

Application to the "Prix de thèse des Systèmes Complexes 2019"

Réseaux d'interactions écologiques, stabilité et résilience des écosystèmes

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One of the central goal of ecological science is to identify how ecosystems will respond to global changes. However, this task is made difficult by the complexity of ecosystems, as their elements do not live in a vacuum but are bound by many interactions (e.g. between species, or between species and abiotic factors – soil quality, nutrients, etc.). These interactions constitute complex networks, whose structure determines how the ecosystem will respond to environmental changes. This response can be smooth and gradual, but may sometimes also be rapid, with unexpected large changes once a threshold in stress has been passed. For example, in some arid systems, cases of rapid desertification have been observed following a small increase in grazing pressure. These sudden transitions arise because of strong, facilitative interactions between plants. Fortunately, not all ecosystems exhibit such large shift following environmental changes, and it has been shown that other structural patterns in interaction networks can have a stabilizing effect on a given ecosystem.

To anticipate how ecosystems will respond to global changes, it is thus essential to study the structure of interaction networks, understand how it changes in space and time and how it affects the dynamics of ecological systems.

The first part of my thesis focuses on the consequences of a specific pattern being present in species interaction networks: positive feedbacks. Positive feedbacks occur when a species affects its own dynamics because of interactions with the other elements of a system – for example, when a plant improves local soil conditions, thus favoring locally its own recruitment. A high number of theoretical and empirical work suggests that feedback loops underpin large and sometimes irreversible transitions in ecosystems (sometimes named *critical transitions*, or *phase transitions*). This first part draws from theoretical expectations about critical transitions to identify where and when feedback loop may produce large shifts in ecosystems.

A transition in a system often implies the presence of two or more discrete alternative states, between which the ecosystem can switch. As a result, the observation of different, well-defined discrete states in the observations of such a system is expected around the environmental conditions where the transition occurs. This first chapter applies this principle of detection to plant communities of subalpine meadows occurring in two iconic Californian national parks, Yosemite and Sequoia N.P. I show that discrete states are present in the multivariate species composition of wet and dry zones of these meadows. Local detailed environmental covariates (e.g. soil surface composition, etc.) suggest that these states could be linked to plant-soil positive feedbacks, and thus be related to the presence of critical transitions.

Many studies have shown that strong positive feedbacks between sessile species can produce the emergence of specific spatial patterns at the landscape scale, which characteristics change with environmental stressors. Metrics characterizing this spatial structure could thus constitute indicators of proximity of a critical transition. In practice, this approach has produced many indicators of transitions (named *early-warning signals*), which are simple metrics capturing some aspects of the landscape spatial structure (e.g. lag-1 autocorrelation). Despite the abundance of data on which these indicators could be used – mainly due to the increase in availability of remote-sensing imagery – these indicators have yet to be widely tested on empirical systems. To facilitate this work, I present as the second chapter of my thesis a synthesis of these indicators, along with guidance on how they can be used on empirical data.

Critical transitions are a very specific type of response to perturbations. It is probable that many other ecosystems exhibit more gradual changes because of different interaction patterns between their parts. To understand how a given ecosystem may change, it is thus fundamental to map interaction networks between species and their environment, and understand how these networks vary in space and time. These are the objectives of chapters 3 and 4, which use plant communities as model systems.

Studies have shown that grazing is one of the main drivers of the relative frequency of positive interactions between plants (e.g. facilitation) over negative interactions (e.g. competi-

tion for resources). However, this has only been shown in simple experimental systems with few species, which may not represent well the complexity of empirical communities. To test the effect of grazing on interactions in complex plant communities, we used in Chapter 3 a novel approach based on association networks. These networks represent spatial associations between species by a positive link when two species tend to aggregate in space, and by a negative link when they segregate in space. The relative importance of these two types of links within an association network have been suggested as a good indicator of the balance between competition and facilitation in a plant community. We analyzed changes in this balance along grazing gradients in the Crau natural reserve (Bouches-du-Rhône), leveraging existing gradients around five large size sheep-folds (more than 1,500 sheep). Our results show that grazing has a major influence on interactions in plant communities, by making them switch from being dominated by competition towards a state where interactions are weak and random.

The last chapter of this thesis focuses on the dynamics of plant-plant interaction networks after perturbation. An ecological community is classically defined by the abundances of a set of species in a given place. However, two communities may have the same species but differ in the way these interact, calling for a more general definition of what constitutes an ecological community. In particular, the temporal dynamics of interactions may be uncoupled from that of species composition. In this chapter, we put to the test this 'uncoupling hypothesis' by comparing the regeneration after perturbation of species composition to that of plant-plant association networks.

We leveraged a 'natural experiment' in the Crau plain in which we compared plant communities from sites that have been perturbed by grazing at known dates – ranging from 5 years ago to 1,800 years ago (roman sites). This allowed us to document the recovery of plant communities through time after perturbation. Results show that the impact of perturbations on species composition becomes attenuated through time, becoming nearly undetectable 1,800 years after the perturbation. However, the effect of the same perturbation is still large in plant-plant association networks. Anthropogenic perturbations thus affect more durably the way plant species interact within a community, rather than the identity of the species that are present in this community. This challenges the simplistic definition of an 'interaction-less' community, and calls for a more integrative definition that acknowledges the complex interactions between species.

In summary, I used principles and tools developed for complex systems to help us reveal and anticipate the effects of global changes on ecosystems, with a focus on protected areas. My work shows that this requires not only new approaches to analyzing empirical data, but also changing the way we describe ecological systems.