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Ecological interaction networks, stability and resilience of ecosystems

Alexandre Génin

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Biologie des populations et écologie

École doctorale GAIA

Unité de recherche ISEM

RÉSEAUX D'INTERACTIONS ÉCOLOGIQUES, STABILITÉ ET RÉSILIENCE DES ÉCOSYSTÈMES

Présentée par Alexandre Génin

Le 13 novembre 2018

Sous la direction de Sonia Kéfi

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UNIVERSITÉ
DE MONTPELLIER

RÉSEAUX D'INTERACTIONS, RÉSILIENCE ET STABILITÉ DES
ÉCOSYSTÈMES

ALEXANDRE GÉNIN

Alexandre Génin: *Réseaux d'interactions, résilience et stabilité des écosystèmes*, November 2018

*Nous, de l'ancienne équipe, nous avons fait de notre chair
une sorte de métal extraordinaire,
à l'épreuve de l'ordure,
mais perméable à l'étoile.*

Jean Giono, bivouaquant avec SAMIVEL (Samivel, 1944)

REMERCIEMENTS

M'accepteriez-vous comme stagiaire pendant cette période ?

Il y a sept ans (!), je contactais Sonia et Vincent pour faire mon stage de Licence, avec la ferme idée d'essayer l'écologie, dont mon expérience à l'époque se limitait à quelques heures de cours se comptant sur les doigts des deux mains. Loin de moi l'idée que cette expérience allait être le démarrage d'une montagne russe pleine d'émerveillements, m'emmenant dans des contrées chaudes ou froides, me faisant travailler sur des bestioles allant de 5 grammes à deux tonnes, ou encore utiliser des outils aussi simples qu'un papier et un crayon, ou aussi complexes qu'un supercalculateur. Pour avoir su susciter l'étincelle initiale, me communiquer leur enthousiasme et m'avoir fait démarrer dans l'écologie scientifique, je leur suis infiniment reconnaissant.

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Eric Imbert et Vincent Devictor. J'ai eu un grand plaisir à discuter de mes travaux avec les membres de l'équipe Eco et Sols (INRA Montpellier), notamment Tanguy Daufresne, Simon Boudsocq et Mickael Hedde, mais aussi Vincent Miele et Stéphane Dray du LBBE (Lyon) ainsi que l'équipe du cluster MBB ici à Montpellier. Un grand merci également à tous mes collègues américains, à commencer par Steven Lee et Eric Berlow qui m'accompagnent déjà depuis quelques années dans ce projet de thèse. Ce fut un grand plaisir également de collaborer avec Sabiha Majumder, Sumithra Sankaran et Vishweshia Guttal, tant en France qu'en Inde.

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SUMMARY OF THE WORK

This thesis is the result of modelling, field work, data analyses and writing carried out between September 2015 and August 2018.

RESEARCH OUTCOMES

5 Part of the work presented in this thesis have appeared previously in the following first-author publications.

- Génin, A., Majumder, S., Sankaran, S., Danet, A., Guttal, V., Schneider, F. D. and Kéfi, S. (2018), Monitoring ecosystem degradation using spatial data and the R package ‘spatialwarnings’.
10 *Methods in Ecology and Evolution*.. This publication is included as Chapter 2 in this thesis.
- Génin, A., Majumder, S., Sankaran S., Schneider, F.D., Danet, A., Berdugo, M., Guttal, V. and Kéfi, S. (2018), Spatially heterogeneous stressors can alter the performance of indicators of regime shifts, *Ecological Indicators*. In press.
15

Part of the work presented in this thesis have also been communicated at the following international conferences: Ecosummit, Montpellier 2016 (Chapter 1) and Ecology Across Borders (British Ecological Society meeting) 2017 (Chapter 3).

20 TEACHING

During this period of time, it has been a pleasure to supervise two students who carried on to ecology graduate programs:

- Mylène Jury, undergraduate student who helped me carry out part of the 2016 field work season.
- 25 • Alice le Priol, Master’s student (two months), who assisted me during the 2017 field work season, and produced an analysis of the variations of plant functional-traits along grazing gradients.

My PhD experience have also been greatly enriched by two years of teaching, with topics spanning Integrative Biology (approx 130h), Statistics applied to Biology (approx 15h) and Functional ecology (15h).

5 DATA COLLECTION

I carried out the collection of a dataset documenting the turnover of vegetation communities around currently-used and abandoned sheepfolds in La Crau (Bouches-du-Rhone). This program totalled approximately 4-5 months of full-time field work, and was carried
10 out in collaboration with researchers at IUT d'Avignon and staff at the Réserve Naturelle des Coussouls de Crau.

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Part I

INTRODUCTION

O.1 PREAMBLE

Following global changes, species populations will disappear, grow or move in space. The species composition and the functioning of ecological communities will change. Anticipating these changes has thus naturally taken a central place in ecology (Mouquet *et al.*, 2015).

The task is daunting, however. While species abiotic requirements can be reasonably used to predict where and when a species can disappear (Devictor *et al.*, 2008), community scale keeps being the realm of contingency and sudden reorganizations (Lawton, 1999). Lakes can shift from clear to turbid as a nutrient threshold is crossed (Scheffer *et al.*, 2003). The introduction of a predator or an invasive species can suddenly dramatically reorganize a community (Ellis *et al.*, 2011; Estes *et al.*, 2011). Arid ecosystems can turn into deserts as grazing pressure crosses a threshold (Kéfi *et al.*, 2007). Fish stocks can suddenly plummet (Vasilakopoulos & Marshall, 2015). Plant-pollinator interactions can collapse following external disturbances (Lever *et al.*, 2014; Dakos & Bascompte, 2014).

These dramatic responses arise because ecological systems are not simple but complex, *i.e.* composed of many interacting elements. Species in a community do not live in a vacuum, but are bound together by interactions. Because many ecological communities are diverse, the web of interactions between species may be unfathomably intricate and difficult to analyze – echoing Darwin's vision of the ecological community as an "entangled bank". This is very real issue as, to date, the consequences of the loss or arrival of a species in a given community remain extremely hard to predict: many species introductions for pest control had and still have unpredicted negative consequences (Carvalho *et al.*, 2008).

Despite their complexity, ecological interactions can exhibit specific structural patterns, that determine the response of the whole community to disturbance. For example, ecological systems can exhibit positive feedback loops – in which a characteristic is amplified because it feeds back on what causes it (Wilson & Agnew, 1992). Where strong feedback loops are present, the effect of an external perturbation, even if small, can be amplified. For example, the positive interactions between plants in arid ecosystems are known to play a great role in their response to perturbations (Kéfi *et al.*, 2007). Plants facilitate each other by growing in tight clusters that raise the availability of water within them (Rietkerk *et al.*, 2004), up to a certain

point in stress. Past this point, facilitation cannot counterbalance stressors and an increase in stress, even small, can trigger an irreversible desertification process.

Not all ecological communities are wired in such a way as to show dramatic shifts. Other studies have also shown that ecological interactions can have specific structures that confer robustness to species extinctions (Lever *et al.*, 2014; Verdú & Valiente-Banuet, 2008; Memmott *et al.*, 2004) and allow them to persist in time despite external disturbance (Stouffer & Bascompte, 2011; Thebault & Fontaine, 2010).

Much research has naturally been devoted to identifying where on this spectrum a given ecological community falls i. e. identifying its potential response to perturbations, and measure its resilience – its capacity to recover after a perturbation.

A first approach has focused on the particular case of ecological systems exhibiting "threshold" responses, where a change in environmental conditions, even small, can produce a wide shift in one or more coarse characteristic of the ecological system (e. g. total biomass). These often arise when positive feedback loops are present in species interactions (Kéfi *et al.*, 2016). This body of research, to which this thesis contributes, has produced generic methods and indicators of degraded resilience for this specific case.

This approach is appealing by its simplicity, yet only applies to specific cases where a specific pattern in interactions is already known (feedback loops). For many communities, interactions between species are unknown and must be mapped. Since the early 2000's and the rise of network science (Barabási & Pósfai, 2016), many tools and frameworks have been created to do so and analyze ever-more complex interaction networks (Morales-Castilla *et al.*, 2015; van Borkulo *et al.*, 2015; Poisot *et al.*, 2012; Delmas *et al.*, 2017). Ecological interactions, in the context of a network, are represented as links between nodes (e.g. links representing trophic interactions between species or nodes in a food web). Identifying specific patterns in these networks that are known to affect the resilience of the community could be a way to anticipate the effect of disturbance on a given ecological community.

However, this view has been criticized (de Ruiter, 2005) as too simplistic, as the link between disturbance and interactions is, in fact, a two-way street: ecological interactions may affect the response of a given community to perturbations, but interactions themselves change with perturbations (Figure 0.1). Indeed, many striking reorganizations of ecological communities entail a rewiring of ecological

interactions on top of a change in species abundances. For example, work on plant-pollinator interactions have shown that not only they can determine the community response to disturbance (Memmott *et al.*, 2004) but also be affected by disturbance themselves (Memmott *et al.*, 2007b). In plant ecology, decades of work have shown the change of interaction strengths between plants along environmental gradients (Callaway, 2007). Describing the response of communities to disturbance thus requires monitoring species abundances as well as interactions between species (Gray *et al.*, 2014).

A tight, and two-way relationship thus exists between the structure of ecological interactions, and the resilience and response to perturbations of the community (Figure 0.1). The way these are studied is quickly changing as new methods and increasingly-detailed datasets become available to ecologists. This thesis aims at contributing to the quickly-changing approaches to these topics.

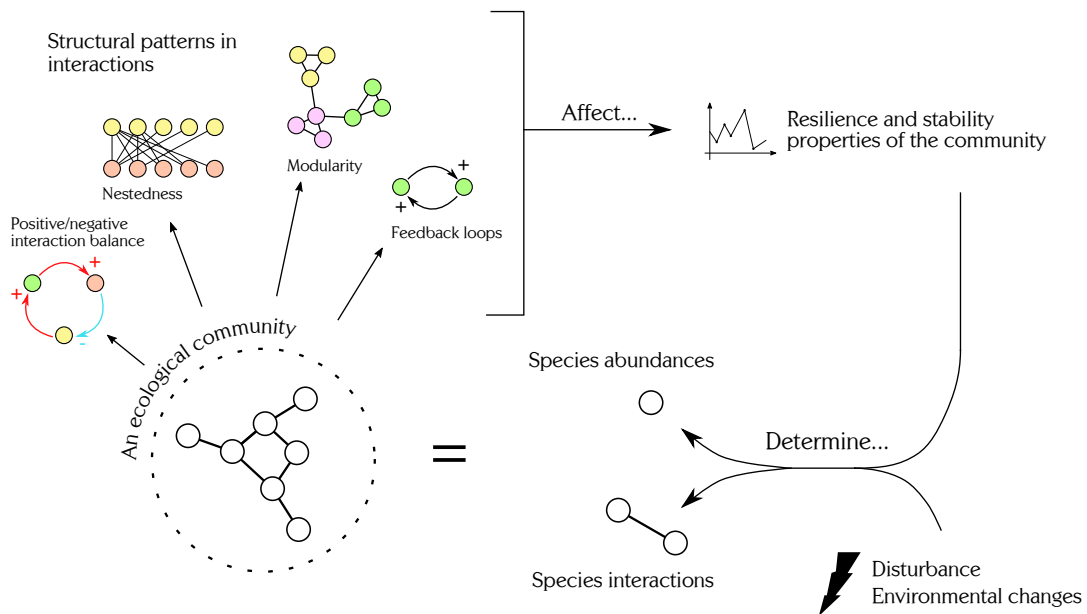


Figure 0.1: An ecological community is defined by a set of species and their interactions. These interactions can show structural patterns that determine the resilience and stability properties. The latter, combined with the characteristics of disturbance events, affect back the species abundances and interactions, effectively changing the original ecological community.

0.2 CONCEPTUAL CONTEXT AND STATE OF THE ART

0.2.1 Describing and measuring the response of communities to disturbance

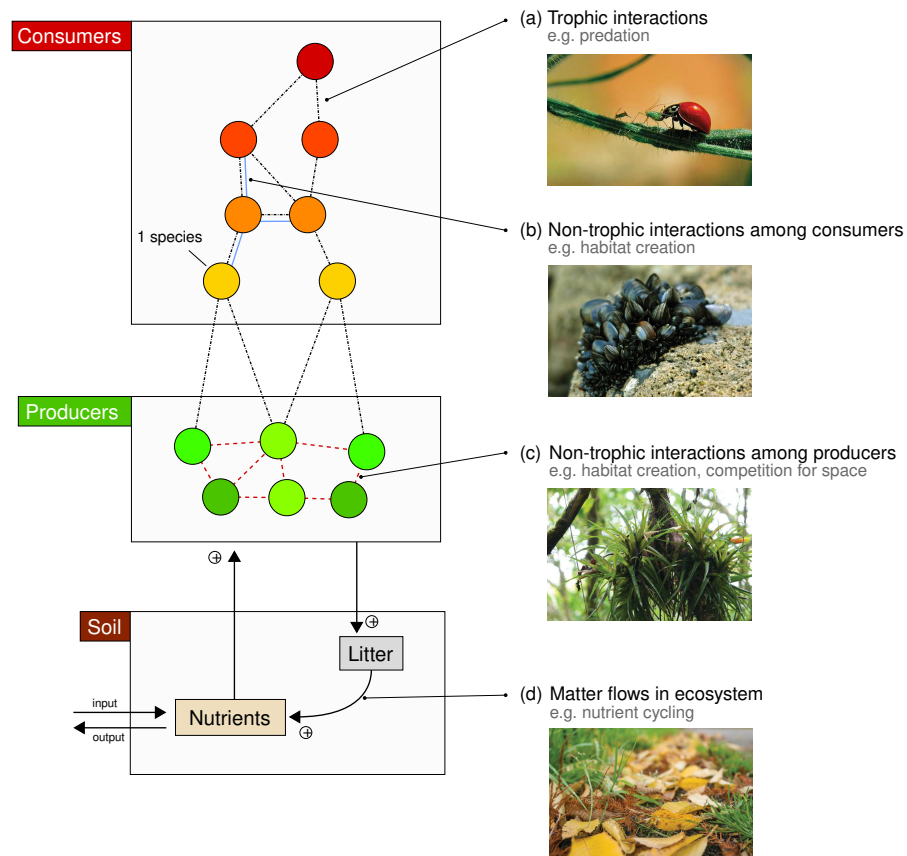


Figure 0.2: Interactions in ecological systems are present at several levels and between elements of different nature. The classic notion of interaction in a given ecological community involves two species, and can be trophic (a) or non-trophic (b,c). However, interactions can also occur between species and their environment (d) as species often modify local abiotic conditions. For example, in the diagram, a positive feedback loop is present between producers and soil quality (litter, nutrients). Taken altogether, these interactions form interaction networks, where nodes are species.

Ecological interactions between species, or between species and their abiotic environment (Figure 0.2), can determine the response of a given ecological community to disturbance. To describe correctly this response, it is required to introduce a set of useful concepts such as stability and resilience.

0.2.1.1 *Stability and resilience in ecological systems*

The concept of stability is notorious for having multiple definitions in ecology, which impedes comparison between studies (Table 0.1). For example, a survey of the literature by Donohue *et al.* (2016) revealed that in model systems, stability is most often considered to be *asymptotic stability*, i.e. the rate of return to equilibrium of a system subjected to an infinitesimal perturbation of its state. This definition of stability is purely deterministic and does not involve any notion of temporal variability, which is what is most often considered as stability in empirical studies (Donohue *et al.*, 2016). However, two ecological systems could have the same asymptotic stability, but different temporal variabilities, for example because they are subject to different perturbation regimes.

This discrepancy in the use of the stability concept is one example among many, as pointed out by the multiple reviews about its use of in ecology (Pimm, 1984; Ives & Carpenter, 2007; Borrelli *et al.*, 2015; Donohue *et al.*, 2016; Grimm & Wissel, 1997). To help reduce misunderstandings across studies, authors have suggested making more precise stability statement (e.g. Grimm & Wissel, 1997), or including multiple aspects of stability at the same time in a given study (Donohue *et al.*, 2013).

Because it is related enough to sometimes be considered a component of stability (Donohue *et al.*, 2016), the concept of resilience – put simply, the capacity of a given system to recover after a perturbation – has followed a similar path. Authors such as Holling (1996) have pointed out the dual definition of resilience in the literature, separating out *engineering resilience* – how *fast* an ecosystem recovers after a perturbation – from *ecological resilience* – the maximum amplitude of disturbance that a system can absorb while maintaining its structure. More recently, authors have also sought to clarify further the concept of resilience (Hodgson *et al.*, 2015), and in particular define a standardized way to measure it on data (Ingrisch & Bahn, 2018).

Despite this diversity of definitions, stability and resilience have proven to be useful concepts to describe and understand the response of ecological systems to perturbations. In particular, *stability landscapes* (or *resilience landscapes*, Hodgson *et al.*, 2015) underpin much work aiming at measuring resilience in empirical systems, and describing their response to perturbations.

Stability measure	Aspect quantified	Domain of most frequent application	Note
Constancy (inverse of Variability)	Magnitude of variation over time/space	Empirical work	
Persistence, Robustness	Appearance/extinction of species over time.	Variable	Robustness often quantifies the number of extinctions after a species is removed from a system, i. e. the number of secondary extinctions
Resistance	Capacity to remain unchanged under disturbance	Empirical work	
Asymptotic stability	Rate of return to equilibrium after infinitesimal perturbation	Theoretical work	
Engineering Resilience	Speed of return to equilibrium after a realized perturbation	Variable	This metric itself can be measured in different ways on empirical data, Ingrisich & Bahn (2018)
Ecological Resilience	Maximum perturbation before a system exhibits qualitatively different functioning	Variable	

Table 0.1: Diversity in the measures of stability and resilience: a non-exhaustive list of stability metrics, with their usual domain of application in ecological work (data from Donohue *et al.*, 2013).

0.2.1.2 *Measuring resilience*

ECOLOGICAL SYSTEMS AS STOCHASTIC DYNAMICAL SYSTEMS

Approaches from dynamical systems theory have heavily influenced the theoretical developments around the notion of stability. In this framework, a system's state is described by a set of *state variables*. For an ecological system comprising a set of different species, the natural state variables could be the set of abundances of every species. The value of these variables is subject to changes because of internal properties of the ecological system – e.g. population growth – but also because of external factors – e.g. environmental conditions.

Put more formally, in this framework, an ecological system is often modelled mathematically by a differential equation of this form:

$$\frac{d\mathbf{X}}{dt} = f_{\theta}(\mathbf{X}) \quad (0.1)$$

where, \mathbf{X} is the set of state variables defining the state of a system. The function f_{θ} , which often depends on a set of parameters θ , defines the intrinsic properties of the system. For example, the following seminal overgrazing model (May, 1977; Noy-Meir, 1975) describes vegetation growing under grazing pressure:

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - c\frac{V^2}{V^2 - V_0^2} \quad (0.2)$$

The vegetation biomass V (a state variable) here defines the state of the system, while r (reproductive rate), K (carrying capacity), V_0 (half saturation of grazing rate) and c (grazing rate) are parameters.

In this framework, ecological systems can display stable states, which are specific values \mathbf{X}^* of the state variables at which the state of the system does not change over time (in the absence of noise). These stable states depend on the values of the parameters θ used in the function f_{θ} , and for a given set of parameters, multiple stable states can exist. The above overgrazing model displays such multiplicity of stable states along a gradient of changing values of c (Figure 0.3).

This modelled view of an ecological system is purely deterministic and does not include stochasticity, i.e. chance events or fluctuations that can happen in a given system. In practice, ecological systems are never purely deterministic and stochasticity always contributes to

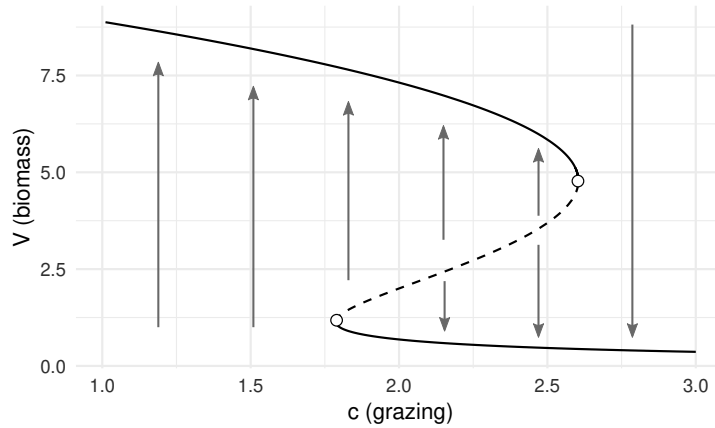


Figure 0.3: Bifurcation diagram of the overgrazing model (with $r=1$, $K=10$, $V_0=1$), along a gradient of c values. Continuous lines indicate stable states, and the dashed line indicates the limit of the two basin of attractions where multiple stable states are present for the same grazing values. This line delineates two basins of attraction, which are the set of values from which a system will converge to a particular stable state (grey arrows). White dots indicate *critical points*, at which one of the multiple stable states becomes unstable.

the observed state of a system at a given point in time, hence to its apparent stability.

In a model system with a deterministic response f_θ , the parameters θ and the form of the function f define how a system will change given in current state. Assuming a simple model where the state is defined by a univariate continuous value X , the response of the system can be visualized by defining a potential U :

$$\frac{dU}{dX}(\theta) = -\frac{dX}{dt} \quad (0.3)$$

Tracing the values of U for different values of X yields a "stability landscape", where stable states are represented by the bottom of valleys which are basins of attraction. Intuitively, the temporal evolution of the system can be described by a ball rolling down this landscape, i. e. towards stable states. For a given value of the system parameters (e. g., grazing rate c in Figure 0.4), a system can have multiple states, as manifested by several valleys in its stability landscape.

Using this landscape analogy, the engineering resilience (i. e. the time of return to equilibrium) is captured by the slope of the potential. The ecological resilience can be interpreted as the height of the basins of attractions, i. e. how much the system needs to be perturbed to switch to a different state. The shape of this landscape, and how it

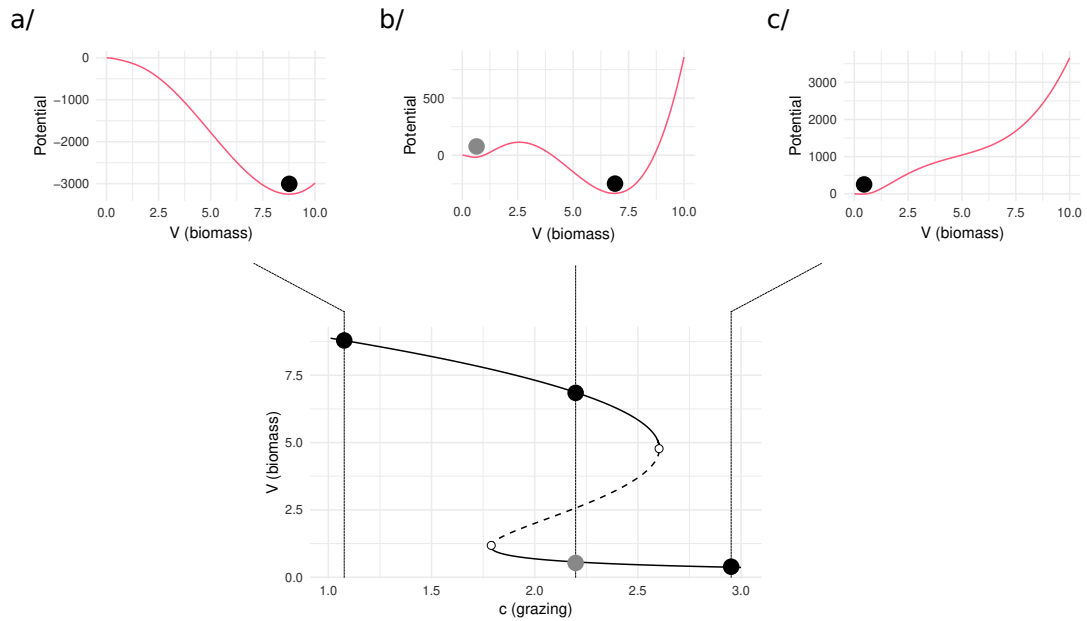


Figure 0.4: Potential curves of the overgrazing model (red curves). Stable states in the bifurcation diagram correspond to the bottom of valleys in the potential curves (black and grey dots). As the environmental conditions change (here, the grazing c), the shape of the curves change and the position and number of stable states change.

varies as environmental conditions (parameters) change defines the resilience of the system.

