data sets. The reason why this is problematic and worth a closer look and further discussion lies in the "unit of analysis" of the macroecological distributions.

Most macroecological distributions focus on species, individuals, which belong to a certain species or biomass of a certain species as unit of analyses. Examples for well-studied distributions are the species abundance distribution (SAD), the species-area-relationship (SAR), the intraspecific spatial abundance distribution or the link degree distribution in species networks. The taxonomic unit of a *species* is hence central in macroecology.

The informative value of the distribution heavily depends on a meaningful choice of the unit of analysis. Meaningful hereby includes both well-defined as well as consistently defined. Species are regarded as the fundamental unit of evolution, seen as a phenomenon of nature rather than a man-made concept and meant to describe the "biological segregation of the total genetic variability (...) into discrete packages (...), which are separated from each other by reproductive barriers" (Mayr, 1996). More complicated is the concrete detection of species. Sexually reproducing species are usually defined as the largest group of organisms in which two individuals can produce fertile offspring together - a definition, which works well for a large number of species, but fails when looking at hybridisation or ring species. Asexually reproducing species have to be distinguished by more fluid criteria of similarity including DNA sequence, karyotype, morphology behaviour or ecological niche.

Hence species, the basic unit of analysis for most macroecological questions, is an ambiguously defined concept. Moreover, as there is a tendency for sexually reproducing organisms to be larger and higher up the food chain than asexually reproducing species, there is a non-random bias in the definition of the fundamental unit when looking at ecological communities.

This bias is further fortified by the fact, that species which are easily observable are generally described in greater detail and with clearer distinction than less easily observed organisms. The granularity of species observations is hence further biased by the human scale of perception, favouring a greater resolution for larger species than for small species. Often, smaller species are even lumped into

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higher taxonomic units, such as in a food web distinguishing the common rabbit (*Oryctolagus cuniculus*) from the European hare (*Lepus europaeus*), and lumping the perennial ryegrass (*Lolium perenne*) together with the Kentucky bluegrass (*Poa pratensis*) - two common grass species found on middle European lawns - into a node called "grasses" (compare Fig. 10.2).

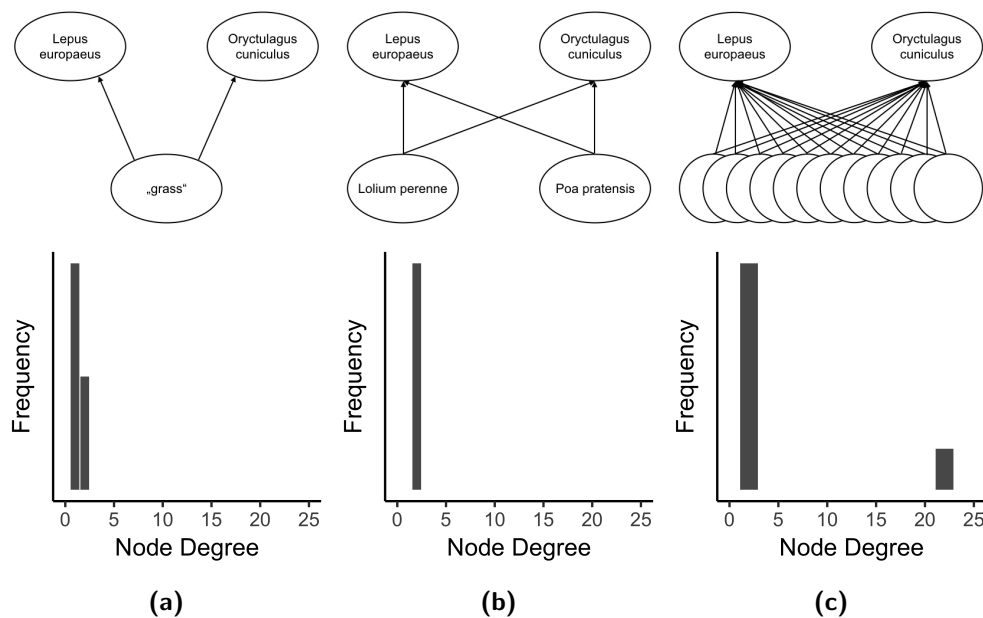


Figure 10.2: Three representations of a food web with one rabbit and one hare species, feeding on grass. The simplest representation is to lump all grass species into one data point (a). If one knows, that the two most common grass species in European lawns are present, one can decide to treat them separately (b). In reality however, lawns and meadows are usually very diverse with regards to their species composition (c), even though the different grass species look very similar at first sight. The corresponding degree distributions are visualised below the respective food webs.

