

Summary

It is common knowledge that the millions of species that inhabit the Earth have adaptations that enable them to survive in different environments. Fish have gills which allow them to breathe under water, while the wings of birds allow them to fly. These adaptations are, as different as they may be, a different solution to the same problem: the problem of staying alive and reproduce in a world where species are under the constant pressure of natural selection. Perhaps less well known, but maybe not surprising when thought about carefully, is that the often complex networks of interactions between species, e.g. between plants and pollinators or between predators and prey, have certain non-random properties as well. These ‘network structural properties’, i.e. specific ways in which the interactions within networks are arranged most likely allow the often large numbers of species in ecosystems to coexist. Just like similar adaptations may be found in a wide variety of species, e.g. gills or gill-like organs in aquatic animals and wings on birds, insects, and bats, similar network structural properties may be found in a wide variety of ecosystems. Similarities that may occur simply because they are, like adaptations, a solution to the same problem: the problem of coexistence in systems where species heavily influence each other’s probability of survival.

While we are beginning to understand more about the structural properties of ecological networks, i.e. the networks of interactions between species, and how they might allow large numbers of species to coexist in complex ecosystems, the Earth and its ecosystems are changing at increasingly rapid rates due to human activities. In some cases, these changes are relatively simple in the sense that they affect a large group of species similarly, e.g. the effect of pesticides on a large group of insect pollinators, while in other cases these changes may be complex, e.g. the effects of climate change on the phenology and distribution of species which in turn leads to alterations in strengths of interspecific interactions in a way that is unique for each interaction. Ecosystems may respond in various ways to such changes (regardless of whether their effects are simple or complex). When conditions change gradually, the state of some ecosystems (e.g. the size of populations) may change likewise, in a smooth, gradual manner. Other systems may respond strongly to change within a narrow range of environmental conditions, but are relatively insensitive to change outside of this range. Particularly sudden shifts may occur when ecosystems have multiple alternative states. Such systems cannot change smoothly from

one state (e.g. large population sizes) to an alternative state (e.g. a state in which some or all species are extinct). Instead, a sudden shift or ‘critical transition’ occurs when environmental conditions pass a critical point. To return back to the original state after such a transition, a return to conditions prior to the transition is often not sufficient; instead, a larger change in conditions is needed until another critical point is reached at which the system shifts back to the original state, a phenomenon called ‘hysteresis’.

While the outcome of critical transitions is relatively predictable when a few leading species or species groups determine the state of an ecosystem, this may not be the case when ecosystem dynamics are determined by many interacting species. The consequences of critical transitions in such complex ecosystems might be severe, for example, when leading to the extinction of a large number of species. Not all critical transitions, however, will have dramatic consequences. Complex ecosystems may potentially shift to many different, alternative states. Some of those may imply minor, harmless changes in the state of a system, or invoke positive change, whereas others may have catastrophic consequences. The amount and type of change needed to cause a transition and a system’s future state after an impending critical transition depends in complex and often unknown ways on how ecosystems are organized, i.e. on the feedback mechanisms within it, and thus on the structure of ecological networks and/or how this structure might be changed by changing environmental conditions. Assessing or mitigating the risks associated with critical transitions in complex ecosystems thus requires a fundamental insight in the interrelationships between the structural properties of ecological networks, the dynamics of ecosystems, and the way in which these properties and dynamics might be affected by changing environmental conditions.

Despite a longstanding interest in ecological networks and more recent advances in detecting commonalities in the structure of ecological networks (**Chapter 1**), the common ground between studying the structure of ecological networks and the potential causes and consequences of critical transitions in complex ecosystems remains largely unexplored. One of the causes of this lack of exploration is, most likely, that stability is a multi-faceted concept that may be defined in various ways, e.g. the robustness of ecological networks to the random removal of species, a system’s temporal stability and/or speed of recovery from disturbances, and the amount of change in abundances or environmental conditions needed to cause a critical transition (**Chapter 1**). Most studies on the structure and stability of ecological networks have focused on stability concepts that are unrelated with critical transitions, while studies of critical transitions have often focused on the dynamics of individual populations rather than on the complex networks of interactions between species that maintain them.