In particular, one central challenge in resilience ecology has been to identify where and when multiple stable states (i. e. multiple valleys
 5 in the potential) are present in empirical ecosystems. When they are, irreversible shifts can occur as one of the stable states is lost (Figure 0.4), and stochastic perturbations can have long-term consequences by making a system shift from one state to another. For this reason, much research has sought to find methods that link the character-
 10 istics of the stability landscape with empirical patterns (Scheffer & Carpenter, 2003).

POTENTIAL ANALYSIS

Following the potential analogy, the state of a system will always tend towards stable states (the ball rolls down into the valleys of the stability landscape). As a result, it is more likely to be observed close
 15 to its stable states than away from them. This intuition has been formalized for a system defined by a single state variable by Livina *et al.* (2010).

Considering a simple system defined by a single state variable X , repeated observations of the same system will yield a set of values whose empirical density P_x can be computed (e.g. through kernel density estimation). If the temporal response dX/dt of a system is
 5 subject to white noise of amplitude σ , then the potential U has a one-to-one relationship with the above empirical density through:

$$U(x) = -\frac{\sigma^2}{2} \log P_x \quad (0.4)$$

This relationship implies that the stable states of a given system, i.e. the bottom of valleys in the potential U , should correspond to modes in the empirical distribution of observed states. In particular, if
 10 a system has two well-separated stable states, then two modes should be observed in the empirical distribution of states (Livina *et al.*, 2010).

This formal link between observed state and potential has had great success in ecology and many studies have used it to interpret multimodality as potential alternative stable states in ecological systems.
 15 For example, Hirota *et al.* (2011) identified tropical forest and savanna as alternative stable states that can coexist under similar levels of rainfall, based on the presence of multimodality in the distribution of tree cover. Similar studies have been carried out for a variety of ecological systems such as boreal biomes (Scheffer *et al.*, 2012b), fish
 20 stocks (Vasilakopoulos & Marshall, 2015), arid systems (Berdugo *et al.*, 2017) or small rock pools (Buschke *et al.*, 2013).

Yet the observation of multimodality in empirical systems only weakly supports the presence of alternative stable states. The presence of the latter entails the presence of bimodality in data, but the
 25 reverse is not necessarily true. Bimodality in data could be underpinned by the presence or absence of an unmeasured factor that has not been taken into account. The presence of multi-modality, however, remains useful as exploratory analysis to identify where potential alternative stable states – i.e. non-linear responses to perturbations –
 30 are present. We use this approach in Chapter 1 to identify potentially fragile plant vegetation communities in the subalpine meadows of Sierra Nevada (California, USA).

CRITICAL-SLOWING DOWN AND INDICATORS As a system gets closer to a critical point, the potential landscape flattens. This is particularly
 35 apparent in the fold bifurcation (Figure 0.4). In this case, at the critical point, one stable equilibrium disappears and the system

may shift to a potentially very different state (i. e. a valley in the potential "fills up" and disappears). In practice, this translates into a phenomenon called *critical slowing-down*.

As a system slows down, specific aspects of the system are expected to arise in its temporal and spatial properties (Scheffer *et al.*, 2001). Namely, an increase in auto-correlation is expected to occur, because its state at a given time (or position) will tend to be more similar to its state in the previous state (or nearby position). Small perturbations will also have a larger effect as the system takes more time to return to its equilibrium (decreased *engineering* resilience), producing an increase in temporal and spatial variance. These two metrics were the first suggested in the literature, but others have then been developed since (e. g. skewness (Guttal & Jayaprakash, 2008), information-based metrics Dakos & Soler-Toscano (2017), etc.).

Measuring these indicators (or *early-warning signals*) of critical slowing-down on empirical data could in principle inform on when and where a given ecosystem has a decreased resilience, in particular when it happens because of an upcoming shift to another stable state. For this reason, a large body of literature investigates empirical data for such changes in critical slowing down. While they have been observed with reasonable certainty in experiments (Veraart *et al.*, 2011; Drake & Griffen, 2010; Clements & Ozgul, 2016), their relevance for empirical data remains controversial. Studies have found empirical evidence showing an increase in these metrics before observed shifts in temporal data (Dakos *et al.*, 2008) and spatial data (e. g. Eby *et al.*, 2017). Yet many of these cases identify shifts after the fact, which questions whether indicators based on them can serve as accurate forecasting tools (Boettiger & Hastings, 2013). Progress on these issues could come from assessing the predictive capacity of these indicators on more empirical datasets. Chapter 2 contributes to these questions by implementing the computation of spatial indicators in common statistical software (R). A more extensive review and summary of indicators is also available there.

Because they are only based on the generic properties of critical-slowness, the above indicators can potentially apply to a large variety of ecological systems. For this reason, they have received much exposure in the ecological literature. However, other indicators of resilience are based on spatial patterns that arise in specific systems, where interactions between species in a given ecosystem have a specific effect on spatial structure.

SPECIFIC INDICATORS One of the main sources of the presence of alternative stable states is the presence of positive feedbacks between elements of a given system. For example, in some arid systems, vegetation tends to favor the local recruitment of new individuals (see also Section 0.2.2.2). In other words, vegetation favors its own recruitment, hence the positive feedback. This has been suggested as a major mechanisms underlying the dynamics of arid systems (Kéfi *et al.*, 2007), which are thought to show irreversible transitions associated with the presence of alternative stable states. Because this positive feedback between plant individuals at local scale has a spatial component, it produces a spatial distribution of vegetation with specific characteristics. Some of these characteristics have been shown to vary as stress increases and when an irreversible transition is approaching. For example, the shape of the distribution of vegetation patch sizes has been suggested as a possible indicator of upcoming irreversible transition, hence decreased resilience (see Chapter 2 and Kéfi *et al.*, 2007, 2012). Others have also suggested to use the shape of vegetation patches as possible indicators of degradation (Rietkerk *et al.*, 2004).

These metrics and indicators try to detect upcoming shifts in an ecological system, for the cases where a particular pattern is present in interactions: a feedback loop. This is an example of a structural pattern in an ecological network that determines how the community will respond to perturbations. However, for most ecosystems, the interactions themselves – between species, or between species and their local environment – are not known. It is thus often necessary to map them in empirical systems.

0.2.2 Mapping interactions in ecological systems

0.2.2.1 Inferring interactions in ecological communities

The study of interactions between organisms has always been at the core of ecology, but it is only in the past several decades that research
 5 has sought to map them systematically in empirical communities – i. e. drawing a list of all pairwise interactions between species in a given community. An advantage of doing so is that these interactions can be viewed as elements of an *interaction network*, where nodes represent species and links interactions. By viewing them as networks, a
 10 great number of visualisation and statistical tools become available.

Trophic interactions have been the first to be mapped as part of a network (Proulx *et al.*, 2005). This has changed in the past couple of decades as ecologists have also focused on other types of interactions such as interactions between plants and pollinators or between hosts
 15 and parasites (Ings *et al.*, 2009). Recent studies have also used networks including several types of interactions (Kéfi *et al.*, 2015; Poccock *et al.*, 2012).

Mapping interactions can be straightforward when direct observation is possible (although measuring an interaction strength is often
 20 more difficult). For example, plant-pollinator interactions can be mapped by direct observation of pollinators' visits to plants. When direct observation is impossible, using proxies is required to reveal where an interaction is present or not (Morales-Castilla *et al.*, 2015). Such a widely-used proxy is the spatial distribution of species. The
 25 intuitive idea is that two species that interact in a negative way (e. g. through competition or by producing hybrids with reduced fitness) should be segregated in space. Conversely, two species that interact positively should often co-occur in the same site.

This approach stems from investigations of the effect of competition on the biogeographical distribution of species. Cody and Diamond's
 30 work in 1975 (Cody & Diamond, 1975) was not the first to apply co-occurrence analyses ¹, but marked the beginning of a heated debate on their computation and interpretation in empirical data (Sanderson & Pimm, 2015). The authors interpreted "checker-
 35 board distributions", where two species rarely ever co-occur on a set of islands, as evidence for competition. This interpretation was disputed by Connor & Simberloff (1979) on statistical grounds, and

¹ Notable previous works include Pielou & Pielou (1968) (association of insects) or Cole (1949) (methodological aspects of measuring associations)

later rejoined by Diamond (Diamond & Gilpin, 1982). This debate has spawned along the way a great body of research investigating the link between the geographical distribution of species and their interactions, much beyond the original, species-on-islands problem.

5 In particular, Connor & Simberloff (1979) pioneered the use of null models. Null models are "pattern-generating models" (Gotelli & Graves, 1996), that serve as a reference to produce the patterns that would be expected given the absence of process of interest. For example, in the absence of any interspecific interactions, one could
10 consider that individuals of a pair of species would distribute at random in a set of sampled sites. To this day, null models are still widely used to infer potential interactions from the spatial distribution of species (Box 1).

Historical co-occurrence studies mostly focused on singling out
15 species from a regional pool that potentially competed with each other. For example, Cody & Diamond (1975) mostly focused on competition (among guilds of New Guinea pigeons). Recent co-occurrence approaches are based on the same principles, but differ in at least two key aspects. First, emphasis is put on positive interactions as
20 well as negative interactions. Second, recent studies do not focus on single interactions but rather view them as part of a network with a given structure. This structure can be analyzed and described, and ecologists have borrowed many tools from network science to do so (Delmas *et al.*, 2017). For example, both these aspects are present in
25 a recent co-occurrence framework suggested by Morueta-Holme *et al.* (2016).

These methods produce sets of positive and negative associations between species, i. e. association networks ² (Figure 0.5).

² sometimes also named more explicitly "spatial association networks", (e.g. Saiz *et al.*, 2017)

Box 1: An example null-model-based analysis of species co-occurrences

Classical co-occurrence analyses are done on occurrence (presence/absence) data, that is represented as a matrix of ones and zeros:

	sp. 1	sp. 2	sp. 3	sp. 4
site 1	0	0	1	1
site 2	1	1	0	1
site 3	0	1	0	1

First, a metric is used to describe how associated two species are. For example, such a metric can simply be the count of co-occurrences when sampling is discrete, a measure called the *natural metric* by Sanderson & Pimm (2015). Other metrics with slightly different properties are also used in the literature (e.g. the checkerboard score (Stone & Roberts, 1990), χ^2 -statistic (Soliveres & Maestre, 2014), (partial) correlation coefficient (Morueta-Holme *et al.*, 2016)). The metric can be most often computed pairwise between each species independently, yielding observed pairwise associations A_{ij} . Here, using the number of co-occurrences as our association metric, we get the following A_{ij} for the data above:

	sp. 1	sp. 2	sp. 3	sp. 4
sp. 1	.	1	1	1
sp. 2	1	.	0	2
sp. 3	0	0	.	1
sp. 4	1	2	1	.

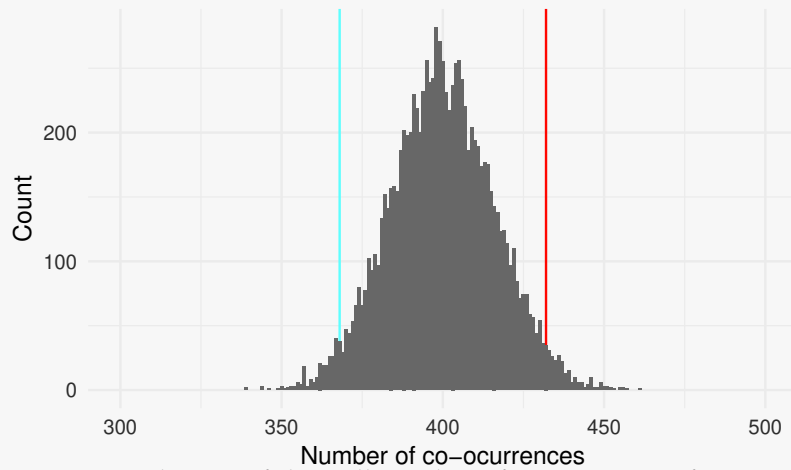
Note that for occurrence data, intra-specific co-occurrence cannot be computed, as this requires recording co-occurrence between individuals of the same species (see Chapter 3).

The observed pairwise co-occurrence metric is then compared to a null model. The goal of the null model is to produce a set of null site \times species matrices that correspond to the expected spatial distribution of species in the absence of interactions. To do so, many studies use constrained permutations of the original site \times species matrix to obtain expected null occurrences of species, but recent approaches also use independent data (e.g. from species distribution models, Morueta-Holme *et al.* (2016)).

Regardless of the chosen method, a set of N presence/absence matrices are obtained, from which a distribution of N pairwise association values $E_{ij,1} \dots E_{ij,N}$ can be computed.

Significant pairwise number of co-occurrences are then retained in the original association values A_{ij} , depending on whether they fall in one of the tails of the null distribution.

Box 1: An example null-model-based analysis of species co-occurrences (cont.)



Box 2: Distribution of the null number of co-occurrences for a pair of species. If the observed number of co-occurrences is above the 97.5% quantile of the null distribution of co-occurrences (red line), a positive association is retained. A similar test yields negative associations in the lower tail of the null distribution (blue line).

Because this method is akin to carrying out a test (with $\alpha=0.05$ in the above example) for each pair of species, correcting for multiple tests is often done using the e. g. Benjamini-Hochberg correction. A strength of association is sometimes also defined as the SES (Standardized Effect Size) of the observed value compared to the null distribution.

This process produces an association matrix which holds either significant association strengths (which can be positive or negative), or qualitative values representing a positive or a negative association between each pair of species (Figure 0.5).

Viewing interactions as part of a network has produced many new methods for the inference of interactions from spatial patterns. Many of them entail regressing a model of the whole interaction network instead of relying on separate pairwise analyses. For example, some statistical models aim at modelling the effect of the presence of a given species on the probability of presence of another, on top of possible environmental covariates (Pollock *et al.*, 2014; Ovaskainen *et al.*, 2010). This method leads to coefficients potentially reflecting directed species interactions (Figure 0.5). Other model-based methods include Markov networks (Harris, 2016; van Borkulo *et al.*, 2015) which produce undirected networks, or bayesian networks (Milns *et al.*, 2010; Delalandre & Montesinos-Navarro, 2018) which produces directed networks.

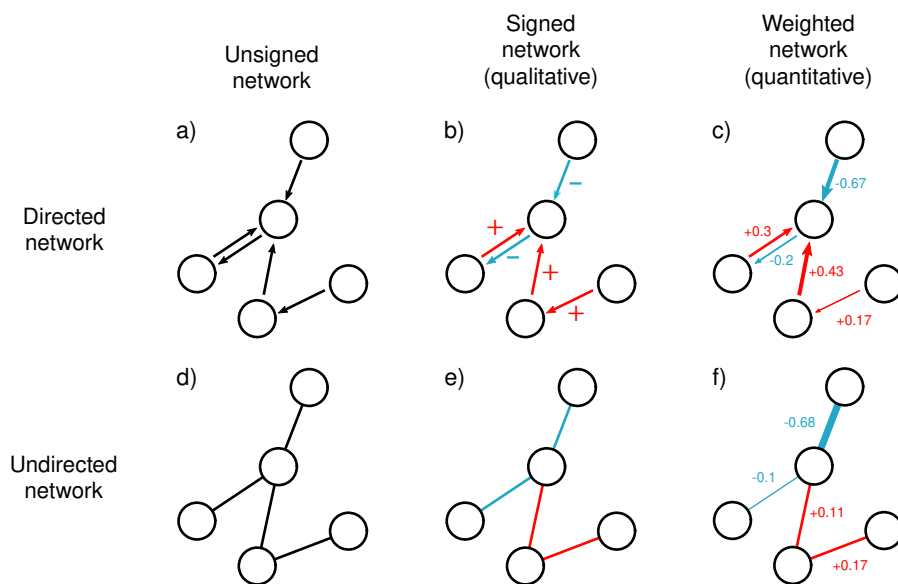


Figure 0.5: Types of networks found in co-occurrence analyses. Networks can represent directional interactions (a,b,c, e.g. food-webs), or undirectional interactions (d,e,f). The same classification applies to association networks derived from co-occurrence analyses, which represent associations as signed, qualitative directed or undirected links (b, e). Weighted networks can be also obtained, in which each association has a given strength (c,f). In most studies, the networks obtained through co-occurrence analyses are signed and undirected (i. e. of type e or f).

Despite ever-more refined methods, co-occurrence networks often fail to accurately reflect interaction networks (Barner *et al.*, 2018; Freilich *et al.*, 2018). This is due to a variety of possible reasons:

- The effect of interactions on co-occurrence patterns have been shown to vary with the scale of sampling (McNickle *et al.*, 2017;

Araujo & Rozenfeld, 2013). Different sampling schemes may thus yield different interaction strengths between species.

- Species often co-occur because they share a given habitat, resulting in positive associations that do not reflect interactions. When the habitat cannot be considered constant, typically when working at biogeographical scale, controlling for this effect may prove very difficult (Morueta-Holme *et al.*, 2016).
- Other assembly processes such as dispersal limitation may also blur the link between co-occurrence and interactions. Two species may for example never co-occur, simply as a result of their inability to colonize shared sites (Connor *et al.*, 2013).

Many of these general limits apply to analyses carried out at scales much above the size of the organisms. Working at local scales, where patterns are more strongly driven by biotic processes, and where habitat may be considered constant may yield co-occurrence networks that reflect better ecological interactions between species. This is the main reason why co-occurrence is often used as a proxy for interactions in plant communities.

0.2.2.2 *Plant-plant interaction networks and co-occurrence approaches*

Because plants are sessile organisms, the potential effect they have on other species and on their environment tends to be most intense around their canopy. As a result, interactions tend to produce a spatial pattern.

A typical example is the case of "nurse" plants in arid ecosystems. In these systems, nurse plants are often bushes, which facilitate the recruitment and/or the survival of other species by improving local conditions under their canopy. For example, this improvement can occur as a result of shading (which limits evapo-transpiration Valiente-Banuet & Ezcurra, 1991) or making water from deep soil layers available to plants with shallow roots (Horton & Hart, 1998). In this case, facilitation produces a pattern of spatial association between the nurse plant and their facilitated species (their *protégées*), because the latter have an increased performance and survival under the former's canopy. It seems thus natural to adopt the inverse perspective and use spatial associations between plants to infer facilitative interactions³.

³ It is noteworthy that not all facilitation is the result of such an asymmetric relationship between a nurse plant and facilitated species. For example, improvement in

The accuracy of such co-occurrence methods to infer interactions between species have been challenged in the general case (Barner *et al.*, 2018; Freilich *et al.*, 2018). Yet the sessile nature of plants, along with experimental evidence of correlation between co-occurrence and facilitation (Graff & Aguiar, 2011), suggests that they may be informative for the specific case of plant-plant interactions in the field.

Verdú & Valiente-Banuet (2008) stands out as a pioneering study in this domain, in which the authors focused on the spatial distributions of nurse plants in a Mexican desert. The authors actively surveyed relationships between nurse plants and protégées and retained an association between these two groups if one plant was found (at least once) under the canopy of another species. The structural properties of this bipartite, facilitation network were then analyzed and linked with resilience properties of the community.

Most studies building association networks are based on data documenting the presence or absence of a set of species at different sites (often different points along a transect). An observed metric of association is computed (e. g. C-score, López *et al.* (2013), χ^2 Soliveres *et al.* (2014), number of co-occurrence Saiz & Alados (2012)), then compared to random expectation to retain significant associations. This random expectation is derived from permutations of the original dataset (López *et al.*, 2013) or an analytical approximation (Saiz & Alados, 2012, 2011; Saiz *et al.*, 2017; Alados *et al.*, 2017).

This method yields a network with positive and negative links between species (nodes), which contrasts with Verdú & Valiente-Banuet (2008) where a bipartite network was used. The network structure can then be described, and its changes along space or in time analyzed.

pollination through a shared pollinator can result in facilitation and spatial association between two plants with similar life forms (Johnson *et al.*, 2003).

0.2.3 *Ecological networks and their response to disturbance*

0.2.3.1 *Structure of ecological networks and community stability*

Several levels of description can be considered to describe networks, either at the node level, at the whole-network level or an intermediate
5 scale.

We can first consider node-level – i. e., species-level – properties. Species may have different patterns of interactions within a network. Species can have variable degrees (numbers of links), and the strength of these links may vary from species to species in weighted networks.
10 In co-occurrence networks, the degree and strength of the interactions of a given species with others may characterize its role within a community. For example, a nurse species within a network would have many positive links – because it is spatially aggregated with many different species –, i. e. a high degree (high number of positive links).
15 A high degree here is correlated with a greater influence on the community dynamics. The role of species structuring communities has been explored using such network descriptors (e. g., *Stipa tenacissima* in arid systems, Saiz & Alados, 2011).

Intermediate-scale properties can also be considered in a network.
20 For example, small subgraphs, or *motifs*, describing interactions between triplets of species have been used to describe the local structure of interaction networks. The relative frequency of these different motifs have been shown to determine network-level properties of food-webs (Klaise & Johnson, 2017). In signed, undirected networks
25 such as association networks, a similar, triplet-based description has been used to compute the structural balance of association networks. Signed networks are expected to be balanced, i. e. have an excess of specific triplets, which has been supported by recent evidence in plant-plant association networks (Saiz *et al.*, 2018). Feedback loops are
30 also a type of intermediate pattern which may have a strong influence on the dynamics of the community.

Finally, many network-level characteristics have been shown to deviate from random expectation in empirical networks. In particular, many empirical interaction networks have characteristics that could
35 increase the robustness of the ecological community – i. e. its ability to maintain a high species diversity despite disturbance. In particular, mutualistic networks such as facilitation networks between plants exhibit a higher amount of nestedness (how much specialist species interact with a subset of those with whom generalist species interact),

which confers the whole community a higher robustness against random species extinctions (Verdú & Valiente-Banuet, 2008; Bascompte *et al.*, 2003). In food webs, modularity (how well a network can be separated in different groups) is thought to have a similar stabilizing effect (Thebault & Fontaine, 2010; Stouffer & Bascompte, 2011). High nestedness have been found in plant facilitation networks (Verdú & Valiente-Banuet, 2008), and it is thought to increase the robustness of the community, but (to our knowledge) no other study explicitly link network-level patterns in plant-plant interactions with the stability of the community.

It is noteworthy that new ways of analyzing and describing networks appear at a quick pace, as evidenced by the rapid increase in methodological papers on network analyses in the last decade (Pellissier *et al.*, 2017; Delmas *et al.*, 2017; Wells & O'Hara, 2013; Graham & Weinstein, 2018; Poisot *et al.*, 2012). New structural patterns that are relevant for ecology may thus be found in the future as methods progress.

Regardless of the scale they describe in a network, many of these metrics are related to the potential response to disturbance of ecological communities (Table 0.2). However, in most cases, the relationship between networks structural patterns and stability is only supported by theoretical studies (an exception is the study by Gilarranz *et al.* (2017), which shows experimentally the effect of modularity on robustness).

This view of interactions as fixed entities determining the response to perturbations has received much criticism (e. g., de Ruiter, 2005). Interactions themselves are known to vary in time, e. g. as a result of annual cycles (Olesen *et al.*, 2008), but also as the result of perturbations. It is thus necessary to understand how they change after disturbance.

0.2.3.2 *Changes of networks along gradients of stress*

Current global changes will impact the abundance of extant species as well as their interactions (Memmott *et al.*, 2007b; Tylianakis *et al.*, 2008). To understand how ecological networks may respond to these changes, it is necessary to know what drives their structure across space and time. To this end, much work have thus focused on documenting how interactions vary along environmental gradients (Tylianakis & Morris, 2017), and developing statistical methods to do so (Poisot *et al.*, 2012; Pellissier *et al.*, 2017).