Ecological data sets are hence not only incomplete, due to the complexity of ecological systems, but also highly skewed, due to the ambiguous definition of the term species and the bias towards larger species due to the scale of human perception and resulting differences in the ease of observation. This poses a critical problem to theory development in macroecology. If the process of translating real-world phenomena into data sets and aggregating them into distributions (Fig. 10.1, left side) is such ambiguous, that one food web can be represented by such a variety of degree distributions (Fig. 10.2), the decision which theory about

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underlying mechanisms behind the macroecological phenomena (Fig. 10.1, right side) is more fitting than the other becomes a subjective process, depending on the choice of aggregation of units of analysis.

To understand the complication around the concept of a species more thoroughly, we need to look at another interplay between theory formation and data collection: the dialogue between scientific concepts and empirical observations.

10.4 Epistemological excursus: the dialogue between scientific concepts and empirical observations

Fig. 10.3 shows an idealised representation between real-world phenomena, empirical observations and scientific concepts.* Real-world phenomena are translated into empirical observations, which give rise to scientific concepts, which themselves ideally are able to predict further real-world phenomena. This is an idealised flow diagram as scientific concepts can only be validated against empirical observations and not real-world phenomena (compare Fig. 10.1). More important for our discussion is the relationship represented by the grey ellipse on the right side of the figure. While it is commonly agreed that scientific theories or concepts influence model building and further theoretical derivations, we argue, that they also influence the observations they are derived from themselves. The scientific concept of units of analysis determines what we attempt to measure in nature - hence what we measure is very much a product of our theory.

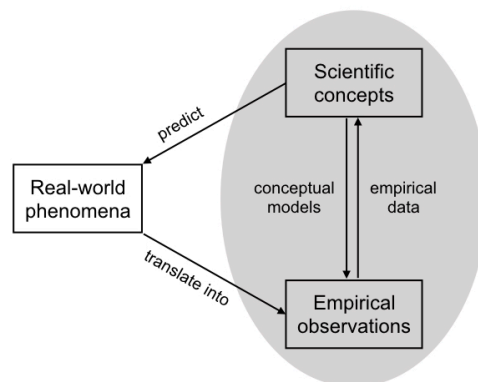


Figure 10.3: Conceptualisation of the dialogue between scientific concepts and empirical observations when studying real-world phenomena.

*Emphasis lies on the world idealised. We are aware of the subtleties around the existence of anything like a real-world-phenomenon. For the sake of the argument however, we want to assume the presence of real-world phenomena, which may or may not be well-represented by empirical data based on our observations, as a working hypothesis.

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10.4. *Epistemological excursus: dialogue between concepts and observations*

More concretely, we might attempt to explore the world open-mindedly, simply describe species sizes, abundances and behaviours without drawing on hypotheses, which functionality they have in the system – but in fact, we are biased by the concept of a species itself. We have developed the scientific concept of species, because it seemed useful to reduce natural complexity, but at the same time, we observe species, because of the prevalence of the scientific concept of a species. Scientific concepts are hence not the result of empirical observations, but rather scientific concepts and empirical observations form a dialogue.