In this thesis, we merge network theory with theory on critical transitions and show that an important trade-off between different aspects of stability may occur in pollinator communities (**Chapter 2**). The networks formed by the interactions between mutualistically

interacting plant and pollinator species are known to be highly nested, i.e. specialists tend to interact with a subset of the species interacting with the more generalist species. Earlier work has shown that such a structure may promote indirect facilitation, i.e. species indirectly support each other through interactions with other species, and the stable co-existence of species. We suggest, perhaps unsurprisingly, that such indirect facilitation also makes pollinator communities more resilient to changes in environmental conditions, e.g. an increase in the use of pesticides. This increase in resilience may, however, come at a cost; when pollinators continue to facilitate each other under increasingly harsh conditions they may eventually collapse simultaneously, because they depend on each other for survival. Recovery from such a simultaneous collapse may require a relatively large improvement of conditions. Findings that may have large implications for our view on the sustainability of pollinator communities and the services they provide in a time when pollinator populations are rapidly declining.

The most commonly studied cause of critical transitions in ecology is a positive, reinforcing feedback that amplifies change when changing conditions or abundances pass a critical value. In the aforementioned pollinator communities, for example, a decline in pollinator abundances may negatively affect plants, which in turn is bad for pollinators and leads to a further decline in pollinator abundances. Studies on the structure and stability of complex ecological networks, on the other hand, often put (implicitly) more emphasis on delayed negative feedbacks, i.e. negative feedbacks with a time lag, usually occurring as the result of an uneven number of negative interactions in feedback loops of two or more species, as a potential cause of instability. Food-web theory and observations in real ecosystems, for example, suggest that destabilizing oscillatory dynamics caused by strong predator-prey interactions are damped by many weak interactions. Transitions towards such dynamics, and more complex, chaotic dynamics, may occur when delayed negative feedbacks gain in strength relative to more immediate negative feedbacks (**Chapter 3**). Inspired by previous work on critical transitions and the structural stability of dynamical systems, we describe a variety of transitions, associated with different types of boundaries in parameter space, that may occur when such stabilizing, damping patterns are undermined. Inspired by previous work on critical transitions and the structural stability of dynamical systems, we describe a variety of transitions, associated with different types of boundaries in parameter space, that may occur when such stabilizing, damping patterns are undermined and explore how structural network patterns, i.e. species number, connectance, and variability in interaction strength, might influence the occurrence of such transitions. To illustrate that abrupt transitions towards alternative stable states, oscillatory or other more complex dynamics may occur even under basic dynamical assumptions, we assume that the functional response of predators, i.e. the relation between a predator's intake rate and prey availability, is linear. Future work may build on this study to include also more complex, non-linear functional responses.

The dynamics of ecosystems are determined by the interplay between many stabilizing

and destabilizing feedbacks and one may assume therefore that it will hardly be possible to detect a change in a system's proximity to a critical point. Earlier work has, however, shown that an increasingly slow recovery from small disturbances may be indicative of a loss of resilience prior to critical transitions. Various indicators of this phenomenon known as 'critical slowing down' may therefore serve to detect an increase in the likelihood of critical transitions. Predicting what comes after a critical transition is, however, terra incognita altogether. In **Chapter 4** we take a first step into this unexplored territory and show that the relative simplicity of the dynamics of mutualistic communities may allow us to look beyond impending critical transitions and foresee a community's future state. To make such predictions, we take advantage of the increasingly slow recovery from perturbations prior to critical transitions. Such disturbances have a size (i.e. the total amount of change) and a direction (i.e. the relative amount of change in each species) in the phase space of complex systems. The more similar a disturbance's direction to the direction in which increasingly small perturbations may cause critical transitions, the stronger the effect of critical slowing down. Provided that there are no oscillating, chaotic or other complex dynamics, a system's future state will most likely lie in the same approximate direction. This 'direction of critical slowing down' may thus provide us with an indicator of a system's future state, and may help us assess whether impending critical transitions may have large, systemic consequences. As an indicator of the direction of critical slowing down we propose to use the direction in which the distribution of fluctuating species abundances becomes increasingly asymmetrical, but other methods to determine this direction may be possible as well.

The major, unanswered questions in ecology are often separated in two main classes: the fundamental ones, aiming to understand the basic processes shaping and occurring in ecosystems, and the applied ones, e.g. aiming to identify or reduce the risks associated with changing environmental conditions (**Chapter 5**). In a time when ecosystems are confronted with rapid environmental change, it is, however, becoming increasingly clear that predicting the consequences of changing environmental conditions requires a fundamental understanding of the processes occurring in ecosystems. In particular, because such changes are likely to bring ecosystems outside of the range in conditions for which data are available. Questions on the stability of ecosystems in the context of such changes are thus both applied and fundamental because their answers require the development of novel theories and hypothesis. In this thesis, I hope to have provided novel ideas and insights that might help to address the question of whether changing environmental conditions are likely to lead to large-scale systemic regime shifts in complex ecosystems. An emerging property of complex ecosystems that may be referred to as 'systemic risk'.