Level of network description	Structural pattern	Description	Ecological relevance	References in ecology
 Network level	Connectance	Percentage of realized links in the network	Linked with community stability and robustness	May (1972) Dunne <i>et al.</i> (2002)
	Modularity	How well a network can be subdivided into compartments with few interactions between them	Increases community persistence	Stouffer & Bascompte (2011) Thebault & Fontaine (2010)
	Nestedness (bipartite networks)	Nestedness quantifies how well specialist species interact with a subset of those with whom generalists interact	Increases community persistence and decreases the number of secondary extinctions	Thebault & Fontaine (2010) Verdú & Valiente-Banuet (2008)
	Distribution of interaction strength	Quantifies the sequence of interaction strengths in the network	Weak interactions increase community persistence	Neutel (2002) Berlow <i>et al.</i> (2004)
	Structural balance (signed networks)	A balanced network can be well-devided into groups with positive links within them and negative links across groups.	Link with stability (? no ecological evidence)	Saiz <i>et al.</i> (2018)
	Positive/negative interaction balance (signed networks)	Percentage of positive links vs. negative links in a network	Positive interactions may favor coexistence (evidence from plant networks)	Saiz <i>et al.</i> (2017)
 Intermediate level	Feedback loops (signed networks)	A feedback loop occurs when a node has a indirect positive effect on itself through one or more other nodes	Can determine the community response to perturbations and underpin alternative stable states	Kéfi <i>et al.</i> (2016)
	Motif distribution	Motifs are types of three-way interaction patterns in a network	May affect the persistence of the community	(Klaise & Johnson, 2017)
 Node level	Node degree	May identify key species for community dynamics	Linked with community dynamics	e. g. Saiz & Alados (2011)
	Node average interaction strength (signed network)	May identify role of a species in community dynamics (e. g. competitor vs facilitator)	Linked with community dynamics	e. g. Saiz & Alados (2012)

Table 0.2: Some structural patterns found in interaction networks and their link with community stability or dynamics.

Plant ecology has a long tradition of studying how interactions vary along gradients of stress, which predates by a wide margin the use of ecological networks. In plant communities, one of the outstanding debate surrounds the prevalence of competition vs. facilitation in plant communities (Callaway *et al.*, 2002). Whether facilitation or competition dominates in a given community is thought to strongly determine the temporal dynamics of a community, by producing potential sharp transitions (Kéfi *et al.*, 2012) or dampening the effect of stressors (Callaway, 2007; Wilby & Shachak, 2004). This balance could thus have a central role in determining how the community responds to external disturbance, and many studies have sought to describe and predict how it varies along gradients of stress (Callaway *et al.*, 2002; Maestre *et al.*, 2009; Smit *et al.*, 2009; Holmgren & Scheffer, 2010).

With the use of co-occurrence networks in plant ecology, this topic has benefited from a new, correlative approach to quantify the facilitation/competition balance in plant communities. Co-occurrence networks in this context can be summarized into a ratio quantifying the relative frequency of positive and negative links (Saiz & Alados, 2012, , Chapter 3). A positive ratio is most often interpreted as a dominance of processes linked to facilitation over competition in the local community. This new approach, because it does not depend on tedious pairwise experiments to infer plant-plant interactions, could allow documenting a much increased variety of plant communities along environmental gradients. It has been successfully carried out to show that facilitation promotes diversity in arid systems (Saiz *et al.*, 2018), and that the competition/facilitation balance at the network scale varies along gradients of grazing (Saiz & Alados, 2012) and aridity (Alados *et al.*, 2017).

Many of these studies based on co-occurrence networks focus on arid ecosystems, where facilitation is known to have a strong effect on community dynamics. Few studies concern more mesic systems, despite an ongoing discussion as to whether facilitation should also be important in those systems (Holmgren & Scheffer, 2010). Using an approach based on co-occurrence networks, Chapter 3 contributes to this debate by focusing on the relative importance of competition vs. facilitation in plant communities along grazing gradients of La Crau (France).

0.2.3.3 *Perturbations and temporal dynamics in networks*

Few studies have focused on the temporal variations of interaction networks. Most of this work has focused on plant-pollinator networks, probably because of their ease of sampling when compared to other
5 types of networks, which makes them easily replicable in time. These studies have shown that these networks do show temporal variations in time throughout the year (CaraDonna *et al.*, 2017; Olesen *et al.*, 2008), and respond favorably to restoration efforts (Kaiser-Bunbury *et al.*, 2017). In vegetation studies, despite the known existence of
10 year-to-year variations in interaction strengths (Tielbörger & Kadmon, 2000), no study (to our knowledge) focuses on the temporal variations of interaction networks in plant communities. This is the object of study of Chapter 4, which focuses on the recovery of potential interaction networks in plant communities after disturbance.

15 Despite new methods (Blonder *et al.*, 2012), understanding how ecological networks vary in time, and how they recover from perturbations appears as a new challenge for network-based analyses of ecological communities.

0.3 OBJECTIVES AND RESEARCH QUESTIONS

As we have seen through this introduction, interaction networks in ecological communities present specific structural patterns (feedback loops, nestedness, etc.) which determine their response to disturbance. However, disturbance itself may affect the abundance of species and the strength of interactions. This thesis focuses on different aspects of this loop, using plant communities as model systems.

The first chapters focus on a structural pattern which is specifically relevant to ecosystem management and conservation: feedback loops. When these are present in a community, possible large shifts may occur despite small perturbations, leading to ranges of environmental conditions where ecosystem resilience can be impaired.

Specifically, **Chapter 1** asks *Can active feedback loops be identified from multimodality in diverse ecological communities ?* To this end, we build on theoretical approaches based on potential analyses and reveal fragile areas where feedback loops may produce non-linear responses. This work is based on the analysis of a dataset collected in 2011 and 2012 in California, USA (to which I participated), in collaboration with USGS research teams (WERC). **Chapter 2** is a synthesis effort of the current state of the literature on empirical measures of resilience – or early-warning signals – into a widely-distributed R package. With this work, we aim at enabling users to *assess the robustness of early-warning signals on empirical data*, by providing a standard and reproducible workflow for future studies focusing on indicators of resilience.

The two first chapters focus on detecting the effect of a particular structural pattern – feedback loops – on the response to disturbance. The two remaining chapters adopt the inverse perspective, and evaluate the effect of perturbations on the structure of interaction networks. In particular, they focus on the effect of perturbation on a specific structural pattern that has been the object of a decade-long debate in vegetation studies: the positive/negative interaction balance. These two chapters are based on an extensive dataset that is the result of field work carried out – in collaboration with many assistants! – over the course of this PhD program in La Crau, France.

Chapter 3 specifically aims at answering the following research question: *How does biotic stress alter community-scale positive/negative interaction balance ?*. We answer this question using a recent approach

based on association networks, and apply it to a dataset documenting plant communities in 16 grazed sites in La Crau, France. Using a chronosequence approach, a temporal perspective is adopted in **Chapter 4** to ask *How resilient are plant-plant association networks ? How*
5 *does it compare to other facets of the community ?*.

0.4 NOTE TO THE READER

This thesis comprises an introduction, four chapters, and multiple appendices. Chapter 1 and 2 can be read independently, but it is probably best to read Chapter 3 before Chapter 4 as the latter builds upon
10 methods explained in detail in the former. Appendices complement individual chapters with background information about the study sites (Appendix 2), or more extensive mathematical details about specific topics (Appendix 3). Before each chapter, a small transition reminds the reader of where the work is situated in the overarching
15 topic of the *link between resilience and ecological interactions in ecological communities*, along with some details about the ecological system under focus.

Part II

CHAPTERS

IDENTIFYING POSITIVE FEEDBACKS IN
VEGETATION COMMUNITIES OF REMOTE AREAS:
INSIGHT FROM SUBALPINE MEADOW
5 VEGETATION COMMUNITIES

CONTEXT OF THE WORK

It is essential for conservation to be able to anticipate how a given ecological system will respond to perturbations. Where ecological systems are resilient, small perturbations in species densities and environmental conditions produce small changes in the state of the system. However, some systems can exhibit large changes in their state, even after a small disturbance. This often occurs where a specific structural pattern exists in the interactions of a given system: feedback loops. It can happen, for example, when two species enhance each other's recruitment (e. g. through facilitation, Kéfi *et al.* 2007).

Identifying feedback loops from ecological patterns may be challenging. Previous approaches have attempted at doing so based on the criterion of multi-modality: where feedback loops are active, the distribution of observations of a given ecological system may exhibit multiple modes (Livina *et al.*, 2010). This approach has been carried out on simple, aggregated data (e.g. total forest cover, Hirota *et al.* 2011), but it remains unclear how it could be extended to multi-species assemblages. We suggest a way to do so in this chapter, and apply it to iconic conservation areas: the national parks of Sierra-Nevada, California.

The Sierra-Nevada is located in inner California (USA) and represents a the dominant mountain range of the state. In these areas, covered mostly by forests of mixed pine species, meadows occur locally wherever topology favors the local accumulation of water (Weixelmann *et al.*, 2011). These meadows, despite representing a small fraction of the total protected areas, represent islands of essential habitat with specific, endemic species of amphibians such as the Yosemite toad (*Anaxyrus canorus*) and the Yellow-legged Frog (*Rana muscosa*). Many accessible meadows are used for recreation, and others, including remote ones are used to establish grazing camps. This use

has been sparked a debate about the appropriate use of meadows in wilderness areas, and called for an assessment of the impact of grazing on subalpine meadows vegetation communities (Lee *et al.*, 2017).



Figure 1.1: Subalpine meadow often appear as clearings within a continuous pine forest. They occur where water accumulates and favors a diverse herbaceous community. Photo: Steven Lee (USGS)

These issues motivated the collection of an extensive survey of 47
5 meadows, spread out within Yosemite and Sequoia National Parks
in 2011 and 2012¹. This survey documented on a regular grid the
species composition within grazed and ungrazed meadows, along
with values of the main identified gradient – water content – and a
set of variables describing the local abiotic conditions.

10 Despite the effort to document the impact of short-term stressors
on meadow ecosystems, it remains unclear how they will respond
to long-term changes such as climate change. It is also unclear as to
whether stressors may have a large or irreversible effect on the species
composition of meadows.

15 To provide hypotheses on how these vegetation communities could
respond to stressors, we reused and extended previous approaches
that aim at identifying non-linear responses in ecological systems
(Livina *et al.*, 2010).

¹ I participated to this survey in spring 2012 as part of my Master's degree.

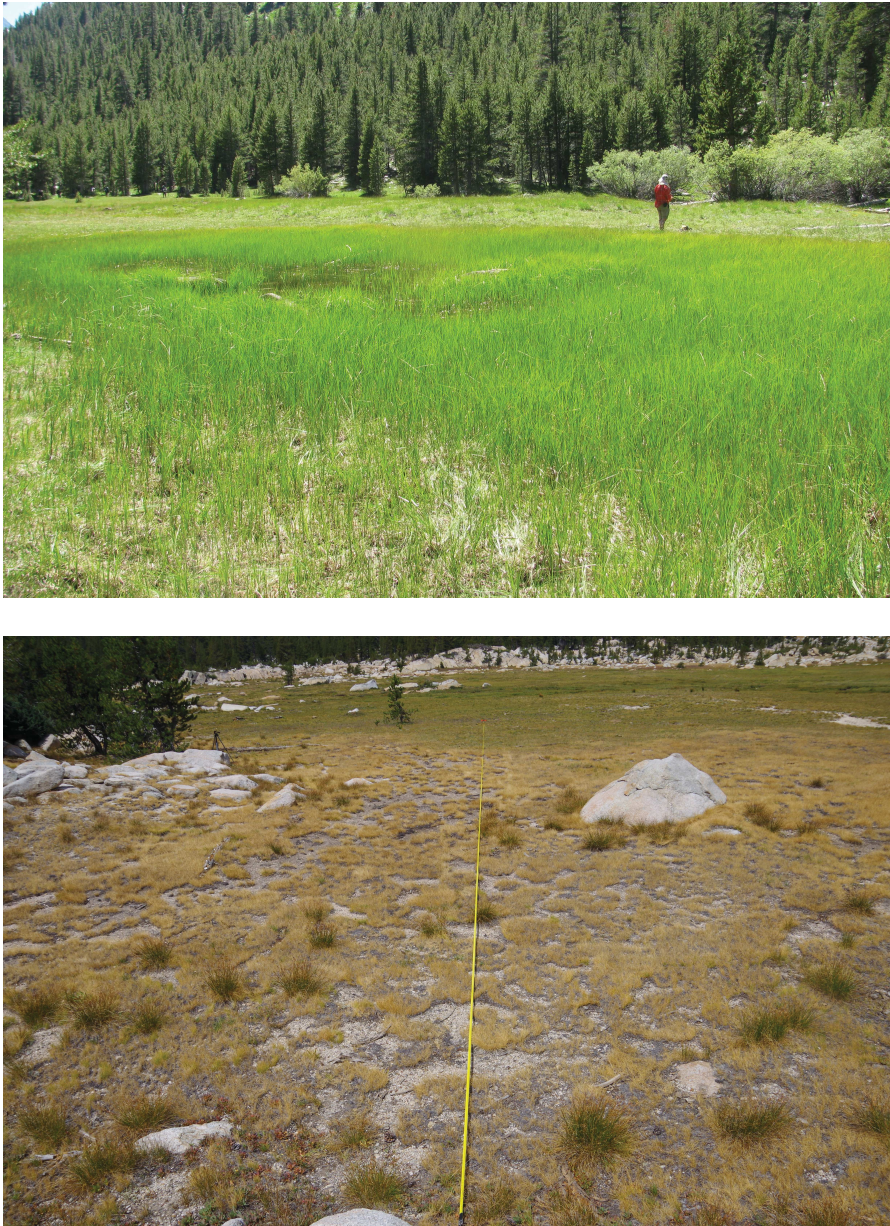


Figure 1.2: The species composition of meadow vegetation communities responds first and foremost to changes in local water availability. The photo on top pictures a community of *Carex* in a regularly-flooded meadow area, while the bottom photo shows a community of *Carex* (a different species) in dry areas of meadows. Photos: Steven Lee (USGS)



Figure 1.3: General view of a meadow (people for scale). The vegetation turnover is visible in the variations of the shades of green, from the stream to the edge of the meadow. Photo: Steven Lee (USGS)

This chapter has been submitted as the article 'Plant community patterns reveal areas of low resilience in subalpine meadows', A. Génin, S. R. Lee, E. L. Berlow, S. M. Ostoja, and S. Kéfi. The work presented here is a ongoing revision prior to resubmission.

1.1 INTRODUCTION

It is essential for pro-active management to identify how ecological systems respond to environmental changes (Suding & Hobbs, 2009). In many ecosystems, small changes in environmental conditions or small perturbations produce small changes in the observed state of the ecosystem. However, in others, the same events can result in large and/or irreversible changes in the ecosystem state. It is thus very desirable to identify where and when a given ecological system has such a decreased ability to recover by itself from perturbations, i. e., a decreased resilience.

In principle, identifying precisely how a given ecosystem responds to perturbations requires documenting its temporal response as external conditions are slowly changed, or perturbation events are performed (Bestelmeyer *et al.*, 2011; Petraitis, 2013). Such data could correspond to time-series from either observations or experiments (Scheffer & Carpenter, 2003). However, in most natural ecosystems, obtaining datasets or setting up experiments at the appropriate scales can be both costly and difficult. Instead, researchers often adopt a ‘space-for-time’ substitution approach, where the state of a given ecological system is recorded in multiple locations along an environmental gradient, but at a single or several very close points in time (‘snapshot’ data).

Many studies have used this type of dataset to identify apparent non-linear responses of ecological systems to changes in environmental drivers (Hirota *et al.*, 2011; Scheffer *et al.*, 2012a; Vasilakopoulos & Marshall, 2015; Eby *et al.*, 2017) by interpreting the changes in the distribution of state values (e.g. distribution of measured tree cover) along an environmental gradient. These studies assume that, on average, a given system is more often observed close to the states that persist the most in time, i. e. its most stable states, than away from them. As a result, at a given point along a gradient, the observed distribution of states of a given system should be centered around its stable states (Livina *et al.*, 2010). For example, a system with one stable state is expected to show a unimodal distribution centered on a single average value – its stable state (Box 1.1).

When an ecological system exhibits a linear response along a gradient, this average state changes proportionally to the change environmental conditions along the gradient (panel a1 in Box 1.1, Ratajczak *et al.*, 2018). In contrast, when the response is non-linear, small

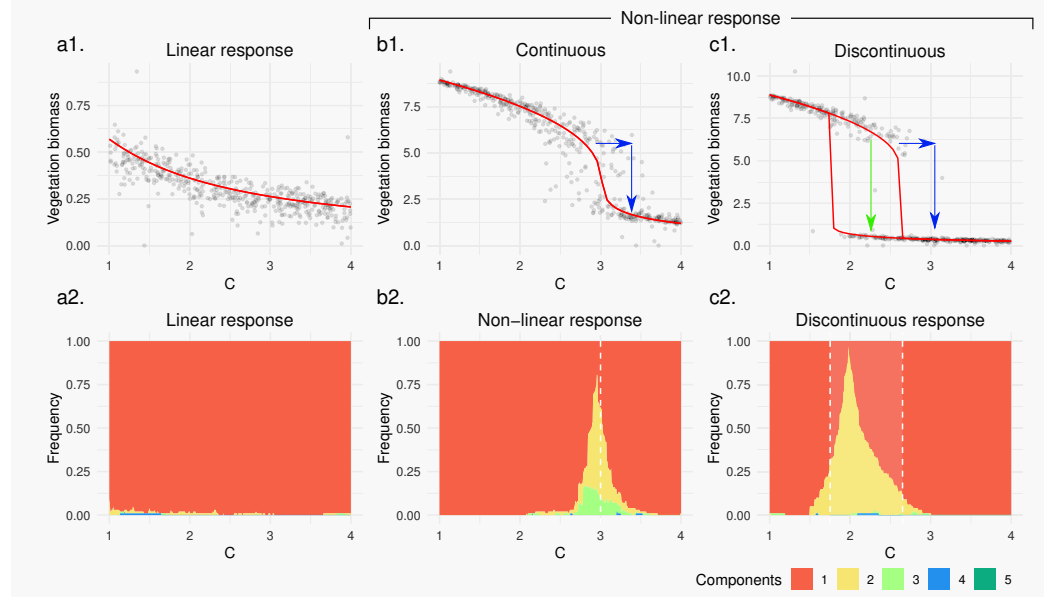
changes in conditions can result in a disproportionate changes in the system's average state, sometimes resulting in a sharp shift as a threshold in environmental value is crossed (panel b1 in Box 1.1). Some ecosystems can also exhibit multiple modes in their observed
 5 distribution of states at a given point along the gradient, i. e. multiple alternative states (panel c1 in Box 1.1). These may be underpinned by external factors, such as an unmeasured variable, which controls whether the observed value is closer to one state or the other. However, internal factors such as feedbacks may also maintain a given
 10 ecosystem in one of these alternative states – they are then effectively alternative *stable* states (Petraitis, 2013). In this case, even a short disturbance event may have long-lasting consequences, by making an ecosystem switch durably from one state to another. Large shifts can also occur despite a small change in drivers' values, if the ecosystem
 15 is pushed outside of the range where those multiple states exist.

For a given system, identifying changes in the number of modes – the *modality* (Petraitis, 2013) – of the empirical distribution of state values may thus identify where non-linear responses occur along a gradient. These areas may be of special interest to carry out further
 20 research or experiments, as perturbations or small changes in environmental conditions may have there a larger effect than expected (Box 1.1).

Using this modality criterion, we investigated where apparent non-linear transitions occurred in vegetation communities of subalpine
 25 meadows of Sierra Nevada (California, USA). Many of these meadows are located in two major national parks, Yosemite and Sequoia/King's canyon, and exemplify ecological systems under strong scrutiny, where it is very valuable to anticipate the effect of stressors. However, due to their remoteness, it is often impractical to monitor meadows
 30 for temporal changes: using snapshot data to infer the potential effect of stressors is thus very relevant in these ecosystems.

Meadows within the Sierra Nevada occupy a small portion of the total area, but they stand out as highly productive riparian islands within a rugged, semi-arid landscape (Barbour *et al.*, 2007). In those
 35 meadows, the species present in vegetation communities respond very closely to changes in the moisture content of the soil (Allen-Diaz, 1991; Weixelmann *et al.*, 2011), making it the dominant environmental gradient at the meadow scale (Lowry *et al.*, 2011). This general response to water content can compound locally with other factors
 40 to determine the response of local vegetation communities, such as

Box 1.1: The link between modality and non-linear responses



To illustrate the link between multi-modality in the observed states and the type of response of a system, we can consider the seminal model of overgrazing by Noy-Meir (1975). This model is able to produce various types of responses along a gradient of grazing (C values). Non-linear transitions arise when strong positive feedbacks are present in the system (b1, c1), which are visible in the deterministic response of the model (red line). The black points indicate "snapshot" values, which would be observed by sampling along the grazing gradient different instances of this system (with added noise) at the same point in time.

Using a moving-window approach, we can characterize the modality of the distribution of observations using component analysis (described in Methods). When a distribution tends to be more bimodal, the frequency of counts for two components increases, which arises in the vicinity of non-linear responses (b2, c2). Identifying changes in modality in empirical data could improve the understanding of where along an environmental gradient a non-linear response of the system may occur. In such cases, a small change in conditions can trigger a large change in the system's state (blue arrows). An acute disturbance event, such as a reduction in plant biomass, may also trigger a durable change to an alternative state when discontinuous responses are also present (green arrow).

disturbance by animals (Klikoff, 1965; Lee *et al.*, 2017), soil coarseness (Ankenbauer & Loheide, 2017) or nutrient content (Ratliff, 1985). These interactions have the potential to create non-linear responses of the community along the water gradient. For example, the presence of *Carex filifolia* sods has been correlated with increased soil nutrients
 5 of *Carex filifolia* sods has been correlated with increased soil nutrients (Ratliff, 1985), suggesting a possible positive feedback between veg-

etation and soil quality. Reducing vegetation cover in some communities could impair regrowth for a much longer time than elsewhere in meadows. It is thus essential to identify where these occur and their spatial extent in meadows in order to carry out informed management, in particular in the current context of recurrent disturbance such as droughts (Belmecheri *et al.*, 2015; Adams *et al.*, 2015).

Using the example of meadows as a case study, we show how and where non-linear responses of plant communities can be identified in subalpine meadows. Combined with an extensive survey of local surface characteristics, we identify possible drivers underpinning these non-linear responses to guide future experiments and management decisions.

1.2 METHODS

1.2.1 Analyzing changes in modality along a gradient

Characterizing the modality of a given set of observations can be done by analyzing the distribution of mass of a kernel-estimated density (Müller & Sawitzki, 1991). This approach essentially identifies whether a density tends to be composed of multiple 'lumps' or components (multimodal density) rather than a single component (unimodal density), and has been identified as more robust to outliers compared to previous approaches (Silverman, 1981).

To analyze changes along the main environmental gradient, we used a moving window approach. For each set of observations of the dataset falling within the window, we first computed the empirical density of the observations with a gaussian kernel of a given bandwidth σ (fixed for the whole analysis). We then rescaled the density so that its maximum was one, and considered n_{cut} thresholds regularly spaced between zero and one. For each threshold, we considered a "slice" of the density and counted the number of observed disjunct components (Figure 1.4). For a given density, this process yields a set of n_{cut} counts of components. A density that is better-described by a given number of well-separated components will show this number for a higher number of chosen thresholds. How these counts vary along an environmental gradient can inform about changes in the modality of the distribution of states. The typical example could be a density switching from being unimodal to more bimodal (exhibiting

then an increased number of counts with two components) around a certain value of the environmental gradient.

This method can be applied to univariate densities (Figure 1, top; Box 1), which is what is classically done when the state of the system is defined by a single value (e. g. Hirota *et al.*, 2011). However, it can also be applied to multivariate densities, obtained through multi-dimensional kernel density estimation (Figure 1b), which is very relevant to cases where the state of the system is not well-defined by a single value (e. g. total biomass) but several (e. g. abundances of individual species).

n_{cut} should be set to a large value to identify differences in height of the density (we used 512 here, which was enough to detect changes in modality along the gradient). We refer to this process as "component analysis" later in this work.