This might sound like a purely theoretical claim, but it is actually relevant in many scientific disciplines. Physics at first appears like the field of research, where such complications don't arise due to its clear and distinct hierarchy of entities (such as bodies, elements, atoms, protons & electrons and quarks) and embedding in mathematics. However, nothing less than a shift in the theoretical understanding of the behaviour of matter in unusual phases or states, for which three researchers were awarded the 2016 Nobel Prize in Physics, led to the development of new materials and applications and opened up new fields of research. The three physicists used advanced mathematical methods from topology to explain what happens in surfaces, which are so flat that they can be considered two-rather than three-dimensional. Their findings have both helped to understand previously inexplicable phenomena such as the Quantum Hall effect, and have built the foundation for the development of superconductors and the creation of integrated circuits, which are present in every computer and smart-phone today. Their findings furthermore led to the development of materials called topological insulators and brought condensed matter physics to the forefront of research in physics (Rathi 2016, see [Nobel Committee for Physics 2016](#) for a detailed explanation of the findings). Hence while at first, empirical observations, which couldn't be explained by prevailing theory, led to the exploration of new theoretical understandings of the behaviour of matter, the breakthrough of the three Nobel laureates in the development of scientific concepts shaped empirical and applied research, enabled new practical applications and led to the creation of new concepts for a range of areas of physics.

This interrelation between concept and observation is common in all data-driven sciences. It is also the reason for the fact, that a well-defined definition of

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scientific concepts is absolutely crucial not only for data analysis and theory development, but for data collection itself - a necessity not given for the whole of macroecology.

10.5 Implications for theoretical ecology

We have analysed that for any scientific discipline to develop meaningful theory, unbiased and clearly defined scientific concepts are crucial, and that in macroecology, this prerequisite is violated by the ambiguous definition of species. What does this imply?

First, one has to distinguish situations from where the complication actually arises from those, which are less critical. It has been discussed in the beginning, that species definitions differ between types of species. Hence we would expect that there occurs no problem for macroecological theory development, in case the research focusses on similar species, with equal species definitions, similar data collection methods and similar observability (e.g. due to similar sizes). Indeed, past research has shown, that theories behind for example species area relationships or community biomass distributions tend to predict empirical distributions well if species stem from one trophic level (e.g. birds or grasses), but fail as soon as one aims to span different trophic levels ([Harte, personal communication, 2013](#)). This finding supports the argument that the discussed issues with macroecological theory development can be neglected in case similar species are regarded. Hence this confinement is actually little problematic for research problems which can be studied separately at different scales - as it is the case for example for upscaling and predicting biodiversity within single groups of species.

Second, in case one explicitly aims at crossing levels of different types and sizes of species (such as for example in food web ecology, where theories explaining patterns across trophic levels are sought), the above made argument however doesn't hold. The definition of a new unit of analysis, a unified species term, is required, which is unambiguously defined across the whole data set. While there is no clearly defined protocol for species representation in food webs and often, the resolution at different trophic levels is based on the availability of observations, some food web research has developed around the concept of a

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functional group (Dunne, 2009). A functional group is a set of species which share alike characteristics, occupy the same niches and perform equivalent tasks. In the case of food web ecology, this are species, which share the same set of predator and prey species. It has been argued, that functional groups are equally or potentially even more meaningful measures of biodiversity, as they correlate better with ecosystem functionality and have hence a higher informative value for conservation and management (Cadotte et al., 2011). Moreover, to return to the question of an unambiguous unit of analysis for macroecology, their definition is independent of size or reproductive mode and hence more useful for research across scales. There are however two problems included in basing for example food web research on functional group. On the one hand, also the concrete definition of a functional group remains dependent on the scale and detail of observation as well as the context in which the group is observed - two species might share their set of prey in one habitat, but differentiate their diet according to preferences in case a larger variety of prey species is available in another habitat. Hence ambiguity and dependency on observation effort remains. On the other hand, even if a functional group could be well-defined within the realm of food web ecology, it might look different in the realm of biodiversity research (think of two species with the same set of predators and prey, but with different abiotic habitat preferences) or the realm of species as ecosystem engineers (species with same predators and prey, but one has a constructive, the other an erosive effect on the environment). Hence gaining clarity about the unit of analysis across species types might come at the loss of clarity and comparability of findings in different ecological subdisciplines or with regards to different ecological questions - thus uncertainty remains.

The third implication is a derivation from the other two. We have seen, that the ambiguity is less problematic, as long as research is constrained to a certain set of similar species (hence within a certain context), and that the context-dependency with regards to different scales of species can only be (partly) resolved by accepting context-dependency with regards to the research question respectively the ecological subdiscipline. Hence, context-dependency is unavoidable in ecology.

This ubiquitous context-dependency is by no means surprising. Ecology is the science of species interactions, hence the study of contexts themselves. Further-

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more, the emergent features of species interactions, namely ecosystems, can be parts of systems themselves - just think about the plant ecosystems in tropical tree crowns, or the gut ecosystem living in any mammal individual. The emergent hierarchies of life overlap, and we simply lack the mathematical tools to analyse and predict these nested systems. Despite the fact that ecology will benefit from more fine-grained data, better sampling techniques do by on means guarantee the development of unified macroecological theories - because, as argued in this chapter, the unit of analysis remains ambiguous and context-dependent, as well as nested at different levels in emergent hierarchies.

The solution for macroecology is hence to embrace this context-dependency. While probably, with the advance of empirical methods and larger and better resolved data sets, many of today's ecological theories will be unified in the future, no single unified theory based on species distributions will emerge. This seeming disadvantage however allows for insights about the nature of hierarchies in ecology by enabling the distinction of different interwoven levels in ecological systems.

While this problem of the units of analysis being emergent features themselves is especially problematic in ecology, it is also relevant in other scientific disciplines. For an example we turn back to physics. The universe is made up of galaxies, which consist of planets, which emerge from the interaction of elements, which are built up of atoms, which are made of protons, electrons and neutrons, which themselves consist of quarks. While it is certainly possible to distinguish more levels of hierarchy, the separation between scales appears to be quite distinct. Entities are generally studied separately at their level in the hierarchy and there is not much debate around the definition of the units of analysis. However the situation is much more blurred than it seems to be at first sight. Electrons for example, are considered as fundamental particles in free space. Inside materials however, they can exhibit very different properties and behaviours due to complicated interactions with other particles - and the electron loses its property of being a fundamental particle. In physics, these cases of crossed scales are more rare and can often be treated more easily than in ecology - in the case of electrons in materials, the redefinition of their weight solves the mathematical complications. Nevertheless, this example shows, that the problem, that funda-

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mental entities are not always unambiguous and clearly defined is not unique to ecology but affects all scientific disciplines.

It has been shown that context-dependency is intrinsic to ecology as well as to ecological theory. This both complicates macroecological methodology by requiring careful treatment of the units of analysis and impedes the development of truly unified theories, due to ambiguity and interdependencies. At the same time, exactly this complexity is the nature of our world, and the beauty of the living planet.

Life is complex, and in fact there are way more ambiguities in ecological data sets than discussed so far. Most data sets are so called cumulative data sets, where presence-/absence measures of individuals, species, interactions or biomass are time- or spatially averaged or cumulated (Dunne, 2009). In reality however, neither species abundances nor interactions are static properties. Especially the latter are heavily dependent on the current configuration of the community, the presence and absence of preferred prey species, the spatial distribution of individuals and further restrictions in prey availability and starving pressure. What is established as a feeding link in a food web representation is in fact only a propensity of a species to predate on another, which exceeds a certain threshold leading to an observation in the field. Nevertheless, theoretical ecology has developed a large diversity of models and theories which have shown to give good predictions both for specific systems and across systems and scales, which have tremendously advanced the field and natural sciences in general (Hastings and Gross, 2012). Hence the same complexity that is complicating ecological theory development at the same time enables insights in large-scale relationships, as detailed not well-understood mechanisms don't necessarily matter.

Hence despite the discussed fundamental problems, theoretical macroecology has proven to be useful to gain insights in the natural world and thereby defended its place. Methodological refinements such as large-scale data collection and next generation sequencing are expected to advance the discipline in the next decades due to larger and more clearly defined data sets. Nevertheless it remains crucial to carefully check how far scale-crosses are intrinsic to the respective question and research study and reflect upon the context and possible dependencies when developing macroecological theories.

10.6 Conclusion

This chapter shall remind the macroecologist to carefully reflect on the unit of analysis, especially when crossing ecological hierarchies. It shall also be remarked that this complication is not a weakness of the science of ecology, but should actually be understood as an opportunity to refine ecological concepts and discover a more correct theoretical representation of the world around us.