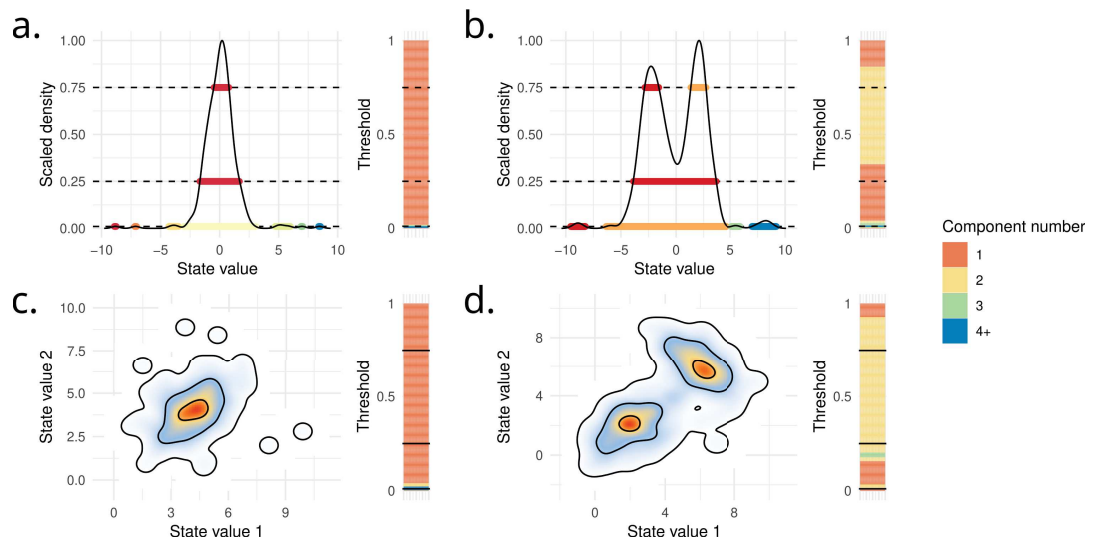


Figure 1.4: Principle of component analysis on synthetic data with added noise. On univariate data (a,c), slicing the density yields a single component for a majority of chosen thresholds. On bimodal data, the same procedure yields two components for most thresholds chosen (b, d). Note that very low thresholds identify spurious components because of outliers in the density, but this effect disappears quickly as higher thresholds are used

15 1.2.2 Meadow sampling

Sampling in subalpine meadows was carried out as described in Lee *et al.* (2017). Within each meadow, surveys were carried out in 2x2m plots, regularly spaced within belt transects laid out every 40m perpendicularly to the main meadow drainage. Ocular estimates of 28

upper soil characteristics were measured (Appendix 2). We measured volumetric moisture content in the soil top 12 cm, as averaged from 5 measurements of a TDR moisture probe. Ocular cover estimates of each plant species was recorded in 8 25x25cm subplots and averaged
 5 to obtain an estimation of the relative abundance of each species in the plot. We then analyzed the response of vegetation communities – in terms of species composition – along the natural moisture gradient in meadows. To attenuate the effect of year-to-year variations in precipitation on the measure of the moisture gradient, we standardized the measured water content within year. Hereafter, water content
 10 values are given in standard deviations (s.d.).

1.2.3 Empirical data analyses

The state of meadow vegetation communities is defined by the relative abundances of all species. Because carrying kernel density estimation cannot be done on data with many dimensions (typically, computational costs become too high after 5-10 dimensions (Blonder *et al.*,
 15 2014), well below the total number of observed species), we had to summarize the variations of vegetation species compositions to a few axes using ordination. In principle, using Principal Coordinate Analysis (also named metric Multi-Dimensional Scaling) is the method of
 20 choice as it preserves as much as possible the dissimilarities between sites. However, it is often empirically found to produce strong arch artifacts on vegetation data, in particular when species turnover is high along a gradient (Legendre & Legendre, 2012). Non-metric dimensional scaling could be considered as an alternative but, because
 25 it preserves only the ranks of the original dissimilarities between sites, the resulting axes summarizing species turnover cannot be used quantitatively. We therefore chose a Correspondence-analysis-based method, Detrended-Correspondence Analysis, which, despite criticisms (Jackson & Somers, 1991), (i) produces axes that can be used
 30 as quantitative variables and (ii) is not subject to arch-like artifacts. We carried out sensitivity analyses to confirm that our results are robust to the use of other dimensionality reduction methods².

We used the two first axes of the DCA and carried out a component analysis in a moving window along the moisture gradient (we set
 35 the window size to 0.5). For the component analysis, we used the bivariate diagonal density estimation kernel $\begin{bmatrix} 0.70 & 0 \\ 0 & 0.62 \end{bmatrix}$, as obtained from

² Unfortunately not shown in this thesis.

automatic bandwidth selection (*bandwidth.nrd* in package MASS). We carried out the component analysis 100 times for each window subset, using a random subsample of 150 of the observations falling within the window to make sure sample size for density estimation was constant along the water gradient.

Because the component analysis identified two ranges of water content with increased support for two components, dry areas and wet areas, we extracted these subsets from the whole dataset and investigated soil attributes that could underpin these bimodal distributions. We refer to dry areas for sites where water content was below -1 s.d. and to wet areas for those where water content was above 1 s.d. We clustered each subset into two groups based on species composition, using hierarchical clustering with a Ward distance on a Bray-Curtis distance matrix. We contrasted the environmental covariates of each group to discuss possible underlying mechanisms for the apparent non-linear response along the water-content gradient. We used two-sample Mann-Whitney tests (*wilcox.test* in R) to contrast the distribution of each plot characteristics across groups, adjusting the p-values for multiple tests using the Benjamini-Hochberg correction. Because sampling was regularly-spaced in meadows, we used the frequency of each group as a proxy for its spatial extent in the meadows.

We carried out the analyses using R (version 3.5.0), along with the R package 'vegan' v2.5 (Oksanen *et al.*, 2018), 'ks' v. 1.11.1 (Duong, 2018) and MASS (Venables *et al.*, 2002).

1.3 RESULTS

In a proof-of-concept model (Box 1.1), simulations show that multiple components arise in cases of non-linear responses of the system, and that they are well-identified by our approach. Empirical data analysis of DCA scores highlighted two ranges of water content along the moisture gradient with an increased support for two components in the species composition of the meadows (Figure 1.5): dry areas and wet areas. At the two extremes of the water gradient, the component analysis yielded an increased count of two components (from nearly zero to 20-40%; Figure 1.6), highlighting a possible non-linear response of species composition to changes in water content in the corresponding areas.

In wet areas, the two groups defined based on species content were contrasted. One was dominated by *Carex vesicaria*, code CARVES,

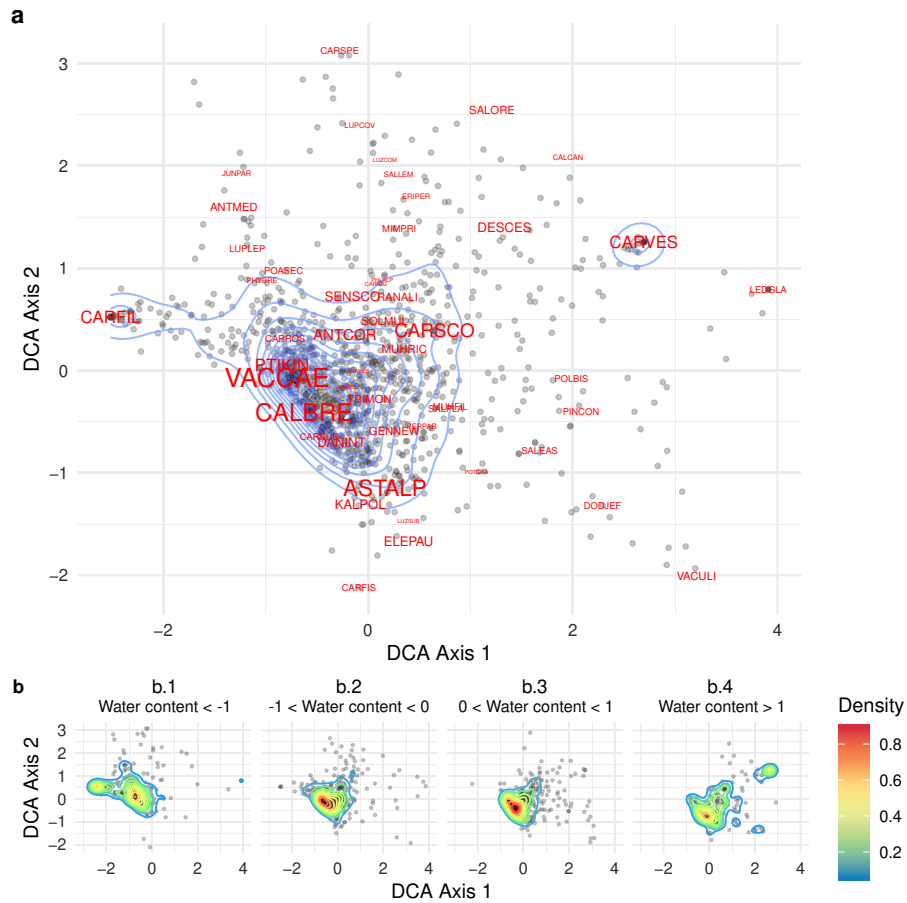


Figure 1.5: Detrended Correspondence Analysis results on the subalpine dataset (a). Species labels indicate where individual species are dominant, with label size proportional to the overall abundance of the species in the dataset. The bottom panels (b1-4) show the same graphs, but only with points comprised within different ranges of water content. Increased modality (i. e. multimodality) can be observed for water contents below -1 s.d. and above $+1$ s.d.

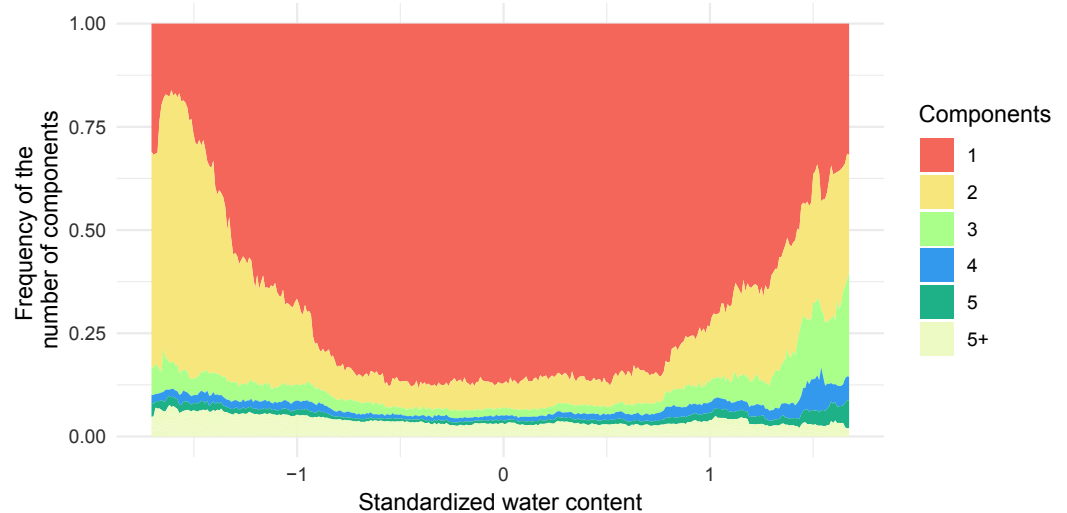


Figure 1.6: Component analysis results on the subalpine meadow dataset. The number of counts for two components in the density is higher in dry and wet areas of meadows, highlighting the possible presence of non-linear responses in these areas.

while the other was a more mesic community that included *Aster alpinum*, code *ASTALP* (Figure 1.7a, b-top). The *C. vesicaria*-dominated group represented 25% of all plots done in wet areas and had different water regime-related attributes: a more saturated and less moist soil, as well as a higher observed cover of silt and bare ground (Figure 1.7b). The covers of dry and flooded soils were significantly different between the two groups but the estimated difference was very close to zero.

In dry areas (plots with water content below 1 s.d.), clustering yielded a group dominated by *Carex filifolia*, *CARFIL* (10% of plots in dry areas), contrasting with another dominated by more mesic plants (e.g. *Vaccinium caespitosum*, *VACCAE*; *Calmagrostis brewerii*, *CALBRE*; Figure 1.8a). The *C. filifolia*-dominated group had a higher ocular cover of coarse particles (sand, pebble) and bareground (Figure 1.8b). It also showed a significant difference in water-regime attributes (cover of dry and moist soil), and disturbance attributes (stock prints, rodent mounds), although they had a very small estimated cover difference (below 10^{-4}).

1.4 DISCUSSION

Patterns suggested two ranges of the moisture gradient where multimodality of species composition highlighted apparent non-linear re-

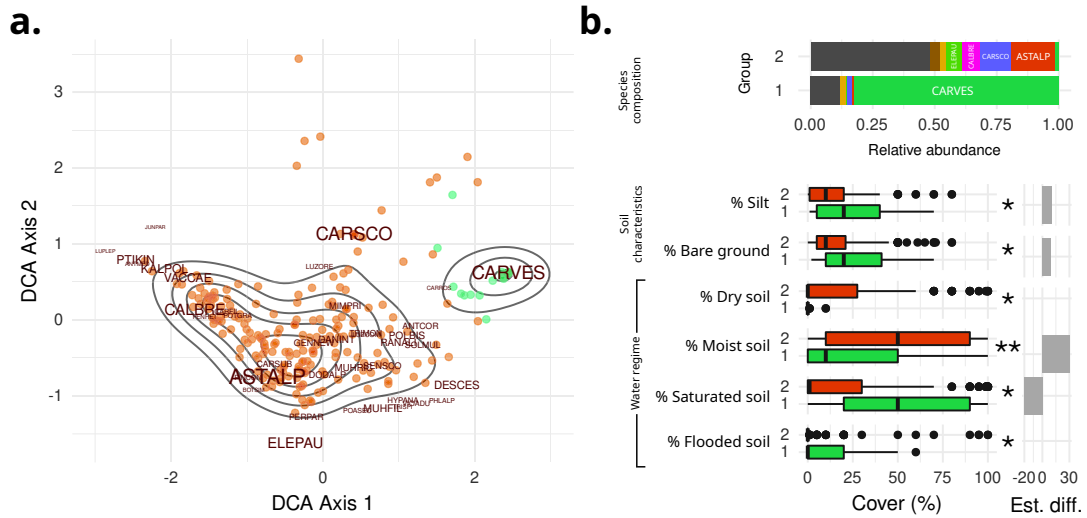


Figure 1.7: (a) Detrended Correspondence Analysis results on the wet meadow subset. Species labels indicate where individual species are dominant, with label size proportional to the total abundance of the species in the subset. A density estimate is added on top of the points. (b) Species composition and differences in plot attributes between the two groups, stars represent significance of a Mann-Whitney test with P-values corrected for multiple tests using the Benjamini-Hochberg procedure (one star for $P < 0.05$ and two for $P < 0.01$). The grey bars show the estimated difference in (pseudo)medians between the two groups.

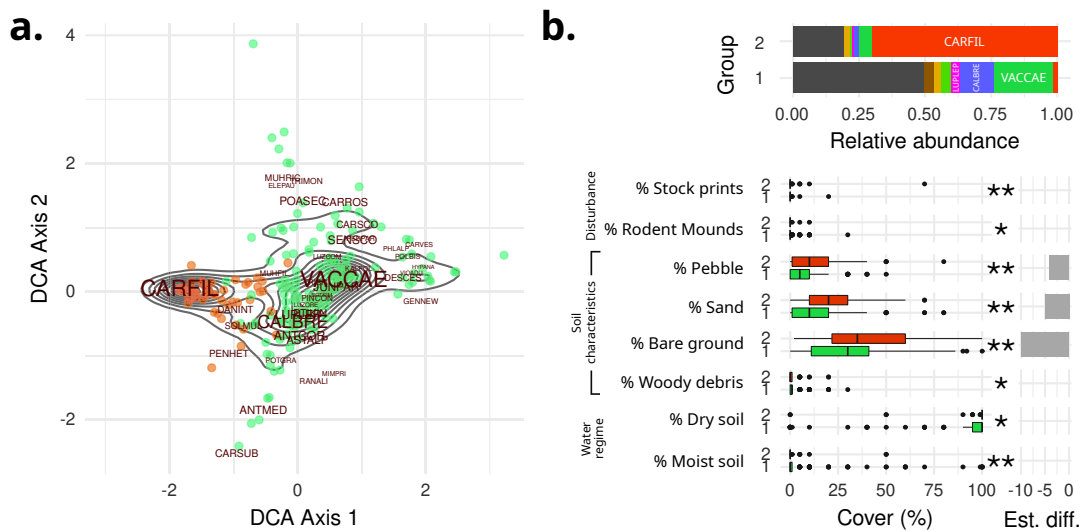


Figure 1.8: (a) Detrended Correspondence Analysis results on the dry meadow subset. Species labels indicate where individual species are dominant, with label size proportional to the total abundance of the species in the subset. (b) Species composition and differences in plot attributes between the two groups, stars represent significance of a Mann-Whitney test with P-values corrected for multiple tests using the Benjamini-Hochberg procedure (one star for $P < 0.05$ and two for $P < 0.01$). The grey bars show the estimated difference in (pseudo)medians between the two groups.

sponses of vegetation to the moisture gradient. These two modes in species composition are correlated to differences in local abiotic conditions and animal disturbances. This pattern could be driven entirely by independent abiotic differences, but at this scale, vegetation itself is also likely to influence the local conditions through positive feedbacks (Wilson & Agnew, 1992). Disentangling causal drivers of multimodality in these areas would require work beyond observational analyses, but it is important to acknowledge this possibility in a conservation context. If vegetation-environment feedbacks are active, i. e. the response of the local vegetation is linked to intrinsic, possibly non-linear dynamics, and not entirely driven by external factors. A small change in annual moisture, or a strong disturbance event could thus lead to unexpected shifts in species composition and different ecosystem functioning. We discuss this possibility in the next paragraphs.

1.4.1 Possible ecological mechanisms behind bimodality in meadows

In wet areas of meadows, our analysis identified a *Carex-vesicaria*-dominated community contrasting with a more diverse community of mesic species. The *C. vesicaria*-dominated community had a larger amount of flooded or saturated soil and more silt, which are typical characteristics of streamside flooded pools with standing water (Baldwin & Hickman, 2012). The mesic community occurring for similar water contents was represented by a more diverse species composition that occurred outside of the areas with standing water. Here, species composition maps well onto independent, external environmental characteristics linked with the absence or presence of standing water. A possible transition from one community type to the other would likely be the result of a major modification of the local water regime.

In dry meadow areas, the analysis identified a *Carex filifolia*-dominated community contrasting with a more diverse mesic community. The *C. filifolia* community was observed to have coarser upper soil particles (sand, pebble), and a higher amount of bare ground. Significant differences were also found in terms of disturbances by animals and water regime. The presence and characteristics of dry communities in meadows is known to respond to external parameters such as rodent disturbance, erosion processes and soil nutrients (Klikoff, 1965). Plants growing in these areas are known to also influence in turn some of these parameters. For example, the sods formed by *C. filifolia*

are known to interact with rodents (Klikoff, 1965), and can improve local conditions by trapping smaller soil particles which hold more nutrients (Ratliff, 1985) and water (Wood, 1975; Ankenbauer & Loheide, 2017). The possible presence of this feedback means that acute disturbance of these areas could have much longer-termed effects than expected and possibly require restoration. Further work focusing on identifying the type of dynamics at play in these dry areas would yield a better understanding of their resilience to local degradations and climate change.

In both wet and dry areas, water-related parameters stood out as possible drivers of non-linear responses. With the increase of temperatures associated with climate change, snow/rain ratios and total spring snowpack are decreasing across the Sierra Nevada (Knowles *et al.*, 2006; Barnett *et al.*, 2008). These long-term shifts have the potential to extensively alter meadow hydrology, to which the identified wet and dry communities may be the most sensitive. Short but acute events such as drought could produce persistent shifts of mesic communities, which tend to be the most diverse, into less-diverse dry communities. The Sierra Nevada has recently experienced one of these events (Belmecheri *et al.*, 2015), which included the four driest years (2012-2015) of the last 2000 years (Adams *et al.*, 2015). While the repercussions of the drought have clearly manifested across Sierra Nevada forest ecosystems (Potter, 2016), the impacts on meadow ecosystems have yet to be thoroughly evaluated. Monitoring changes and setting up experimental research in areas where non-linear responses occur could inform us greatly about such impact.

1.4.2 Method discussion

In this work, we used a descriptive method to reveal where a complex ecological system exhibits apparent non-linear responses, in the absence of temporal monitoring. This method can be readily applied to existing datasets provided that a measure, even noisy, of the main environmental gradient is carried out. To differentiate whether apparent non-linear responses are underpinned by potential positive feedbacks, it remains essential to also have local, detailed data.

We chose to base our component analysis on the two first axes of the ordination because visual inspection revealed the two clusters (Figure 1.5 top), and because we focused on broad variations in species composition (which are contained in the first few axes of

the ordination). A similar analysis could be based on a multivariate density estimation that uses more dimensions (in this case, more axes of the ordination). This could in principle reveal more ranges of the environmental gradient with multimodal distributions. However, observations become increasingly distant from each other (in a multivariate space) as dimensions are added. As a result, the possible increased power brought by added dimensions may come with an increased amount of false positives – i. e. ranges of the gradient with increased multimodality, which does not correspond to ecologically relevant differences in the field. Using only one or two dimensions is a conservative option when investigating multi-modality (Blonder, 2016). Further work investigating this trade-off, along with computationally efficient methods (Blonder *et al.*, 2014) would certainly provide insights to guide the choice of the number of dimensions.

Future refinements of this work should also include sensitivity analyses regarding the choice of ordination, the window sizes and density bandwidths.

1.4.3 Conclusion

In the current context of rapid change and abundant data, a rising number of methods and indicators aim at linking patterns with the stability properties of a given ecosystem (Clements & Ozgul, 2018), based on e.g. time-series properties (Dakos *et al.*, 2014), spatial patterns (Génin *et al.*, 2018a) or in this case, the distribution of states. Although they do not replace experiment-based ecological knowledge (Boettiger & Hastings, 2013), they can provide valuable monitoring tools to anticipate the response of ecological systems to global changes as well as local disturbances, allowing managers and researchers to make more informed decisions in uncertain contexts.

FOSTERING THE DETECTION OF ECOSYSTEM SHIFTS BY IMPLEMENTING SPATIAL EARLY-WARNING SIGNALS

5 CONTEXT

Some ecosystems show non-linear responses to gradual changes in environmental conditions, once a threshold in conditions - or critical point - is passed. This can lead to wide shifts in ecosystem states, possibly with dramatic ecological and economic consequences. Such behaviors have been reported in drylands, savannas, coral reefs or shallow lakes for example, and often arise because of positive feedbacks (Wilson & Agnew, 1992). Important research effort of the last decade has been devoted to identify indicators that would help anticipate such ecosystem shifts and avoid their negative consequences.

15 Theoretical and empirical research has shown that, as an ecosystem approaches a critical point, specific signatures arise in its temporal and spatial dynamics; these changes can be quantified using relatively simple statistical metrics that have been referred to as 'early warning signals' (EWS) in the literature. Although tests of those EWS on experiments are promising, empirical evidence from out-of-lab datasets is still scarce, in particular for spatial EWS. The recent proliferation of remote-sensing data provides an opportunity to improve this situation and evaluate the reliability of spatial EWS in many ecological systems.

25 Despite the abundance of data and the interest of ecologists for testing the accuracy and usefulness of these indicators (Burthe *et al.*, 2016; Gsell *et al.*, 2016), no reference implementation exists. Yet it would favor the reproducibility of results, lower the technical knowledge requires to carry out these analyses, and as a result enable a much wider audience to have access to indicator-based analyses. We created and published such implementation as the R package 'spatialwarnings', and describe it in this chapter.

35 This work is the result of a collaborative effort with the theoretical ecology group at Indian Institute of Science (Bangalore), in particular with Sabiha Majumder, Sumithra Sankaran and Vishweshha Guttal. It

has been published in 2018 in *Methods in Ecology and Evolution* ¹, is under continuous development at its homepage ². 'spatialwarnings' is also widely distributed to R users through CRAN ³.

The tools provided by this package were also used in modelling work, to investigate the role of different types of stressors on the predictive performance indicators. This has resulted in another publication in *Ecological indicators*⁴.

¹ <https://doi.org/10.1111/2041-210X.13058>

² <https://github.com/spatial-ews/spatialwarnings>

³ <https://cran.r-project.org/package=spatialwarnings>

⁴ <https://doi.org/10.1016/j.ecolind.2017.10.071>

2.1 BACKGROUND

Many ecosystems appear to respond in a gradual way to changes in environmental drivers. In contrast, in other ecosystems, once a threshold in environmental condition - or *critical point* - is passed, just a small additional change can provoke an abrupt shift (Scheffer *et al.*, 2001; Petraitis, 2013) (Box 2.1). Examples of ecosystem shifts have been reported for a variety of ecosystems, such as drylands, savannas, coral reefs or shallow lakes (Scheffer *et al.*, 2001).

Because abrupt ecosystem responses can have strong and irreversible ecological and economical consequences (Scheffer *et al.*, 2001), the possibility of shifts has been accounted for in ecosystem management (Stein *et al.*, 2016; Briske *et al.*, 2005; Suding *et al.*, 2004), and methods have been developed to try to anticipate them in empirical systems (Scheffer *et al.*, 2009). In particular, theoretical and empirical studies have shown that ecological systems close to critical points should exhibit specific signatures in their temporal and spatial dynamics (Scheffer *et al.*, 2009; Dakos *et al.*, 2012; Kéfi *et al.*, 2014), leading to the development of metrics, which have been referred to as *Early-Warning Signals* (hereafter EWS) in the literature (Scheffer *et al.*, 2009). EWS provide a relative measure of the proximity to a critical point, and therefore of a possible ecosystem transition to a different state. Computing and monitoring them could therefore help detecting upcoming critical transitions in ecological systems (Scheffer *et al.*, 2009).

Despite their promises, a number of studies have also stressed the weaknesses of EWS. EWS provides information about whether a system is degrading or not, but they do not inform on how far the studied system is from a critical point (but see Majumder *et al.*, 2017; D'Souza *et al.*, 2015). Evaluation of EWS on empirical data has also proved to be challenging, and a number of studies have reported various limitations of EWS when evaluated on out-of-lab data, sometimes due to reasons such as a lack of sufficiently long and finely resolved data sets, or underlying stochasticity (Gsell *et al.*, 2016; Burthe *et al.*, 2016; Chen *et al.*, 2018; Weerman *et al.*, 2012; Moreno-de las Heras *et al.*, 2011; Ashwin *et al.*, 2012). Successful tests on ecosystem data remain rare – especially so for spatial EWS – which questions the usefulness of these indicators as tools to assess ecosystem degradation. The recent increase in the availability and extensiveness of remote sensing

data provides a timely opportunity to test spatial EWS outside of controlled experiments (e.g. Gsell *et al.*, 2016; Burthe *et al.*, 2016; Eby *et al.*, 2017; Butitta *et al.*, 2017; Berdugo *et al.*, 2017; Cline *et al.*, 2014; Ratajczak *et al.*, 2017). In the context of the currently available and
5 upcoming spatially extensive data, spatial EWS have been suggested to be particularly promising because they could allow the systematic monitoring of ecosystems' degradation level based on a few spatial snapshots (Kéfi *et al.*, 2014).

To help fuel investigations around spatial EWS, we suggest here
10 a workflow to guide users of a new package for R (R Core Team, 2018), 'spatialwarnings', to facilitate their application to spatial data from ecological and other complex systems. The package can readily compute the spatial indicators from data, assess their significance, and display the results, all in a convenient format much similar to
15 other usual R tasks (e.g. linear regression).

In the following sections, we first give the required background knowledge on spatial indicators. Using case-studies, we then describe how they can be applied to real and model systems with 'spatialwarnings' (version 1.1). For conciseness, we do not show all textual output
20 in the article, but Appendix 2 presents the code used here in more details.

2.2 THE SPATIAL EWS AND THEIR EXPECTED TRENDS

Current spatial EWS available in the literature come mainly from two different theoretical backgrounds: some are based on the changes of
25 dynamics before a critical point (namely 'critical slowing down'; see below), while others derive from the characteristics of the patchiness of certain ecosystems.

As an ecological system approaches a critical point (Box 2.1), it is expected to take more time to recover from small perturbations
30 (Scheffer *et al.*, 2009), a phenomenon known as Critical Slowing Down (CSD). This is expected to yield an increase in spatial heterogeneity (the spatial variance) of its state variables, as it stays longer away from its average state (Guttal & Jayaprakash, 2009). This deviation can sometimes be biased towards higher or lower values of the state
35 variable, resulting in an additional rise of spatial skewness (Guttal & Jayaprakash, 2009). For example, a forest close to a transition towards

a treeless state could exhibit higher spatial variance in tree cover and a bias towards low cover values (higher skewness) as external stress increases. In addition, because of CSD, a system close to a transition should exhibit higher near-neighbor correlations (Dakos *et al.*, 2010).

5 These three metrics – spatial variance, skewness and autocorrelation – can, in principle, reflect an upcoming critical point in any dynamical system, hence their reference as ‘generic EWS’ in the literature (Scheffer *et al.*, 2009).

Later work has produced EWS based on spectral properties (Carpenter & Brock, 2010), hereafter referred to as ‘spectrum-based EWS’.
10 Because of the slowing down, two points at a given distance from each other should be more similar in systems close to critical points (Kéfi *et al.*, 2014). This change in correlation length can be measured by computing the *r-spectrum* of the data (Couteron, 2002). The *r-spectrum*
15 is based on the Discrete Fourier Transform and decomposes the spatial data into series of periodic sines and cosines of given wavelengths (the inverse of wave frequency) and amplitude. The amplitude coefficient associated to each wavelength characterizes the dominance of this scale in the spatial data. Close to a critical point, a relative
20 increase in the amplitudes of long wavelengths (lower frequencies) is expected compared to short wavelengths (higher frequencies). To summarize this into a single value, one can use the ratio of the average amplitude of low frequencies over the average amplitude of high frequencies (Biggs *et al.*, 2009), the Spectral Density Ratio, which is
25 expected to increase along degradation trends.

Additional EWS have been suggested for ecosystems that exhibit a clear spatial structure, such as drylands or savannas (Rietkerk *et al.*, 2004). Characteristics of these spatial patterns, and in particular the distribution of their patch sizes (Kéfi *et al.*, 2007, 2011), have been suggested
30 to be promising indicators of degradation (Kéfi *et al.*, 2007; Lin *et al.*, 2010; Berdugo *et al.*, 2017), hereafter referred to as ‘patch-based EWS’. In these ecosystems, when stress is low, density is typically high and there can be a patch whose width or height equals the entire area considered, *i.e.* a spanning cluster. As density decreases, this
35 spanning cluster breaks down into smaller ones until a barren ecosystem state is reached (Kéfi *et al.*, 2011; Van Den Berg, 2011; Corrado *et al.*, 2014; Sankaran *et al.*, 2017b). When using spatio-temporal data, this sequential process is reflected in changes of the patch size distribution (PSD) (Kéfi *et al.*, 2011). More precisely, it is expected that,

(i) under low or no stress, a spanning cluster of occupied (vegetated) cells is present. (ii) As stress increases, this single patch breaks down and the PSD resembles a power-law ($x^{-\alpha}$). (iii) As stress increases further, vegetation patches break down and the PSD fits best to a truncated power-law ($x^{-\alpha}e^{-\beta x}$). (iv) In the final stages before reaching a fully empty state, only small patches persist and the patch size distribution is best-described by an exponential distribution ($e^{-\beta x}$) with presence of a spanning cluster of empty cells. Identifying where in these four phases an ecological system lies could thus constitute an indicator of degradation level (Kéfi *et al.* (2011), but see Schneider & Kéfi (2016); Sankaran *et al.* (2017b)).

A recent study has further suggested that this gradual truncation of the patch size distribution could be simplified into a single metric (Berdugo *et al.*, 2017). The idea relies on the fact that many empirical distributions resemble power-laws only for patches above a certain size x_{min} . This *power-law range* (PLR) can be expressed as

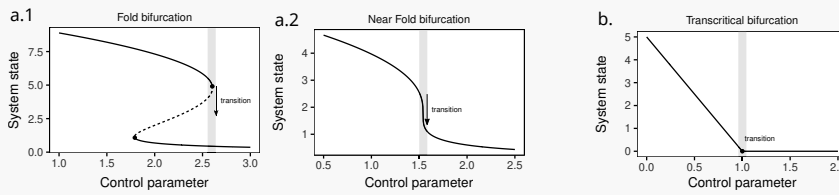
$$PLR = \frac{\log(x_{max}) - \log(x_{min})}{\log(x_{max}) - \log(x_{smallest})}$$

where $x_{smallest}$ represents the smallest and x_{max} the largest patch size observed in the dataset. This metric is expected to decrease as the ecosystem becomes degraded.

It is noteworthy that the interpretation of the expected trends in patch-based EWS depend on the underlying ecological mechanisms generating the patterns; these have been particularly well studied in drylands (Rietkerk *et al.*, 2004; Kéfi *et al.*, 2011; Manor & Shnerb, 2008). Therefore, as for all the other EWS, their use without a good understanding of the ecological mechanisms driving spatial structure could lead to misinterpretations of the trends, since altered or even opposite trends can be observed, both in empirical (Weerman *et al.*, 2012) or model systems (Pascual & Guichard, 2005; Schneider & Kéfi, 2016).

2.3 WORKFLOW AND EWS COMPUTATION

Because working with spatial EWS can be challenging and error-prone, we provide a workflow for the R package ‘spatialwarnings’ to make this type of analyses more accessible and reproducible. Our workflow allows computing EWS from raster data, typically from re-



A behavior of interest in ecological systems are discontinuous transitions via Fold bifurcations (May, 1977; Noy-Meir, 1975), where the prediction of the proximity to a critical point is particularly relevant. In this case, the system of interest has alternative stable states over a range of values of the control parameter (upper and lower solid lines in panel a.1; e.g. high vs low vegetation cover in a rangeland), separated by an unstable equilibrium (dashed line in panel a.1). If a change in the control parameter (e.g. grazing intensity) pushes the system state across the critical point (black dot), the system exhibits a ‘catastrophic shift’ (black arrow) and collapses from its current state (e.g. high cover) to the other one (e.g. low cover).

These transition arise because of the presence of strong positive feedbacks. They can sometimes be present, driving the system close to Fold-bifurcation-type dynamics and leading to a non-linear response, but not strong enough to produce a discontinuity (panel a.2) (Kéfi *et al.*, 2013). Other types of critical points exist without wide shifts in ecosystem states, such as in the case of *transcritical* bifurcation (panel b), for which the typical example in ecology would be the extinction of a species (Clements & Ozgul, 2016; Drake & Griffen, 2010).

In all these cases, EWS are expected to reflect the approach of critical points (panels a.1,c) or upcoming threshold of nonlinear response (panel a.2). See (Boettiger *et al.*, 2013; Boettiger & Hastings, 2012; Boerlijst *et al.*, 2013; Hastings & Wysham, 2010; Kéfi *et al.*, 2013; Dakos *et al.*, 2012; Kéfi *et al.*, 2014) for further discussions about the use and interpretation of changes in EWS.

Box 2.1: Three examples of ecological system responses where EWS can be useful

mote sensing imagery. All tools and example datasets are provided by the associated package ‘spatialwarnings’.

The package can compute three types of EWS as earlier defined: generic EWS, spectrum-based EWS, and patch-based EWS. For each
 5 one, a high-level function returns a suite of spatial indicators. Usual basic functions (`plot()`, `summary()`, etc.) can be used to display the results. Lower-level functions, prefixed by `indicator_` are also offered to compute raw values of individual indicators.

The workflow comprises four steps: (i) prepare the data and check for
 10 periodicity, (ii) compute the EWS from a list of matrices, (iii) assess their significance compared to a random spatial structure, and (iv) display the results (Figure 2.1).

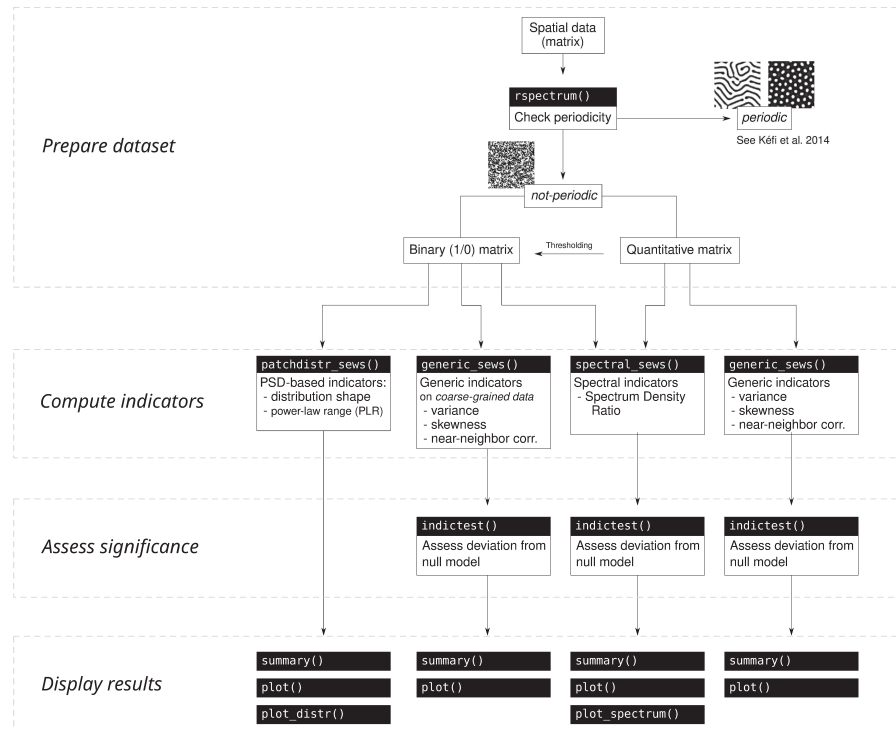


Figure 2.1: 'spatialwarnings' workflow. Black headers indicate the relevant package functions for each step.

In R, 'spatialwarnings' can be installed from CRAN and loaded using the following commands:

```
install.packages("spatialwarnings")
library(spatialwarnings)
```

5 2.3.1 Preparation of input data and periodicity checks

Typical raster data, e.g. from airborne or satellite-based remote sensing imagery, often come as image files with multiple bands. These images can be read in R using standard packages (e.g. 'tiff', 'jpeg') to obtain an array (a three-dimensional set of values), or a more complex raster object (package 'raster'). Indicator functions of the package work on matrix objects, the common denominator of all these data types. A conversion of a multi-band raster object to a matrix object is often required before computing EWS, a procedure that depends on the type of data, the system of interest and the questions addressed (see Appendix 3 and e.g. Liu & Mason (2016) for a more complete reference). In what follows, we assume that the data have been transformed into a matrix object, *i.e.* a raster surface of a single variable.

As with many spatial analyses, the resolution of the raster data should be such that it appropriately captures the scale of the changes in the spatial structure. For example, if the scale of the spatial structure is small, a coarse raster image may not be able to capture its variations.

5 In general, using prior knowledge or carrying out preliminary analyses at different scales when the data is available (Lam & Quattrochi, 1992) can help guide the choice of resolution. In addition, the input raster image must be large enough so that the spatial characteristics measured by the indicators are accurate. Subsetting the input data,
10 where possible, could provide a way of estimating measurement errors.

The indicator functions can also operate on lists of matrices to directly obtain trends. This can be the case when one does not only have a single image of the system under study but several ones corresponding to different moments in time or to different instances of a
15 given ecosystems along an environmental gradient. All indicators can be computed on matrices containing binary (boolean, TRUE/FALSE) data, but some of them can also be computed on continuous (numerical) data (Figure 2.1). A continuous matrix can be transformed into
20 a binary matrix by thresholding or classification. However, this transformation needs to be done carefully depending on the ecological context of the data and is therefore left to the user.

Once a suitable matrix object is obtained, it is necessary to identify whether the spatial structures in the matrix are periodic or not (Kéfi
25 *et al.*, 2014). Some ecosystems, such as patterned bushes in the Sahel, show characteristic changes in spatial periodicity along degradation gradients (Rietkerk & van de Koppel, 2008), which mask the expected increase in EWS before critical points (Dakos *et al.*, 2011). To identify whether an ecosystem shows periodic patterns, a solution is to detect
30 possible modes in the r-spectrum of the image (Appendix 2, Coutron (2002)). The absence of strong modes in the r-spectrum of the input matrices means that the patterns are not periodic and that EWS provided by ‘spatialwarnings’ can be computed (Kéfi *et al.*, 2014). Specific indicators exist for periodic ecosystems (Deblauwe *et al.*, 2011)
35 and may be part of a future ‘spatialwarnings’ release.

2.3.2 Generic EWS

To illustrate the quantification of generic EWS using the ‘spatialwarnings’ package, we reproduce here an analysis performed by Eby *et al.*

(2017) on remote sensing imagery. In this study, the authors used remotely-sensed images along gradients of increasing annual rainfall. The aerial images, stored in the R object `serengeti` were preliminarily classified so that TRUE values (pixels in the image) represent grassland areas and FALSE values represent woodland areas. The transects document the shift of the ecosystem from a grassland to a woodland state around an annual rainfall of 730mm/year. The object `serengeti.rain` contains the rainfall values for each matrix.

Generic EWS – variance, skewness and near-neighbor correlation (as measured by Moran’s I) – can be computed using the `generic_sews()` function. However, the computation of these indicators differs depending on the data type.

When working with binary data (TRUE/FALSE values), variance and skewness only reflect the proportion of TRUE values in the data and do not depend on the spatial structure (Kéfi *et al.*, 2014). Coarse-graining has been shown to be a useful procedure to make these indicators actually reflect the spatial patterns (Sankaran *et al.*, 2017a). This procedure divides the input matrix of size $N \times N$ (for a square matrix) into submatrices of size $s \times s$. The average of the pixels is taken in each submatrix, thus producing a $N/s \times N/s$ matrix with continuous values. Even when a matrix already contains continuous values, in some cases, coarse-graining may nevertheless be required to correctly compute EWS, and is therefore provided optionally. Sankaran *et al.* (2017a) provides more details on the procedure and on the choice of coarse-graining length.

Note that, in the package, coarse-graining is only included by default in the computation of spatial variance and spatial skewness. Near-neighbor correlation can be forced to be computed on coarse-grained data using the `moranI_coarse_grain` option.

Using a subsample $s = 5$ as per Eby *et al.* (2017), we can reproduce their analysis using the following code:

```
serengeti.ic <- generic_sews(serengeti,  
                             subsample = 5,  
                             moranI_coarse_grain = TRUE)  
summary(serengeti.ic)
```

The significance of generic EWS can be assessed by comparing the observed indicator value to a distribution of values obtained from matrices with a randomized spatial structure. The generic function `indictest()` can perform this operation by permuting the position

of the cells in the matrix a great number of times (999 by default). To carry out this operation efficiently, much of the package is implemented in compiled code, and the package will use the global option `mc.cores` to carry out parallel processing.

```
5 serengeti.test <- indictest(serengeti.ic)
  summary(serengeti.test)
```

Calling the `plot()` function on `serengeti.test` displays the results of the computation (Figure 2.2):

```
plot(serengeti.test, along = serengeti.rain)
```

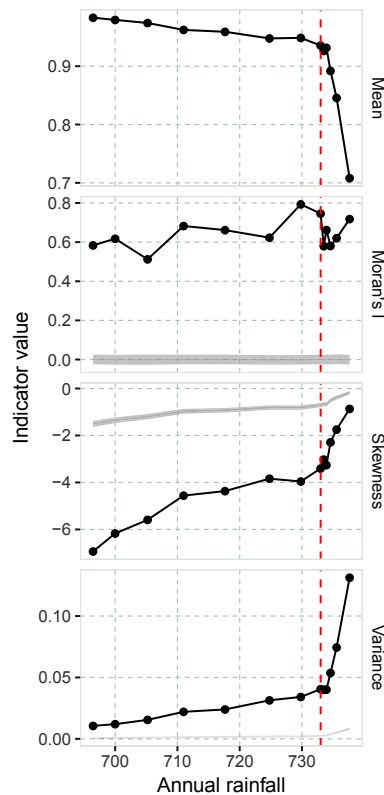


Figure 2.2: Generic EWS trends for the `serengeti` dataset (Eby *et al.*, 2017) along an annual rainfall gradient. This figure is produced by calling the `plot()` function on the output of `indictest()`. First row: mean value of each input matrix (here average grassland cover). 2nd-4th rows: the three generic EWS - variance, skewness and near-neighbor correlation (Moran's I). Black lines represent the observed values, and gray ribbons the 5%-95% quantiles of the null values (obtained by randomizing the spatial structure). The red line displays the value at which the ecosystem shifts from savannah to forest (added using `ggplot2`; see Appendix 1). The three indicators are found to increase prior to the shift.

2.3.3 Spectrum-based EWS

Using the same Serengeti dataset, we can compute spectrum-based EWS using the `spectral_sews()` function:

```
serengeti.spec <- spectral_sews(serengeti)
5 summary(serengeti.spec)
```

Similarly, the generic function `indictest()` can be used to test whether the observed values depart significantly from the null expectation of a matrix with random spatial structure. Calling the `plot()` method on the result of `indictest()` displays the SDR trend with the null expectation (Figure 2.3):

```
serengeti.test <- indictest(serengeti.spec)
plot(serengeti.spec, along = serengeti.rain)
```

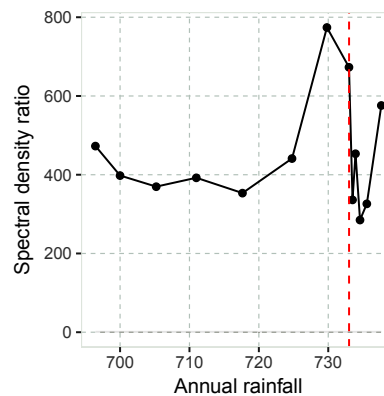


Figure 2.3: Spectral density ratio (SDR) trend along the gradient of annual rainfall in the `serengeti` dataset. The null distribution of SDR values is invisible because it falls within the width of the zero grid line. The red dashed line indicates the value at which a shift in vegetation cover occurs. SDR exhibits a sharp increase before the threshold value in rainfall.

Additionally, individual r-spectra can be displayed for each input matrix using `plot_spectrum()` (Supplementary figure 1):

```
15 serengeti.test <- indictest(serengeti.spec)
plot_spectrum(serengeti.test)
```

All observed r-spectra should show a near-monotonic decrease: a spectrum with a non-zero mode implies the presence of a periodic pattern in the matrix (Appendix 2), in which case the use of the generic and spectrum-based EWS can be unreliable (Dakos *et al.*, 2011; Kéfi *et al.*, 2014), while the shape and size of the patterns may provide more valuable information (Kéfi *et al.*, 2014).

2.3.4 Patch-based EWS

We showcase the use of the patch-based EWS on model data from a Forest Gap model by Kubo *et al.* (1996). In this model of forest spatial dynamics, spatial patterns emerge because of near-neighbor interactions between trees. The dataset, `forestgap`, contains the model outputs along several values of increasing stress, a list of a binary matrices in which TRUE values identify cells with trees. The data frame `forestgap.pars` contains the parameters used in the simulations (d , δ and α).

EWS can be computed using the `patchdistr_sews()` high-level function, for example using BIC as criterion to select the best-fitting distribution:

```
forestgap.patch <- patchdistr_sews(forestgap, best_by = "BIC")
```

The percolation status, patch distribution type and PLR can be displayed as text using `summary()`, or as a graph using `plot()` (Figure 2.4):

```
summary(forestgap.patch)
plot(forestgap.patch, along = forestgap.pars[, "d"])
```

The individual distribution fits can be shown using `plot_distr()` (Figure 2.5):

```
plot_distr(forestgap.patch, along = forestgap.pars[, "d"])
```

2.4 CONCLUSION

Remote-sensing imagery now provides outstanding data sets for ecological analyses, both in terms of spatial and temporal coverage. Satellite imaging archives extend back several decades (e.g. Landsat archive since 1972), and newer programs bring improvements in spatial resolution (e.g. 0.31m for the commercial program WorldView), as well as temporal frequency (e.g. every five days for the freely-available Sentinel archive). This data proliferation makes EWS-based approaches essentially applicable to any ecosystem on the planet. Combined with a good understanding of the process scale and its ecological underpinnings, it could eventually allow mapping ecosystem degradation or recovery trends across large spatial extents.