This thesis looks at species interaction networks and the special case of a food web, which, as discussed above, is strongly affected by the discussed problems. However the case studies of this thesis in particular are purely built on models - in which the term species is clearly and equally defined across the whole community. As nested hierarchies are excluded from the models, too, the discussed complications don't arise in the modelling studies.

It is however important to note, that any of the suggested measures of ecosystem organisation remain to be checked on real-world data, where the complications of ambiguous species definitions and varying observabilities is strongly relevant. It hence remains an open question, whether such macroscopic ecosystem measures can ever be validated in the field, or whether they remain purely theoretical, for the curious fundamental researcher to hypothesise and explore. In any case, they will inform and shape the dialogue between empirical research and ecological theory development.

"In anything at all, perfection is finally attained not when there is no longer anything to add, but when there is no longer anything to take away."

Antoine de Saint-Exupery
Wind, Sand and Stars, 1939

11

Conclusion and Outlook

11.1 Conclusions

11.1.1 How can the degree of self-organisation in ecological systems be quantified?

A complex emergent system differs from a reducible system by the fact, that the behaviour of its macroscopic entities, which usually only follow fundamental laws, is additionally constrained, influenced or shaped by its macroscopic properties emerging from the interactions at lower levels ([Hendry, 2010](#)). Quantifying the role of these macroscopic emerging properties for governing the system's behaviour requires measures which are holistic, capturing structural and functional aspects of the whole system ([Ulanowicz, 1986](#); [Jorgensen et al., 2007](#)). The difference between the macroscopic state of a complex system and a system, which can be reduced to the behavioural rules of the microscopic entities, is the additional amount of information in the emergent state of the complex system. Higher level biological phenomena are brought about by information storage and flow within cells, tissues, organs, organisms and ecosystems. To understand the self-organisation of living systems requires understanding how living systems

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gather, process, store and use information (Nurse, 2008).

Information theory studies the information content and communication in a rigid manner. On the one hand, information theoretic measures are able to reduce large samples to few measures of information content and are therefore suitable to capture ecosystem organisation in a holistic way. On the other hand, different aspects of information, uncertainty and information transfer allow enough flexibility to address different questions around the self-organisation of ecosystems. Therefore, information theory is a promising tool for theoretical ecosystem ecological research and is used to quantify self-organisation in ecological systems in this thesis.

In the different examples discussed in this thesis, it has been shown, that the information stored in model ecosystems does indeed increase over successional and evolutionary time scales in a variety of dimensions and relates to the degree of development and stability of the system (chapter 5 and 7). The information in the system stems from the increased coadaptation of more developed ecological communities compared to random or early successional systems. It has even been shown that the higher developed and more coadapted the systems are (hence the more different they are from a random system in information content and organisation), the stronger the influence of the macroscopic state on the whole system becomes, replacing bottom-up control as a main driver (chapter 6).

Furthermore, it has been shown that concepts about self-organisation and stored information can also be assessed in different contexts such as the dispersal flow of communities across fragmented landscapes (chapter 9).

Overall, the results imply, that information theory is not only conceptually valuable for ecosystem research, but that it can actually reveal differences in the state, stability and resilience of the system at hand. It is hence a promising tool for the assessment of the degree of self-organisation of complex ecosystems, and further empirical research and theory development should focus on its transferability to the empirical systems as well as its conceptual limitations.

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11.1.2 **How does order in ecological systems arise, develop and evolve?**

Ecological communities develop in a dialogue of bottom-up and top-down control. While in a young ecosystem, the behaviour and fitness of the single individuals shapes the system's dynamics, in later successional stages, the macroscopic state exhibits a growing influence on the overall behaviour of the system (chapter 6). The increased degree of coadaptation of the species stabilises the community, allows for higher levels of overall biomass in the system and results in increased importance for species to fit in the system, rather than only being benefited by the current environment.

This observation brings us back to the dual meaning of fitness (compare chapter 1.1.2): fitness is both a characteristic of an individual describing how well it does under the current circumstances, and a measure of how well the organism is able to contribute to the overall functionality of the system. It is therefore, that autocatalytic feedbacks from the system to the individual act as a self-organising driver (as hypothesised for example by [Ulanowicz \(1979\)](#)), leading to the arising, development and evolution of order in ecological systems.