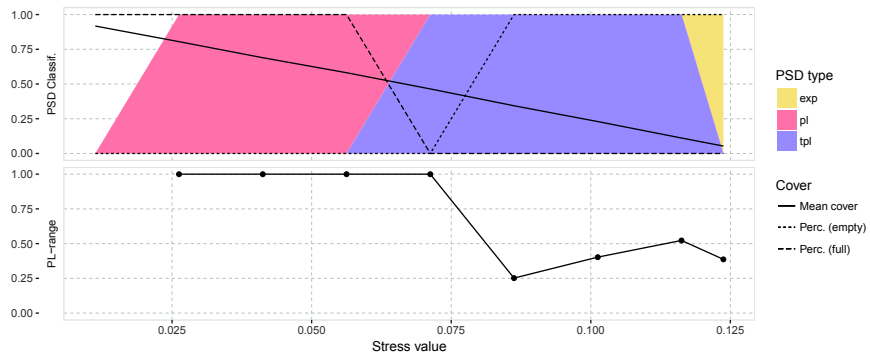


Figure 2.4: Outcome of the `plot()` function called on the output of `patchdistr_sews()`. The upper panel indicates the best fitted PSD and shows whether there is percolation (presence of a spanning cluster) of full (TRUE) or empty cells. Mean cover is displayed as a continuous line. As stress increases, best-fit of PSD switches from a power-law (pl) with percolation of full cells, followed by a truncated power-law (tpl) and an exponential (exp) with percolation of empty cells. The bottom panel shows PLR decreasing along the stress gradient.

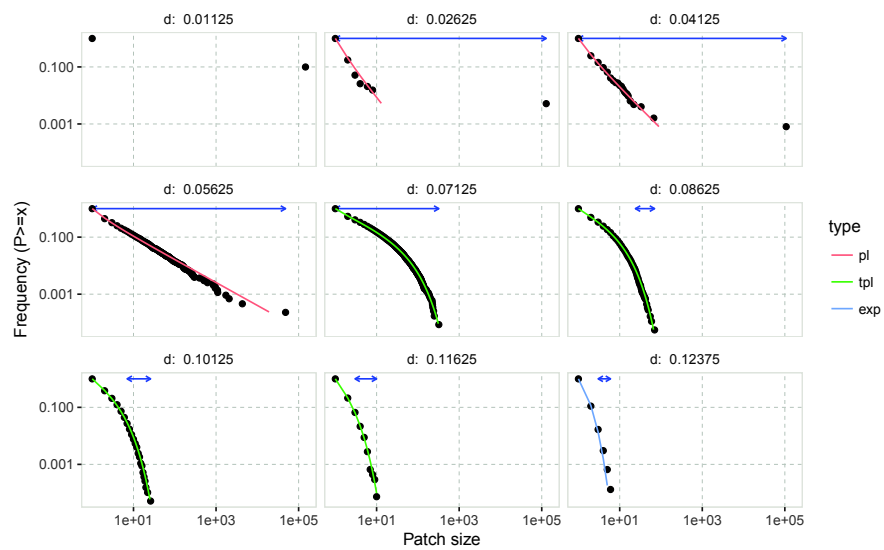


Figure 2.5: Individual PSD fitted to each matrix of the forestgap dataset. As stress increases (top to bottom and left to right), the truncation of the PSD increases and the shape of the best-fitting distribution goes from a power-law (pl), to a truncated power-law (tpl) and an exponential (exp). Along the same gradient, the PLR decreases (represented by the blue double-headed bar on top of each panel).

The ‘spatialwarnings’ package lowers the threshold for conducting state-of-the-art spatial pattern analysis from spatial ecological data and enables a wide exploration of spatial metrics as predictive tools for critical transitions. It is released under a permissive open-source
5 MIT license and invites new indicators, bug reports and other contributions through its git repository <https://github.com/spatial-ews/spatialwarnings>. We hope that its publication will motivate further research to address the ground-truthing of spatial EWS and contribute to the identification of robust measures of ecosystem degradation.
10 tion.

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AG contributed most to the package development, with significant contributions from all other authors. All authors contributed substantially to discussions and writing of the manuscript.
20

THE RESPONSE OF HERBACEOUS PLANT-PLANT ASSOCIATIONS ALONG A BIOTIC STRESS GRADIENT

5 CONTEXT

Many interaction networks exhibit patterns that affect the resilience of the whole community. For example, in some plant communities (Verdú & Valiente-Banuet, 2008), the fact that interaction are nested may prevent species extinctions and maintain a higher diversity. A
10 dominant role of facilitation in a given community has also been identified as the potential source of sharp responses to increase in stress, because they are a necessary condition for positive feedback loops (Kéfi *et al.*, 2016). Identifying whether the dynamics of a community are more dominated by competition or facilitation could thus
15 inform greatly about the potential response of a given vegetation community to perturbations (Callaway, 2007). This is one of the reasons why, since the late 90's and early 2000's, much work has focused on measuring the relative importance of competition vs facilitation in vegetation communities.

20 We contribute to this debate using a relatively new approach based on co-occurrence networks, and describe the variations of the competition/facilitation balance in vegetation communities of La Crau (France) along grazing gradients.

This work is based on vegetation surveys carried yearly during
25 along the course of this PhD program (springs of 2016, 2017 and 2018, and fall of 2017 for soil sampling), totalling an approximate amount of 4 months of field work. It was carried out in collaboration with Thierry Dutoit at *IUT d'Avignon*, along with Axel Wolff and Laurent Tatin from the *Réserve Naturelle des Coussouls de Crau*.

3.1 INTRODUCTION

In many plant communities, much work has shown the fundamental effect of inter-specific interactions on the response of the community to perturbations (Verdú & Valiente-Banuet, 2008). This concerns not only competitive interactions, but also positive interactions. For example, in semi-arid communities, nurse effects are prevalent, in which a bush promotes the recruitment of other herbaceous species under its canopy (Valiente-Banuet & Ezcurra, 1991; Horton & Hart, 1998). Such facilitative effects have been suggested as the drivers of shift-like and irreversible responses of plant communities to perturbations (Kéfi *et al.*, 2007). Knowing where and when facilitative interactions are predominant in a community could inform greatly about its potential response to perturbation.

Species interactions can change along environmental gradients, either directly or as the result of species turnover. For example, a general result seems to be that interactions between plant species tend to be facilitative in abiotically-stressed environments, but switch to competition in less-stressed environments. This result was coined as the Stress-Gradient Hypothesis (SGH) two decades ago (Bertness & Callaway, 1994; Callaway *et al.*, 2002), then further refined by later studies to include different type of stressors and plant strategies (Maestre *et al.*, 2009). For example, the net interaction between a pair of plants can be altered by the presence of herbivores (Smit *et al.*, 2009). Associative protection can arise in grazed conditions, an interaction in which a plant benefits from protection against herbivores due to the repulsive effect of unpalatable neighbors (Baraza *et al.*, 2006; Graff & Aguiar, 2011; Le Bagousse-Pinguet *et al.*, 2012). Typical functional traits leading to decreased palatability are the presence of thorns (Plate 5) or leathery leaves. Variations in a given interaction between two species can thus arise as a result of changes in the nature and strength of stressors, and the combination of their traits.

Because the dominance of positive or negative interactions in a given plant community may determine strongly its performance and dynamics (Callaway, 2007), many studies have aimed at evaluating the relative importance of these interactions in natural communities (Brooker *et al.*, 2008). However, many only consider the variations of pairwise interactions among a limited set of species (e. g., Holthuijzen & Veblen, 2016; Graff & Aguiar, 2011), because the number of pairwise experiments required to measure interactions among a diverse

set of species is very high. Yet even when they are carried out, pairwise experiments may be insufficient to characterize accurately interactions that occur in a natural community (Engel & Weltzin, 2008), because of e. g. indirect effects (an interaction between a pair of species is altered by the presence of another). Predictions from the SGH at the community level have also not always matched what is observed at the species-pair level (Soliveres *et al.*, 2014), because a given stressor may have different effects on each species in a community (Soliveres *et al.*, 2015). As a result, to date, no consensus exists on the main drivers of positive and negative interactions in vegetation communities, despite its central role in community assembly and successional dynamics (Cramer *et al.*, 2008; Verdú *et al.*, 2009).

Recent work has suggested that the observed co-occurrence of a pair of species in a given community could be used as a proxy for the effect they have on each other, i.e. their interaction (Saiz & Alados, 2011). The underlying assumption is that, given a constant abiotic environment, a positive interaction between two species should produce a spatial pattern of aggregation between the individuals of these two species. Conversely, a negative interaction is expected to produce a pattern of segregation. Although co-occurrence-based analyses have shown mixed success in accurately predicting pairwise interactions in general (Barner *et al.*, 2018; Freilich *et al.*, 2018), they have been shown to have some success in predicting community-level properties such as the balance between negative and positive interactions (Barner *et al.*, 2018). Some studies have also suggested that associations could highlight shifts in the processes driving community-assembly (Lyons *et al.*, 2016; Levy & Borenstein, 2013). In addition, the equivalence between spatial aggregation and facilitation has been shown experimentally in plant communities (Graff & Aguiar, 2011). Spatial pattern analyses thus appear as a promising avenue to contribute to the debate over the relative importance intensity of facilitation vs. competition in natural plant communities.

Previous work based on this approach has shown that associations varied according to changes in grazing pressure. In grazed systems, the balance between positive and negative associations can be driven by associative protection, in which a plant's mortality due to grazing is reduced because of unpalatable neighbors. This is expected to produce a unimodal pattern of variation of positive associations (Graff & Aguiar, 2011), where associative protection dominates at intermediate levels of grazing, but is absent when grazing is either low (competi-

tion between plants dominate) or very high (disturbance is too high for interactions to be observed, or associative protection disappears). This pattern has been observed in positive associations (Saiz & Alados, 2012), but given the fact that associations also tend to vary with
5 aridity (Holthuijzen & Veblen, 2016; Alados *et al.*, 2017; López *et al.*, 2013), its generality may be questioned. Other work has also shown that interactions could switch from facilitative to competitive because of grazing, as a result of morphological adaptation (Suzuki & Suzuki, 2012), diminishing the potential role of positive interactions in grazed
10 contexts.

No consensus exists yet on how the relative importance of competition and facilitation responds to grazing, leaving a general uncertainty on the effect of stress on the organization of vegetation communities, beyond the sole change in species composition. In addition,
15 despite authors suggesting that facilitation could also be strong in more mesic environments (Holmgren & Scheffer, 2010), few studies have focused on the latter. Yet such studies could help understand better the prevalence of facilitation in communities, moving away from nurse-plant asymmetric facilitation and more towards symmetric fa-
20 cilitation (where two plants facilitate each other but have similar life-forms, Gallien *et al.*, 2018), and set a reference for studies carried out in stressed environments.

To contribute to filling this knowledge gap, we investigated the variations of the positive/negative association balance, this time in a
25 more mesic, Mediterranean environment: La Crau, France (mean annual rainfall: 540mm). Contrasting with many previous studies, our work focuses on the variations of associations in herbaceous communities composed in majority of annuals (which are often ignored in association studies, e. g. Soliveres *et al.*, 2014). We investigated whether
30 the variations of positive and negative associations matched previous expectations based on the importance of associative protection, i. e. whether there was a unimodal relationship in positive associations along the grazing gradient, and how the community-scale balance between positive and negative associations varied along the gradi-
35 ent. We also investigated the species-level association balances (i. e. whether species tend to engage in more negative or positive associations) to interpret the variations in community-scale trends.

3.2 METHODS

DESCRIPTION OF LA CRAU La Crau is a Mediterranean semi-arid grassland located in the south of France (Bouches-du-Rhône), whose vegetation has been shaped by sheep grazing for at least 2000 years (Henry *et al.*, 2010). For this reason, a diverse community of herbaceous plants is maintained (on average 30 ± 12 species/m² in this study, mean \pm s.d.), with a species composition that varies depending on the grazing pressure. All vegetation is herbaceous with very few perennial higher shrubs, leading to a typical steppe-like visual aspect (Plate 1).

Grazing in La Crau is centered around numerous sheepfolds (pens for sheeps) spread out in the steppe, where sheeps are gathered at night. Sheep activity is most intense around the sheepfold and decreases with the distance from the sheepfold. This results in local changes in the identity and diversity of vegetation communities in an otherwise continuous "Coussoul"-type community (Molinier & Tallon, 1950), dominated by the perennial grass *Brachypodium retusum* (Plate 4). Ruderal nitrophilous plants are most abundant close to sheepfolds, and decrease in abundance as distance to the sheepfold entrance increases. This very-well defined gradient constitutes an ideal setting to test the influence of grazing (and other stresses associated with grazing, such as trampling and redistribution of nutrients) on the associations of vegetation communities.

SURVEYS We selected six sites, i.e. six sheepfolds, for sampling that were spread out in the studied area (Figure 5.6), and displayed typical vegetation turnover as a response to grazing.

We first carried out a quadrat-based survey to document the variations of species covers along the grazing gradient. Each quadrat had an area of 1x1m and was subdivided into a grid of 25 subquadrats (20x20cm each), in which the presence/absence of each species was recorded. The first quadrat was placed as close as possible to the entrance of the sheepfold, avoiding any local disturbance not related to grazing (e.g. presence of a dirt road). The spacing between quadrats followed a geometric series, i.e. the second quadrat was placed at $d_2=2m$ from the first in a general south-east direction (maximal direction of extension of the gradient), then subsequent quadrats were placed such that $d_{n+1} = b * d_n$ where b was between 1.2 and 1.5 depending on the site (Appendix 2). Adjustments in the quadrat spacing or

in the general direction of the transect were made to avoid local disturbances unrelated to grazing.

Computing species spatial associations requires measuring the spatial structure of plant communities at different levels of grazing pressure. In La Crau, the local grazing pressure (i. e. the number of sheep-time/ha) is known to decrease with the distance from the sheepfold, although its exact value has not been determined for most sites. Previous studies (Dureau, 1997) suggest it decreases as the inverse of distance. In the current absence of a quantitative measure of the grazing pressure, we used an indicator-species-based approach to choose the distances at which the spatial structure was documented. Because previous work identified four vegetation "belts" that differ in species composition around sheepfolds (Molinier & Tallon, 1950), we based the spacing of our transects on this classification to make sure we documented a wide range of grazing levels. In a 5x3m area around the quadrats described above, we considered the presence and absence of 16 indicator species known to reflect each vegetation type (taken from Molinier & Tallon (1950) and Gomila (1987)). This allowed us to identify in space where each community type occurred. We then laid out two replicate transects in each vegetation type, separated from at least 10m but no more than 75m so that the local vegetation was under similar levels of grazing pressure.

We documented the spatial structure of vegetation communities using 5 meter-long transects. Each start point and direction of transects were chosen randomly by throwing a pen. For each transect, we laid out a measuring tape, and recorded the length over which every plant individual or part of an individual overlapped to a precision of 2mm (Plate 9 and 10). Positions were determined with an accuracy of 2mm, as estimated from repeated measurements, mainly due to parallax errors when recording plant intersections. For each plant part surveyed, a class of height was also recorded, on a scale ranging from 1 to 5 (classes bounds of 0/2/5/10/20/>20 cm). We also recorded along transects the intersections of pebbles, which drive to some extent the distribution of some species. For example, tillers of *Brachypodium retusum* tend to resprout from under pebbles, leading to a possible increased spatial association between them. However, we did not include the pebbles in the following analyses as we were interested in the associations between plant species.

We replicated this survey in the surroundings of 6 different sites (each site comprised one sheepfold). Because in some sites, some veg-

etation types ("belts") were absent or impossible to identify, not all belts could be documented for every site. Surveys were carried out during the plant growing season (Apr 15 - June 10) which is the time of the year where 80% of species can be detectable and identified (Bourrely *et al.*, 1983), during years 2016 and 2017. This period was included within the grazing season (February - June). Because the structure of plant communities can change along the grazing season, we made sure to distribute the surveys randomly in time.

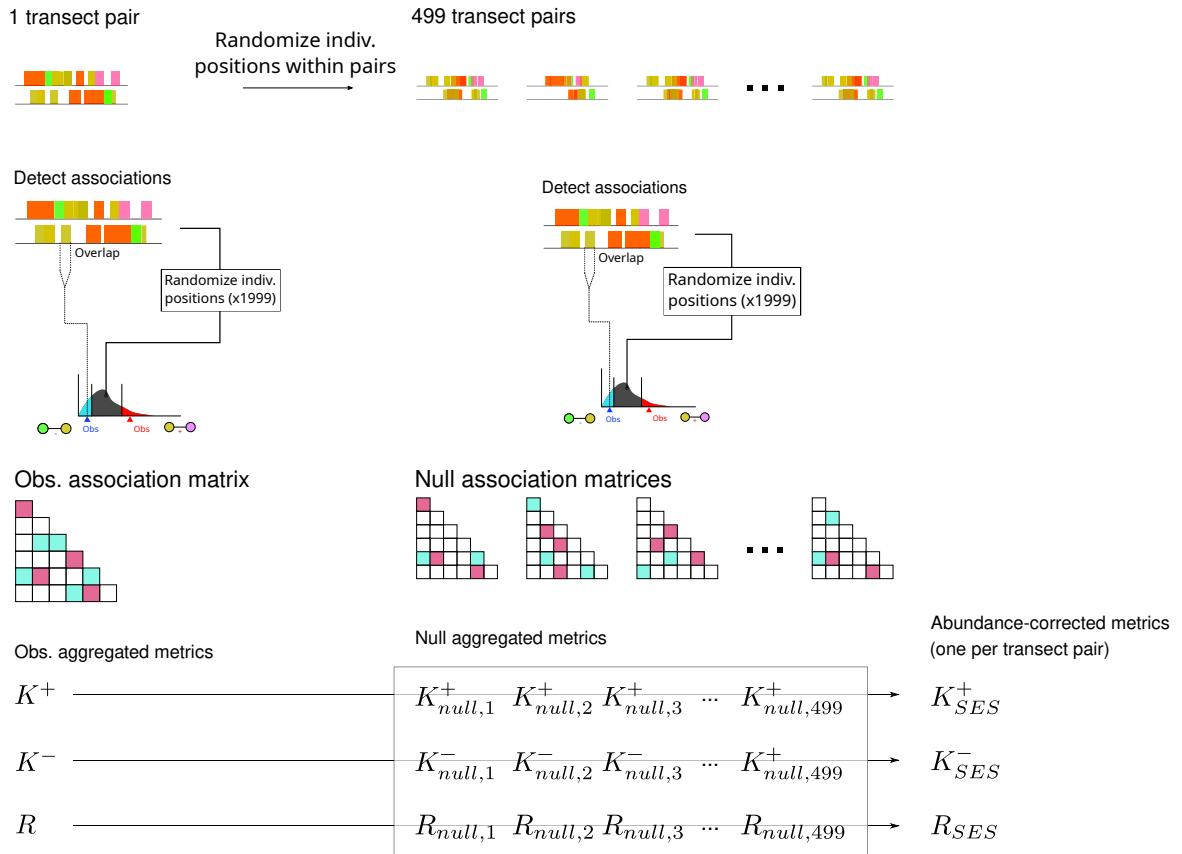


Figure 3.1: Workflow of the association analysis for community metrics. For each pair of transects, outlying associations are detected, which produces an association matrix of $S(S + 1)/2$ coefficients for S species, and three raw community-scale metrics K^+ (percentage of positive links), K^- (negative links) and R (association ratio, see main text). The same analysis is carried out for 499 null transect pairs obtained through the randomization of the original transect pair. This creates a null distribution of community-level metrics, which are used to obtain the deviation of observed metrics to what is expected given the same species identities and covers but random spatial structure.

MEASURING ASSOCIATIONS We analyzed species associations using the transect data and a randomization-based approach. This ap-

proach involves computing a pairwise metric between species on observed data, and comparing it to a distribution obtained from the randomization of the spatial structure.

We computed associations by combining the two *replicate* transects within each vegetation belt, resulting in one set of associations for each pair of replicate transect. We used the total overlap between all individuals of a pair of species (or between individuals of the same species) along the two replicate transects as a measure of pairwise association. We then randomized the spatial structure by assigning to each individual a new, random position along one of the two replicate transects, and recomputed the overlap metric. By repeating this process 1999 times, this produced, for each species pair, a distribution of overlap metrics that depended only on the abundance of the two species in the dataset (Fig. 3.1). The observed total overlap can then be compared to this distribution.

Associations were classified into positive, negative or neutral by using a cutoff value α applied to the distribution. More specifically, a positive association was considered to occur within a pair of species when $1 - \alpha/2\%$ of the null distribution was below the observed value. Conversely, a negative association was retained when $\alpha/2\%$ of the null distribution was above the observed value (Fig. 3.1). For example, using a classic threshold of 5% ($\alpha = 0.05$), a positive association would be retained if the observed overlap was above 97.5% of the null distribution. In this study, we chose to display trends based on $\alpha = 0.25$, but as the choice of this cutoff may affect the results, we carried out a sensitivity analysis to make sure results were robust to a range of thresholds chosen. Given the abundance of all species found in the community and a chosen cutoff value α , this provides information about species that are significantly more frequently found close to each other than expected by chance (positive associations) and species that are less frequently found close to each other than expected by chance (negative associations).

COMMUNITY-SCALE METRICS For each pair of transects, this method yields a number of positive and negative associations, which can be viewed as a network where nodes constitute species and positive and negative associations are signed links between them. We summarized these networks into three community-scale metrics commonly used in association studies: (i) K^+ , the percentage of realized positive associations (out of all the $S * (S + 1)/2$ possible associations that may

be realized for S species¹), (ii) K^- the percentage of realized negative associations and (iii) the relative importance of each association type $R = (K^+ - K^-)/(K^+ + K^-)$ (Saiz *et al.*, 2017; Alados *et al.*, 2017; Arroyo *et al.*, 2015). R is zero when no positive nor negative associations
 5 are detected, and is equal to +1 or -1 when interactions are all positive or negative. In the literature, R has a similar form to the relative interaction index (RII), which has been shown to be a mathematically correct index to measure neighbor-effects (Díaz-Sierra *et al.*, 2017).

The probability of retaining a positive vs. a negative association for
 10 a pair of species varies with the total cover of the two species in the transect (Box 3.1), affecting the values of K^+ , K^- and R . The variations of the raw values of these indexes along a gradient may thus reflect variations in species abundances rather than true variations in plant associations. Abundances-corrected values of K^+ , K^- and R
 15 need thus to be obtained to correctly interpret the variations of associations along a gradient (Pellissier *et al.*, 2017; Tylianakis & Morris, 2017).

To do so, we devised a procedure to obtain a distribution of network-level metrics that reflected expected values given the same identity
 20 and species total covers, but random spatial structure. For each pair of transect, we created 199 'null' transects, with randomized positions of individuals along the transects (allowing mixing individuals between replicate transects). These transect pairs have the same species composition and covers, but associations derived from them only reflect the
 25 distribution of species covers. We then computed the standardized effect sizes of K^+ , K^- and R compared to this network-level null distribution, K_{SES}^+ , K_{SES}^- and R_{SES} as follows (i.e. Z-score; example given for the latter) :

$$R_{SES} = \frac{R - \mu_{R_{null}}}{\sigma_{R_{null}}} \quad (3.1)$$

where μ is the mean of the null distribution and σ is its standard
 30 deviation.

This allowed us to build a null distribution of community-scale metrics, and disentangle their variations due to changes in species covers from the true effect of the gradient. In what follows, we only present the raw variations of R along the grazing gradient for the

¹ Note that this is not $S(S-1)/2$, because our method also allows the detection of intra-specific associations

sake of conciseness, but show the variations of K_{SES}^+ , K_{SES}^- and R_{SES} .