11.1.3 **Which role do complex dynamics and coadaptation play for ecological communities undergoing habitat loss?**

The core value of complex systems modelling lies in the ability to bridge the gap between microscopic behaviour and non-reducible macroscopic emergent systems and to study properties of emergence. Questions addressed often refer to long time-scales, during which specific switches in macroscopic behaviour might occur - like the shift of one stable community to another during the course of evolution. Complex systems modelling however has a further advantage, which can make the technique very valuable also for questions regarding shorter time-scales. To explain emerging characteristics of complex ecosystems (as abundance, distribution and energetics of species), ecologists usually investigate the numerous ecological processes and mechanisms (e.g. competition, speciation or migration) coupled with multitudinous species traits and behaviours (like body size, food preferences or environmental tolerances). This wealth of detail on the local/individual

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in the best case leads to equation rich, non-generic and computationally intensive ecosystem models - and in the worst case can't be parametrised or computed at all. Complex systems modelling reduces much of this complexity by distilling the main driving forces behind individuals' and species' behaviour, which give rise to the same macroscopic patterns we can observe in nature, and then study the role and effect of those main drivers while neglecting anything that is irrelevant for the macroscopic behaviour of the system.

In chapter 8, this advantage of complex systems modelling was used to study the relative importance of individual species traits as well as the degree of coadaptation of a species to the community for species abundance and persistence after habitat fragmentation - a combination, which is very difficult to study with mechanistic models due to missing empirical parameters and computational complications. The results have shown, that even if only looking at the microscopic level of individual species' fates, the coadaptation of the whole system plays a significant role as a predictor for abundance and persistence. Individual species' reproductive, competitive and dispersal ability are not sufficient explanatory variables, but the complex interactions in the community, the self-organisation of the community and the degree of coadaptation of a species need to be taken into account to understand community dynamics in fragmented landscapes and their resilience in the face of major disturbances.

11.1.4 What epistemological value does macroecological research have in general?

Theoretical ecological research is struggling with the dilemma of generality versus specificity ([Fukami, 2010](#)). Ecology had originally started off as a mainly descriptive scientific discipline about species characteristics, their occurrence in different habitats, their behaviour and finally their influences on each other. From these detailed descriptions, a vast range of hypotheses have been developed, attempting to explain specific observations usually limited to small areas or groups of species. Over time, these hypotheses have been refined, integrated and developed into the body of theoretic knowledge ecology is comprised of today. Over the last decades, many attempts have been made to aggregate theory further

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and develop unified theories of ecology, such as Evolution as Entropy (Brooks and Wiley, 1986), the Unified Neutral Theory of Biodiversity and Biogeography (Hubbell, 2001), the Metabolic Theory of Ecology (Brown et al., 2004) or the Maximum Entropy Theory of Ecology (Harte, 2011) - at the loss of the details hidden in the fascinating diversity of organisms, but with the aim in mind to capture the grand scheme of how nature works.

It has been argued, that unified theories in ecology are neither feasible nor desirable (Fukami, 2010). The latter is mainly justified by the need for specific answers to specific questions especially in the realm of conservation and management, where broad overarching theories might not be helpful to understand how for example a particular species with its individual life cycle in the specific habitat can be preserved (Simberloff, 2004). However the fact that unified theories are not feasible is usually simply deducted from the arising difficulties and the lack of fit to empirical data. In chapter 10, it is argued, that there are not only practical, but also fundamental theoretical reasons for the absence of unified ecological theories. Ecological research deals with individuals, their biology and their interactions, from which species and ecosystems arise. In the biological hierarchy of species and ecosystems, scales of emergence blur (think about the gut ecosystem or the ecosystem which can be found in the canopy of rainforest trees, as well as the ambiguous definition of the term species itself and its emergence from reproductive interactions between individuals). It is therefore, that any ecological theory which uses a *species* as fundamental unit of analysis, is intrinsically context dependent and cannot easily be widened across taxonomic scales.