In addition to the variations along the grazing gradient, we investigated the tendency of each species to engage in negative and positive associations. In a similar way to how we derived community-scale metrics, we used, for each species, the percentage of realized positive interactions S^+ (number of positive associations / total possible number of associations for this species) and negative interactions S^- . We then computed the ratio between the two as $(S^+ - S^-)/(S^+ + S^-)$.
As for community metrics, for each species, we corrected these values for species abundances by computing their standardized effect size compared to what was obtained from the null dataset. We compared the SES obtained for each species to the average height of the species (using the midpoints of the height classes) and the average total cover of the species in the transects where it was present.

Box 3.1: Detection bias in plant-plant association analyses

The probability of detecting a significant association (positive or negative) between two species varies with their abundances. To illustrate this, we can consider the simple situation of a transect containing two randomly-placed individuals of different species and identical size s , and consider the association that is retained between the two species depending on the observed overlap. This figure below has been obtained by placing 10,000 times at random two individuals of a given size along a transect, then computing the quantiles of the obtained distribution of overlap.

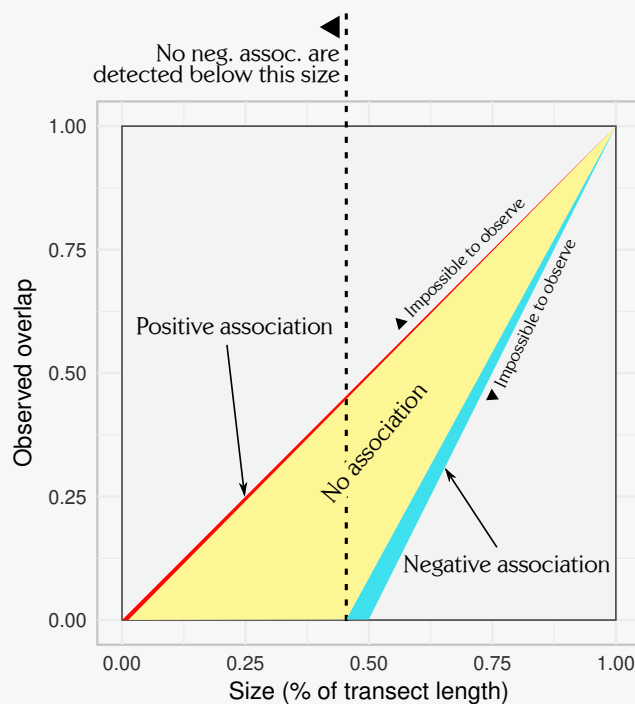


Figure 3.2 Type of association deduced from the observed overlap between two individuals of a given size (for $\alpha = 0.05$). Blue and red bands represent the fraction of the overlap distribution below 2.5% and above the 97.5% quantiles respectively. For a wide range of individual sizes, no negative association can be retained.

In this simple example, negative associations cannot be detected when the cover of the two species is moderately low (below 0.44% of the transect length), regardless of the value of the observed overlap. In other words, even if these two species do not overlap at all, we cannot conclude to a negative association. This arises because the 0.025 ($\alpha/2$) quantile of the null distribution intersects zero, and the overlap metric cannot be negative (as noted by Saiz & Alados (2012)).

As a result, in association networks, all negative associations between rare species are effectively "forbidden links", that can never be derived from data. This has two important consequences on association analyses.

Box 3.1: Detection bias in plant-plant association analyses (cont.)

First, the expected association ratio (R) under random assembly is not neutral (zero) but in fact biased towards positive associations (Figure 3.3), because most natural communities have few abundant species and many rare ones (Harte, 2011; Bazzaz, 1975). This could explain the oft-observed dominance of positive associations over negative ones in studies that do not correct for abundance (e. g. Saiz *et al.*, 2018, 2017; Alados *et al.*, 2017; Morueta-Holme *et al.*, 2016; Lane *et al.*, 2014)).

Second, because the distribution of abundances of species varies along gradients, the null expectation of associations numbers and ratios will vary accordingly, even in the absence of any biological effect. For example, an increase in rare species along a gradient can shift the association balance towards positive values, even with random spatial structure. It is thus necessary to compare the deviation of these aggregated metrics to what is expected given the distribution of species abundances, rather than their raw values (Pellissier *et al.*, 2017).

REGRESSION AND SENSITIVITY ANALYSES We used mixed-effect linear modeling to measure the variations of K^+ , K^- and R (and their abundance-corrected counterparts) along the grazing gradient. We modeled the response of one of the above variables as a linear function of the log of the distance with a normal error structure (e. g. for R , $R \sim a + b * \log(distf) + \epsilon$), and considered site-level random effects on the intercept and slope of the regression. We considered an uncorrelated random effect on the slope and the intercept because given the low number of data points, we could not obtain a relevant estimate of their correlation this correlation was sometimes be 1 and regression diagnostics could not be computed.

We carried out this regression procedure for different values of the association cutoff α and used bootstrapping to derive confidence intervals on the estimate of the slope.

All spatial analyses were carried out in R using custom procedures and the package 'lme4' (Bates *et al.*, 2015) for regressions.

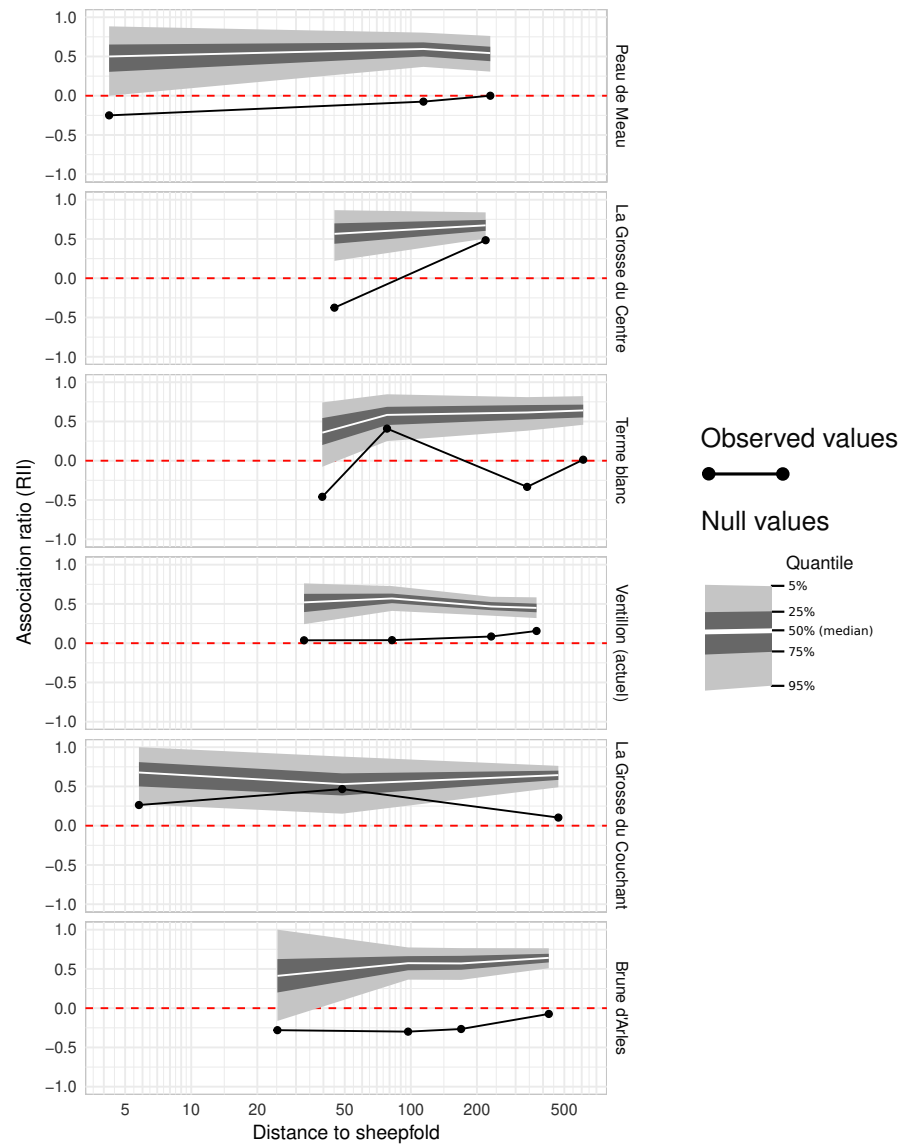


Figure 3.3: Variations of the raw association ratios R and its expected value given the species covers along the grazing gradient (measured by the distance to the sheepfold). Each panel corresponds to one surveyed site (along the rows). The raw association ratio showed mostly flat variations along the gradient, with values close to zero (same number of positive vs negative associations). The expected values of the ratio given the species covers and abundances were always positive.

3.3 RESULTS

Raw variations of R along the grazing gradient were mostly flat and close to zero, suggesting an apparent balance between negative and positive associations (Figure 3.3). This absence of trend was robust to the choice of interaction cutoff α (Figure 3.6) as the effect of distance on the raw ratio was non-significant for a majority of α values. However, null distribution of R values were generally positive along the gradient in all sites, and observed R values almost always below the expected null trends (Figure 3.3, ribbons). In other words, there was always relatively less positive associations than expected given the species richness and covers in transects.

This deviation from random expectation, measured by R_{SES} , changed with decreasing grazing intensity (Figure 3.4). Close to the sheepfold, R_{SES} values were close to the null expectation, while negative values were observed further from the sheepfold. Mixed-effect modelling showed that this decrease was significant for most of the cutoff values α selected (Figure 3.6).

This decrease in R with distance was underpinned by a decrease in the fraction of realized positive associations K_{SES}^+ , combined with an increase in negative associations K_{SES}^- (Figure 3.5). An excess of negative associations was always found, regardless of the grazing level (K_{SES}^- values were always positive). Positive associations were close to random in highly-grazed zones, and a deficit was observed in less-grazed zones (more negative values of K_{SES}^-). These trends were robust for most choices of α cutoff, except for extreme values of α (< 0.10 and > 0.875).

Per-species analyses of associations revealed that most species had a tendency to produce negative associations, as manifested by a negative SES in the association ratio (Figure 3.7). The association ratio of a given species was not significantly correlated to its average height (Kendall's $\tau = 0.041$, $P = 0.5$) but was negatively correlated with its cover when present in a transect (Kendall's $\tau = -0.44$, $P < 0.001$)

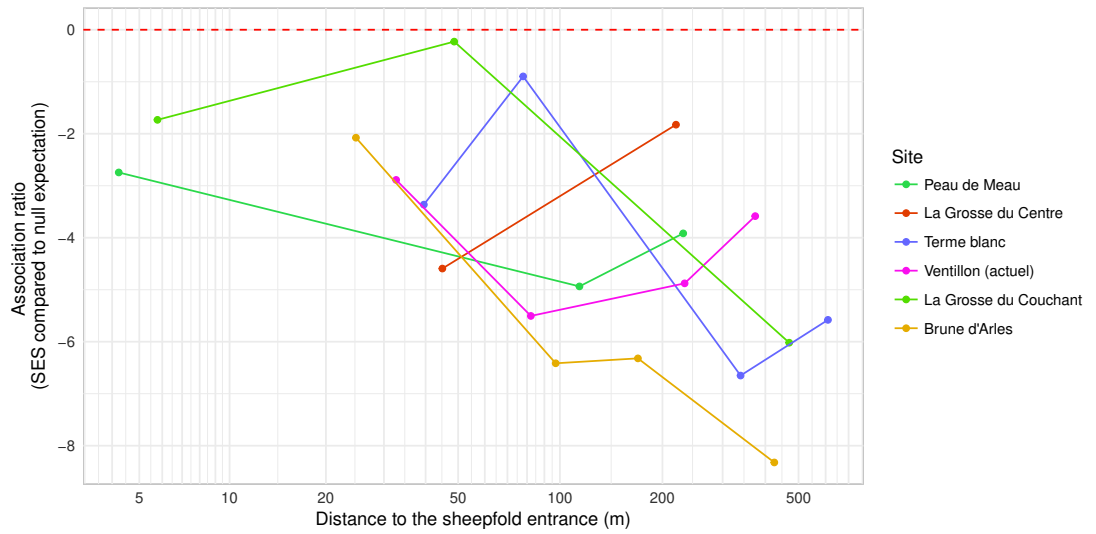


Figure 3.4: Variations in the SES of the association ratio R_{SES}^+ along the grazing gradient. A value close to zero indicates that the ratio value is fully explained by the species composition and covers of the given pair of transect. Negative values indicate a lower association ratio than what is expected given the species covers.

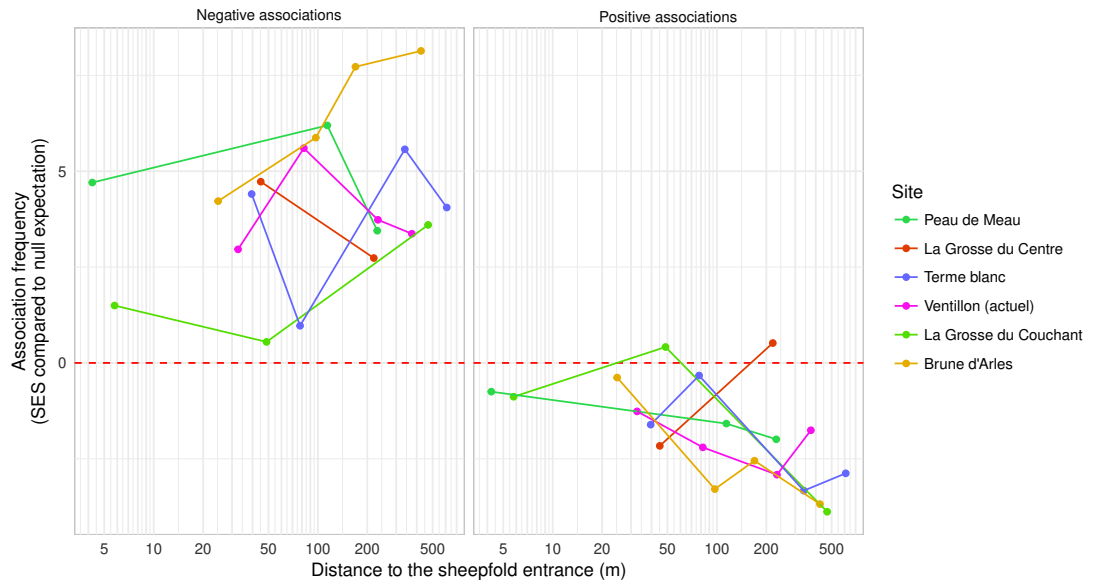


Figure 3.5: Variations in the SES of percentage of realized positive associations (K_{SES}^+) and negative associations (K_{SES}^-) along the grazing gradient. A value close to zero indicates that the observed number of negative and positive associations is close to its expected values given the species composition and covers. Negative (resp positive) values indicate a deficit (resp an excess) in the given type of interaction.

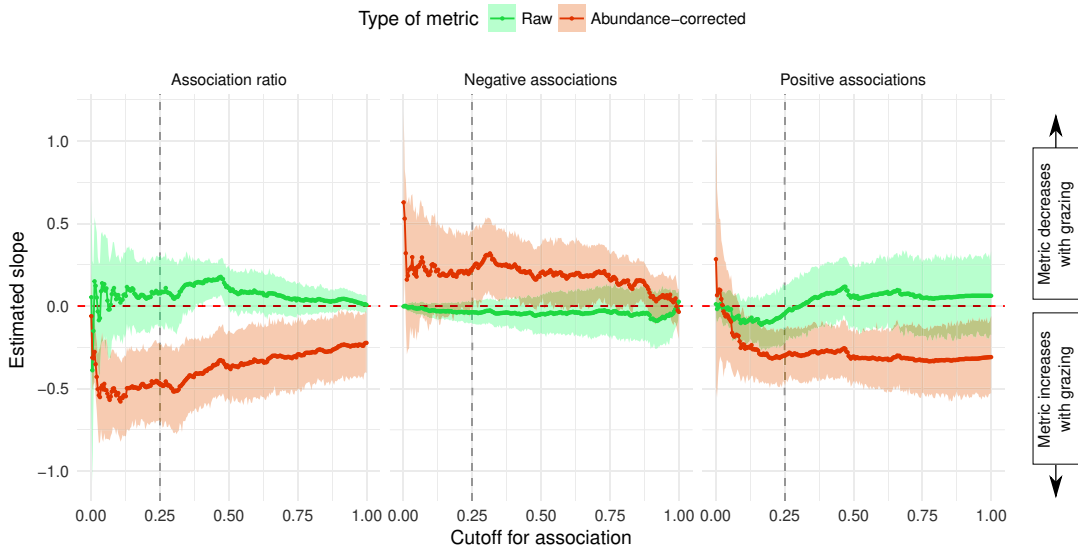


Figure 3.6: Coefficient of regression of the slopes of K^+ , K^- and R (green) and their abundance-corrected counterparts (K_{SES}^+ , etc.) along the grazing gradient (red), as a function of the association cutoff α . Ribbons indicate 95% confidence intervals. The grey vertical line indicates the chosen threshold for Figures 3.3, 3.4 and 3.5. A value close to zero indicates that the distance (i. e., grazing) has no effect on the pattern of association. Negative (resp. positive) values indicate that grazing increases the focal metric (resp. decreases). For example, the raw association ratio R does not significantly vary with grazing for almost all cutoff values (α), but its abundance-corrected version always increases with grazing.

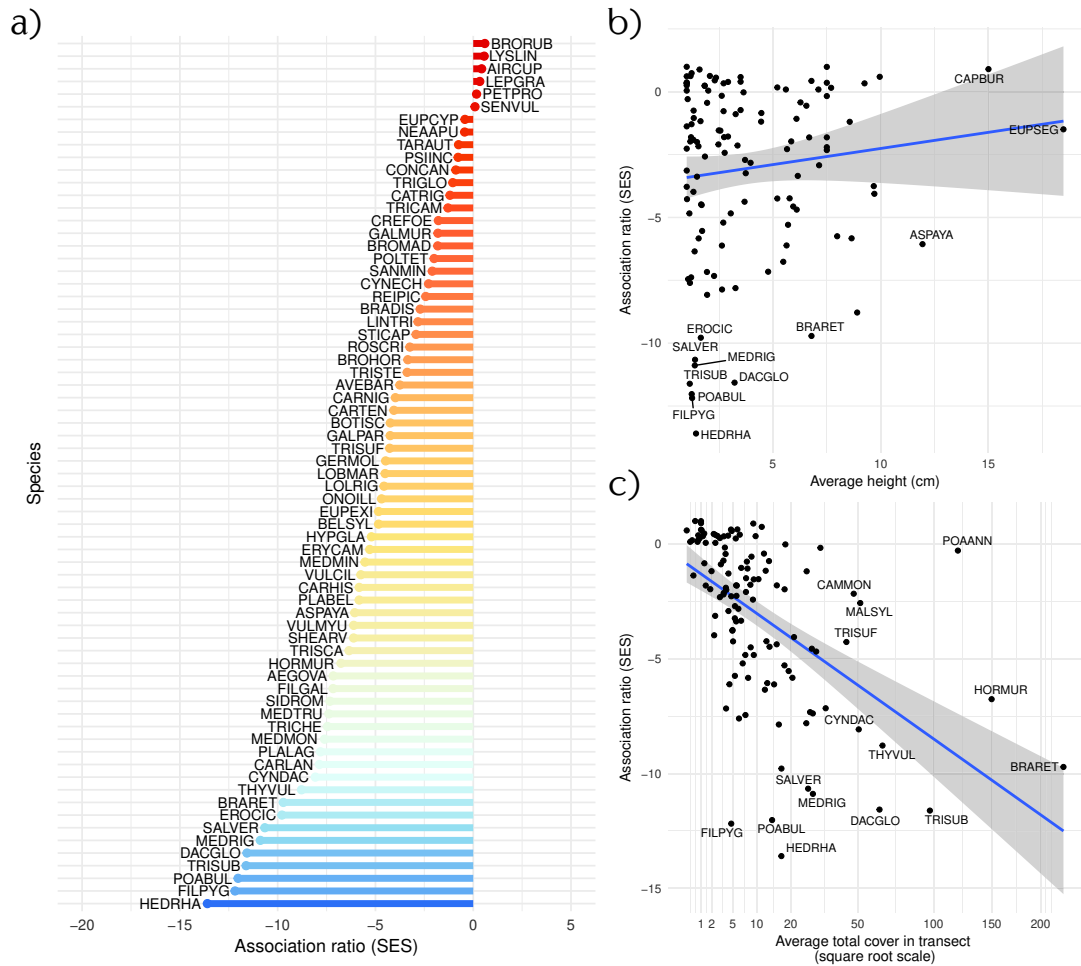


Figure 3.7: (a) SES of association ratio for each species (only species with at least 200 potential associations were included in this graph (see species codes in Appendix 1). (b) Relationship between the association ratio and the average height of the plant. (c) Relationship between the association ratio and the average cover of the plant in the transects where they are present.

3.4 DISCUSSION

ASSOCIATION TRENDS Using continuous transects documenting the spatial associations of individuals, we found non-random trends in spatial associations along a grazing gradient. Although an excess of negative associations was observed at all grazing levels, very highly grazed areas showed less associations between plants. In area with less grazing, the association balance was highly negative, due to a combined decrease in positive associations and an increase in negative associations.

The classical interpretation of plant-plant associations is that positive associations reflect facilitative processes between plants, while negative associations reflect competitive processes. This hypothesis is consistent with our results, as grazing is known to produce a shift from competitive plant strategies to ruderal plant strategies (le Priol, 2017). Far from the sheepfold, competition processes dominate the assembly of the communities, resulting in an increased number of negative associations. Close to the sheepfold, very high stress due to grazing favors ruderal plants with short lifespans (*Chenopodium* spp.) or adapted to frequent disturbance (e. g. *Malva sylvestris* with a deep taproot, *pers. obs*), resulting in a spatial structure that reflects less the effect of interactions and more the disruption of spatial patterns by recurrent disturbance.

How do these trends compare to other association-based studies? We found no unimodal relationship of positive associations along the grazing gradient (contrasting with e. g. Saiz & Alados (2012), although the difference may be explained by methodological differences). This is probably due to the fact that our study is based on the extremely grazed side of the gradient, thus only documenting the collapse of positive and negative interactions under high stress (Graff *et al.*, 2013). Evidence of associative protection can be observed in the field (Plate 5), but it did not occur frequently enough to be sampled by our systematic survey. The seemingly low presence of facilitative interactions could also be explained by the identity and morphological adaptation of species (Suzuki & Suzuki, 2012). Because of the long-term grazing, plants in La Crau are mostly herbaceous species, with no tall (> 30cm) woody shrubs engaging in asymmetric facilitation (Callaway, 2007, e. g. nurse syndrome). As such, species may show a different pattern of associations in communities where more shrubs are present. For example, e. g. *B. retusum* produces mostly neg-

ative associations in this study, but these are mainly positive in Saiz & Alados (2012).

We found that the most competitive plants in term of associations were also among the smallest (e. g. *Trifolium subterraneum*, Figure 3.7), and there was no significant relationship between the average type of association done by a species and its height. This suggests that the resource under competition in the less-grazed communities is not light (which would be manifested in a tendency for competitive plants to be higher), but rather space and/or local nutrients. This interpretation is reinforced by the fact that species with very low association ratios included cespitose grasses (e. g. *Dactylis glomerata*, *Brachypodium retusum*), or ground-covering species (e. g. *Trifolium subterraneum*, *Medicago rigidula*). Future analyses crossing trait data with association-based observations would certainly provide insight into the underlying mechanisms driving associations. In addition, our study only looks at above-ground processes, but underground processes could also explain the patterns.

METHODOLOGICAL ASPECTS In this chapter, we showed that strong variations of the association balance along the gradient were masked by variations of species abundances (Figure 3.3). This highlights the need to have community-scale null expectations when interpreting patterns of associations (Soliveres *et al.*, 2015, e. g.). In fact, since significance of patterns is only tested for the community-scale metrics (R , K^+ , K^-), any α cutoff could be considered at the species level, even one i. e. all associations are included to compute community-scale metrics).