The dilemma between specificity and generality in ecology doesn't have an answer that says either/or - the solution will always be an and. Specific concrete empirical and model studies are necessary to find answers to concrete questions, and the search for overarching patterns and theories is the only way to understand more general aspects of the living world. Both approaches have fundamental constraints which so far prevent us from developing a unified theory of ecology. However, as discussed in detail in chapter 10, empirical research does not only provide the foundation for the development of theory; the derived theoretical concepts also influence what we look out for in nature and thereby feed back on

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11.2. Implications for future research

empirical research. Therefore, despite the fact that a unified theory of ecology is not feasible with the current collection of scientific techniques (especially empirical tools and mathematical methods), the exploration of its possible scope and limits is a crucial inspiration for the development of the science of ecology in general, widening the window through which we look at the world and conduct ecological research.

11.2 Implications for future research

Complex systems modelling builds on assumptions about the rules which govern the behaviour of the microscopic entities. Of special importance is the way in which the entities influence each other, as the interactions give rise to the emergent behaviour of the overall system. To understand this complex interplay in ecological systems properly, further research in different areas of ecology is required.

Empirical research: Quantifying the interaction effect of one individual or species on another is very difficult in empirical studies, but further methods should be developed to gain better insights about realistic distributions of interaction strengths. When it comes to comparing predicted results with empirical data, the effects of species coadaptation should be most visible in short-lived species with short generation turn-over times such as invertebrates and microbes.

Mathematical modelling: When designing model studies, more attention should be given to the role of coadaptation within ecological communities, as it can shape dynamics as much as individual species traits. The presented results have shown in particular, that different types of interaction (both positive and negative) are important and meaningful results can only be obtained if neither is neglected.

Theory development: Ecological theory is context dependent - species, the units of analysis, are not necessarily defined equally when scales or levels of hierarchy are crossed. Hence it is important for the future of theory development to reflect upon the context in which this particular theory is supposed to generate meaningful predictions and to evaluate possible scopes and limitations of theory

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11.3. *Implications for ecosystem management and conservation*

aggregation. The search for a unified theory of ecology has fundamental problems, which might be resolved in the future by advanced empirical methods and new mathematical developments, but which right now might limit its scope to purely theoretical studies. Nevertheless this fundamental abstract research of possible unified theories for complex systems in general and ecosystem behaviour in particular can be an important inspiration for the future of more concrete theoretical and empirical research. It opens the way for *conceptual* unified theories, after which more practical theory unifications can follow.

11.3 Implications for ecosystem management and conservation

Ecosystems are complex, they are comprised of a multitude of agents interacting in many different ways, influencing each other and thus giving rise to stable and resilient emergent ecological systems. Complexity research shows that while the most abundant species often play a large role in shaping the system's dynamics, it can also be the rare, small or otherwise seemingly insignificant species which keep the community in its current state. There are not necessarily any keystone species or processes, whose preservation ensures the preservation of the overall system, as basically any change in the microscopic configuration of the system can feed into feedback loops, trigger chain reactions and kick the system in a different alternative stable state.

If the goal of ecosystem conservation and management is to keep ecosystems in a lively and functional state, it is hence most important to ensure that its self-organising capacities are retained by keeping it away from a less energetic equilibrium state. The most stable state an ecosystem can reach is complete extinction, and it is the openness with regards to energy but also species and matter fluxes which keep an ecosystem in more diverse and functional states. It should therefore be a goal in ecosystem management to conserve fluxes rather than single species. Ensuring the flow of species between subcommunities, the flow of matter and energy through ecosystems and the flow of individuals through the landscape allows the system to experience diverse microscopic interactions, which are the motor of the system's resilience and persistence.

11.4 Implications for sustainable development

In the realm of this thesis, natural ecosystems have been regarded in isolation, but obviously, the reality is even more complex. Human beings are part of the global ecosystem. They are one entity in the overall pool of interacting species, far up in the trophic hierarchy but nevertheless participating in the never-ending assimilation, degradation and cycling of resources in the ecosystem earth. Aiming for an ideal of nature detached from mankind, it being in its pristine state without any interfering human intruders, is an unrealistic attempt. There is no single point on the planet which is not at least indirectly influenced by human behaviour. However even more importantly, placing nature aside from mankind is not even desirable. It is only by recognizing and appreciating our role as small building block *within* this vast diversity of life, that we can make the right decisions about our interactions with nature and manage for shared well-being and sustainable development.

Sustainable development is one of the most important challenges of our time. A complex systems perspective on sustainability generates both warnings and hope. No matter how much you alter, constrain or disturb an emergent system, as long as you don't wipe out the entirety of its microscopic entities, they will always keep exhibiting their intrinsic behaviour and a macrostate will re-emerge. Sustainability is hence inevitable - per definition, those systems, which are resilient and sustainable will be the ones which persist. The question is simply, which kind of sustainable state we will reach, how much diversity and functionality will be left and how well we as a species will do in the system.

It is our task to make the ecosystems around us which we want to be preserved as resilient as possible. As life is intrinsically dynamic, it will not be enough to define one desired long-term state of the socio-ecological system and use it as a conservation goal. The focus has to lie on the establishment of processes which allow to continually apply adaptive management, carefully monitor states and trajectories and iteratively adjust management efforts. Rather than seeking simple principles to guide our actions without reflection, we need to strengthen our capacity to quickly and bravely deal with change - both in our roles as conservationists and in our everyday lives - in order to be most effective as change

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agents in the dynamic, quickly evolving and complex socio-ecological system.

The need for dynamic, reflective and adaptive behaviour is linked to the problem of reductionism versus constructivism discussed in the preface and encountered in all examples in this thesis. The living world is indeed, at least within certain realms and depending on the specific question at hand, reducible to different fundamental rules which govern the behaviour of individuals and species. However it is the interplay *between* the individuals which gives rise to diversity, functionality and resilience in ecosystems. Of course, we as rational agents can also follow simple behavioural rules and thereby contribute to the emergence of a certain socio-ecological system - but this might not necessarily be the specific macroscopic state we envisioned when initially determining our behavioural rules. The macrostate cannot be predicted from the microscopic behaviour, which is why if we want to make use of our intellect to steer the world into the desired sustainable future, we have to use our ability to make rational decisions, to re-evaluate our actions and to continually adapt our behaviour in order to not construct but contribute to the development of resilient sustainable systems.

Ecosystems have an astounding capacity to deal with disturbances, react to changes in the boundary conditions and reconfigure to return to viable functional states - and all this without any steering mind. Our intellect and our ability to project in the future allows us to rationally define our goal and the overall long-term direction we want to follow: a sustainable trajectory for our planet, so that it remains livable also for future generations. It doesn't need intellectual decisions for sustainable development in living systems - but adding our ability to impose top-down constraints in the form of laws and regulations on the socio-ecological system and to continually reevaluate goals and actions, adapt our behaviour and thereby shape the system bottom-up paints a picture of optimism and hope for the future of our planet.

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11.5. *Final remarks*

11.5 Final remarks

The aim of this thesis was to widen the window complexity science provides to look at the world in a non-constructivist fashion, appreciating both reductionism and emergence and ideally contributing to theory unification from the behaviour of a garden pond to the Amazon rainforest. Perfection, in the sense of Saint-Exupery as quoted at the beginning of this chapter, would have been contributed to, not if complexity theory would add *additional* explanations and hypotheses, but *reduce* the large amount of theories about the growth and development of ecosystems to core unifying principles, which are so simple, that there is no longer anything to take away.

Instead it has been shown, that species interactions are the guiding force behind ecosystem organisation, that coadaptation shapes functionality, stability and resilience and that ecosystem development is not either guided by fundamental laws *or* global optimisation criteria, but by both - individual fitness and the system's state determine ecosystem development in a dialogue of bottom-up and top-down control. Simple unifying theories which predict ecosystem development from an initial state and boundary conditions are hence impeded by complexity and emergence, if not intrinsically unachievable with the current mathematical framework. However at the same time, precisely this complexity is the unifying property of living systems across scale and location on our planet.

Ecology has a long way to go on the path towards perfection - but at the same time it is exactly the imperfection, the diversity and the impossibility to pigeon-hole life in labelled boxes, what makes the world to the fascinating and beautiful place it is.

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