Interestingly, the trends along the grazing gradient varied slightly with the choice of cutoff (Figure 3.6). This calls for systematic testing of the full range of α values (0-1) instead of focusing on a specific values (typically 0.05). In fact, different interaction types may lead to different strengths of associations. For example, using a modelling approach, it can be shown that competition for space produces an excess of weak negative associations (Box 3.2). Using different values as cutoff (or different ranges) may select different types of underlying interaction, whose trends along gradients could be different.

This work shows that association-based approaches can be useful to understand the dominant processes occurring in a community (e. g. competition, facilitation). Yet the link between pairwise interactions and spatial patterns remains not fully understood, i. e. which kind of

interactions give rise to which kind of spatial pattern. However, the recent rise of interest around co-occurrence methods (Morueta-Holme *et al.*, 2016) and network analyses (Graham & Weinstein, 2018; Delmas *et al.*, 2017), along with increasingly-exhaustive trait databases
5 (Tavşanoğlu & Pausas, 2018) may greatly enhance their potential.

Box 3.2: What interactions are captured by associations ? A modelling approach.

A quick look at the general distribution of association strengths in empirical data reveals that it follows no well-known distribution but has a complex shape.

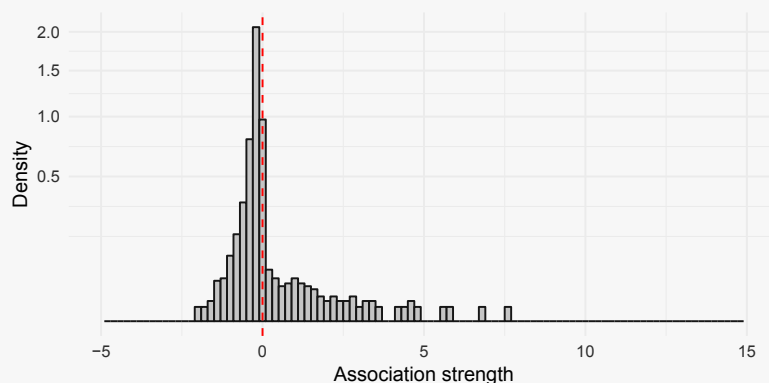


Figure 3.8 Empirical distribution of 1024 randomly-selected association strengths (i.e. the deviation of the observed total overlap between pairs of species to the mean of the random expectation, divided by the s.d. of the random expectation) The y-scale is non-linear (square-root transformation).

A notable feature of this empirical distribution is the excess of weakly negative association strengths. These associations could possibly represent a widespread and common type of underlying interactions. We used a modelling approach to investigate a possible mechanisms underpinning this pattern.

We devised an individual-based model, in which plant individuals are represented as discs that interact on a 2D plane. The details of this model are presented in Appendix 3. Each individual can affect the mortality and the probability of recruitment of a new individual in its neighborhood. In this model, we also included spatial preemption in part of the simulations. When it was present, propagules cannot access the ground under the canopy of other individuals, so no recruitment of new individuals is possible there. We ran a set of 100 simulations, with and without a space preemption effect, in communities of 20 species until equilibrium. At the end of the simulations, this model produces individuals distributed out in space.

Box 3.2: What interactions are captured by associations ? A modelling approach (cont.).

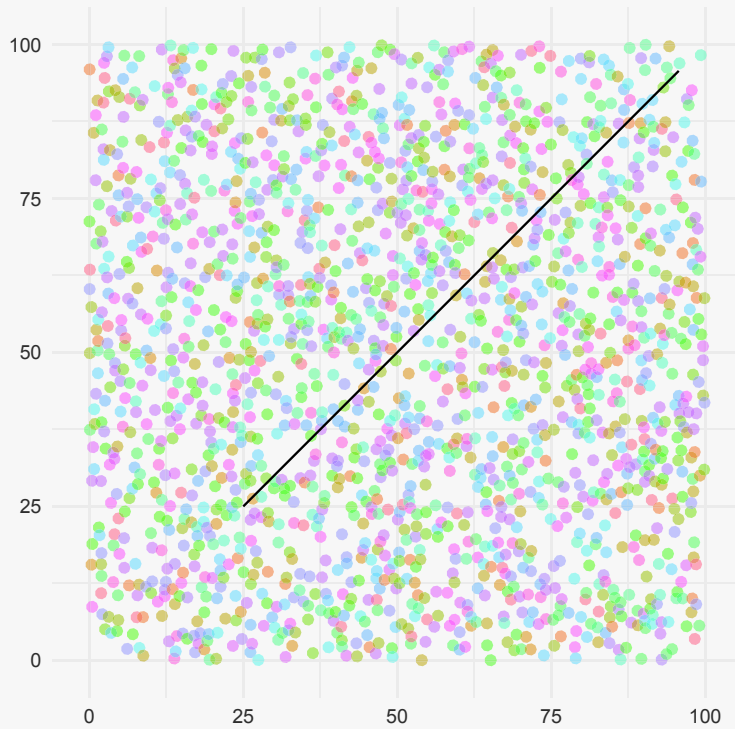


Figure 3.9 Example output of the model. Discs are individuals of different species (color). x/y axes represent dimensions in space. A "virtual transect" of length 100 is being represented with a black line.

Because this model is based on disc-like individuals in a continuous space, we measured associations between species by carrying out "virtual transects", which record the range over which individuals intersect a line. This provided us with the same type of data than what was recorded in the field, so we could carry out the same association-based analysis as what was done on empirical data. From these associations, we can then derive the general distributions of associations with, and without space preemption.

Box 3.2: What interactions are captured by associations ? A modelling approach (cont.).

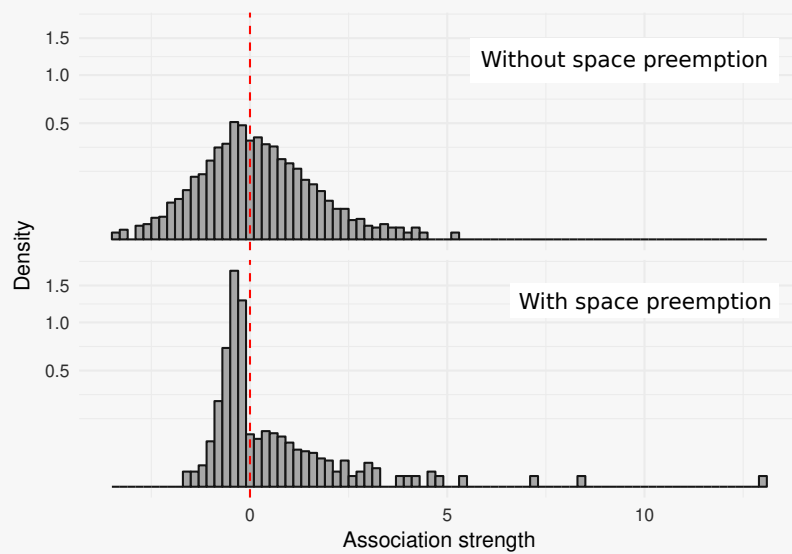


Figure 3.10 Observed distribution of 4096 association strengths from model data, with and without the effect of space preemption.

Adding the effect of space preemption produces a distribution of association strengths that is strikingly similar to what is observed in empirical data (compare with Figure 3.2). This suggests that competition for space appears – or another process limiting recruitment or survival under the plant canopies – appears as one of the main process explaining the distribution of observed associations.

THE RESILIENCE OF INTERACTION NETWORKS: INSIGHT FROM PLANT-PLANT ASSOCIATIONS

CONTEXT

5 As shown in Chapter 3, interactions can vary along gradients of biotic stress. In particular, we showed that strong disturbances produced a decrease in competition for space. This chapter focuses on the long-term temporal dynamics of interactions after the release of the biotic stress, i. e. the resilience of interactions. Very few studies have described the temporal variations of interactions (at local scale), and if
10 so it has often only be done for plant-pollinator networks (CaraDonna *et al.*, 2017; Olesen *et al.*, 2008). This work contributes to filling this gap by describing the temporal dynamics of plant-plant association networks. We focus in particular on a specific structural pattern of
15 association networks: the positive/negative association ratio.

To do so, we adopt a chronosequence approach and document sites that have been previously abandoned at known dates in time. La Crau has a long history of grazing, which allowed us to survey vegetation communities up to approximately 1,600 years after abandonment.
20 Current sites show a strong, established gradient of grazing centered on the sheepfold. After abandonment, the abandoned sites were still grazed but at much lower levels than originally, and without grazing intensity being spatially centered around the sheepfold. This leaves place for a recovery process of vegetation communities that we document here. This process is remarkably slow: Henry (2009) reports
25 that the vegetation was still significantly different from a reference, "Coussoul" community (where *B. retusum* predominates) 2,000 years after abandonment.

This work is based on vegetation surveys carried every year during
30 the course of this PhD (2016, 2017 and 2018, see also Chapter 3 and Appendix 2), with the invaluable help from many field assistants, researchers from the *IUT d'Avignon*, and staff from the *Réserve Naturelle des Coussouls de Crau*. This chapter is still a work-in-progress, and we describe here preliminary analyses of the data set that highlight the



Figure 4.1: The sheepfold Guillaume Orcel, which has been abandoned between 1968 and 1971 (Henry, 2009).

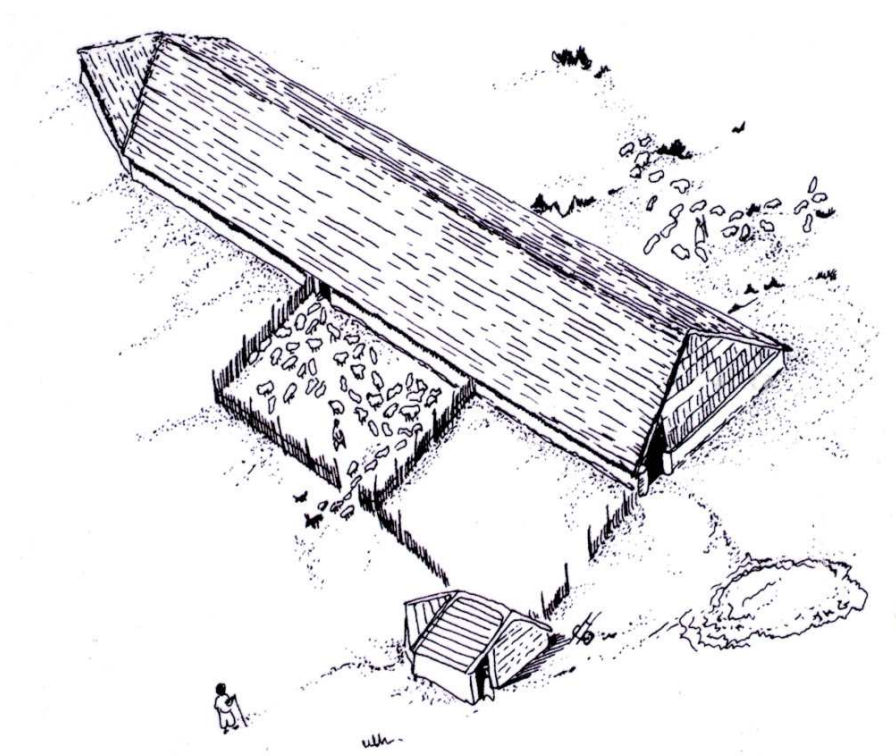


Figure 4.2: Artist depiction of a Roman sheepfold (image taken from an interpretative sign in Peau de Meau). See also Plate 8.

main variations of plant-plant associations and frame the chapter in the relevant literature context.

4.1 INTRODUCTION

Ecological systems are increasingly affected by anthropogenic impacts, leaving many communities disturbed, possibly with very different functioning than their pre-disturbance state. This is in particular the case for an increasing number of vegetation communities located in abandoned agricultural fields (Cramer *et al.*, 2008). Predicting the future trajectory of this type of communities requires understanding the relative importance of multiple community assembly processes (Meiners *et al.*, 2015). These processes determine whether the community will be naturally resilient and recover towards its original, pre-perturbation state (Ruprecht, 2006), or instead diverge and persist in another state through time (Suding *et al.*, 2004). For example, old crops can show an absence of recovery following abandonment, due to competitors impairing the recruitment of the original vegetation (Firn *et al.*, 2010). Disentangling how and where such biotic interactions alter the dynamics of vegetation communities – and their importance relative to other assembly processes – is thus invaluable to anticipate future changes.

Successional dynamics – understood here as the temporal trajectories of communities after a disturbance event (Hobbs & Walker, 2007) – provide an ideal setting to estimate the relative importance of these assembly processes through time after disturbance. A general expectation is that abiotic processes dominate the assembly of the community in the early stages after disturbance, while biotic processes such as competitive exclusion increase in importance in the later stages (Connell & Slatyer, 1977). However, many exceptions to this general trend can be found (e.g. Verdú *et al.*, 2009). For example, the recovery of many old fields is often limited by the low dispersal ability of native species (Fedriani *et al.*, 2018).

To test the relative importance of different assembly processes, recent correlative approaches have built on functional and phylogenetic community patterns (Garnier *et al.*, 2004; Meiners *et al.*, 2015). Where competitive processes are dominant, communities are expected to exhibit overdispersion, i.e. species in the community should be more distinct functionally and phylogenetically than expected through random assembly (Webb *et al.*, 2002; Macarthur & Levins, 1967). Functional and phylogenetic overdispersion – hence a possible increased role of inter-specific competition – has been found in late successional stages (Purschke *et al.*, 2013; Li *et al.*, 2015). Yet these approaches have

been criticized because the mechanistic bases of overdispersion remain debated (Cadotte & Tucker, 2017). These approaches also often ignore the possibility of plant-plant facilitation, which may change the expected successional patterns. For example, Verdú *et al.* (2009) documents a facilitation-based succession which shows phylogenetic overdispersion only in middle successional stages, and not in late-stages.

Progress towards a better mechanistic understanding of the drivers of succession – and in particular of the role played by biotic interactions – may come from applying new, independent approaches. In this work, by using a new approach based on plant-plant association networks (Saiz & Alados, 2011), we aim at describing how potential interspecific interactions vary along succession in plant communities. Association networks describe plant spatial relationships as part of a signed network. When two plants species co-occur more than expected by chance, a positive link is drawn between the two species. Conversely, a negative link is drawn whenever two species co-occur less than expected by chance. Positive and negative links are thought to reflect on average the sign of the interaction between the pair of species. Thus, the relative proportion of negative and positive links in a given association network could inform on the dominance of positive over negative interactions in a plant community. The variations of this interaction balance during succession may shed a new light on succession mechanisms, and in particular (i) provide an independent alternative to approaches based on functional/phylogenetic relatedness and (ii) include facilitation as well as competition in the relevant processes occurring along succession (Verdú *et al.*, 2009).

Association-based approaches are not devoid of criticism (Barner *et al.*, 2018; Freilich *et al.*, 2018). For example, some interactions may produce counter-intuitive associations, such as parasitic interactions, which are negative in essence yet produce a positive association. However, as far as plants are concerned, support for spatial aggregation as the result of facilitation has been shown in experiments (Graff & Aguiar, 2011; Valiente-Banuet & Ezcurra, 1991). Focusing on community-level properties instead of individual pairwise associations may also average out errors at the species-pair level, and provide a more reliable measure of the positive versus negative interaction balance in a given community (Saiz & Alados, 2012; Alados *et al.*, 2017).

We applied the association network approach to a succession of vegetation communities of the plain of La Crau, a locally semi-arid

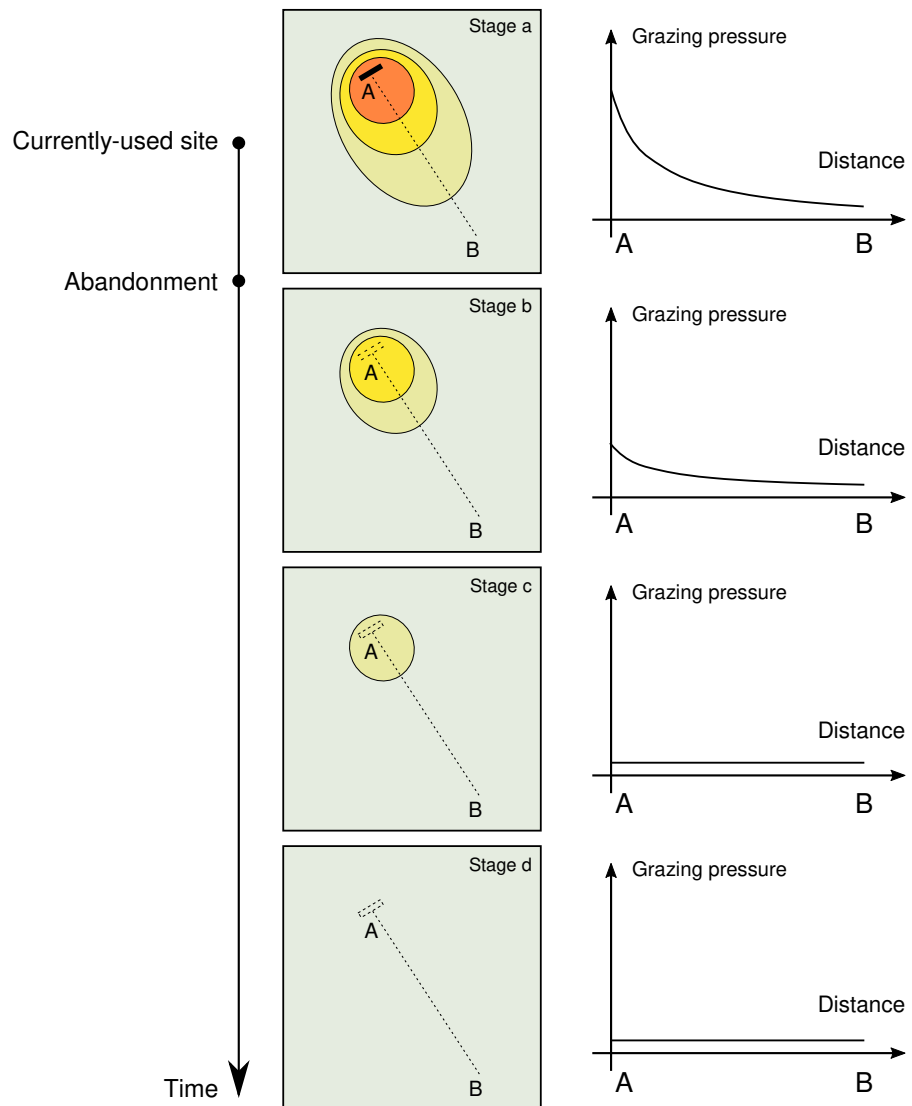


Figure 4.3: Response of vegetation communities at a currently-used site, recovery through time, and hypothesized spatial distribution of grazing pressure. A currently-used site will show a strong local variation of grazing pressure (Stage a), which results in a local change of vegetation communities (colors). After abandonment, a "rewinding" process occurs and the "Coussoul"-community (grey) colonizes back the disturbed areas (Stages b-d). In the early stages after abandonment, the grazing pressure is locally a bit higher than elsewhere as the remains of the sheepfold are still standing and provide shade, where the sheep tend to stay longer (Stage b). We documented the variations of vegetation communities along the line A-B in current and past sheepfolds.

grassland in Mediterranean France. This grassland has been maintained open since the roman era due to a rich sheep husbandry activity (Badan *et al.*, 1995; Henry *et al.*, 2010). In this plain, current grazing is organized around sheepfolds where sheep stay at night. This results in a local gradient of sheep impact through grazing, nutrient deposition and trampling, whose maximal extension is towards the south-east (the direction under dominant winds). This gradient leads to a local spatial turnover of the species composition. Ruderal plants predominate locally around the sheepfold, within a matrix of a "Coussoul"-type community, dominated by stress-tolerant perennial species such as *Brachypodium retusum*, *Thymus vulgaris* and *Asphodelus ayardii* (Molinier & Tallon, 1950). Through history, some sheepfolds have been abandoned, which results in a locally decreased – but non-zero – grazing pressure and the resorption of more nitrophilous vegetation communities, in favor of the original Coussoul community (Figure 4.3). Since abandonment, a succession-like process has taken place, although it is worth noting that despite abandonment, the vegetation of the sites remains grazed – albeit at much lower intensities. Because many sheepfolds have a known date of abandonment, the comparison of these sites today provides an ideal setting to adopt a chronosequence approach by space-for-time substitution, allowing us to document the recovery process of the vegetation community through time.

Our study aims at investigating the long-term changes in plant-plant associations following grazing abandonment, in an attempt to quantify the resilience of the community, both in terms of species composition and inter-specific interactions.

First, we assessed whether biotic interactions (as measured through associations) varied on the same time scale as the species composition of the community and the abiotic characteristics. To do so, we documented plant associations, species composition and soil attributes of vegetation communities at currently-used and abandoned sites in La Crau, and estimated their trajectory through time by comparing these different sites.

We then focused on testing whether associations supported classic hypotheses regarding succession. Approaches based on functional traits in La Crau (le Priol, 2017) have shown that undisturbed communities tend to contain species with higher leaf dry matter content (LDMC) and lower specific leaf area (SLA), suggesting that the species making up the undisturbed communities may adopt compet-

itive strategies (Garnier & Navas, 2013). Given these variations, we hypothesized that associations would switch from weak (low number of positive and negative associations) to strongly negative during late successional stages (high number of negative associations).

5 4.2 METHODS

4.2.1 *Surveys and soil sampling*

We surveyed 6 currently used sites, 4 sites abandoned in the late XXth century, 3 sites abandoned in the XIXth century and 3 roman sites, abandoned between 88 A.D and 430 A.D (abandonment dates
10 were obtained from Henry, 2009; Badan *et al.*, 1995). We describe here broadly the survey protocol for the variables used in this chapter, but more details are available in Appendix 2, along with a presentation of the general ecological context of La Crau.

To compute species associations, we laid out transects using a mea-
15 suring tape, and recorded the beginning and the end of overlap of each plant individual (or part of individual, Plate 9). Transects were laid in pairs – 4 pairs in total per site – at different distances from the sheepfold, separated by at least 10m but no more than 75m so that grazing levels were similar. We placed one pair of transect in
20 each one of four community types identified using indicator species (Appendix 2, Figure 5.9). These community types are known to correspond broadly to a certain level of grazing pressure (Molinier & Tallon, 1950), so by placing one pair of transect in each type, we made sure that we surveyed a wide range of grazing levels.

25 We computed the average distance of placement of each transect pair (excluding one site, "Terme Blanc", where the grazing gradient is unusually long), and used this distance to place pairs of transects at abandoned sites.

We merged each pair of transects together to produce one associ-
30 ation network per pair. This yielded 4 association networks for each site, at increasing distances from the sheepfold. Because of local disturbances unrelated to grazing, or because indicator species could not be found in the field, some pairs of transects could not be placed, resulting in sites with less than four documented association networks.

35 For each site, we sampled soil at the average distance of each pair of transect, and complemented this first set of samples with samples taken at quadrat positions. Each soil sample consisted in 200 g taken

out of a homogeneous mix of 16 subsamples regularly spaced within a 4 m radius circle (Appendix 2). This yielded between 4 and 6 soil samples per site, which were dried for at least 48h at 40°C, then sent for analyses. Soil analyses included pH (in water), cation total exchange capacity (Metson method), total CaCO₃, total organic matter, total phosphorus (Olsen method), exchangeable K, Mg, Ca and Na and total Nitrogen.

4.2.2 Selection and derivation of community statistics

We derived for each transect the total cover of each species, then averaged them for each pair of replicate transect. We used this distribution of covers for the pair of transects to compute the number of observed species and the Shannon diversity index. To obtain a univariate value summarizing broad variations in species composition, we first computed a Bray-Curtis dissimilarity matrix between the species compositions of each pair of transects. We then summarized it into a single univariate value by extracting the first axis of a principal coordinate analysis ran on these dissimilarities. The R package 'vegan' v2.5-2 (Oksanen *et al.*, 2018) was used to compute dissimilarities.

We also computed for each pair of transects the average linear plant volume, i. e. the sum of the size of each individual (or part of individual, Plate 9) multiplied by its height, to obtain an estimation of the above-ground plant community volume. The volume taken by an individual was computed as follows: if individual i overlaps the transect between a_i and b_i , and has a height h_i , then its volume is $(b_i - a_i) * h_i$. Because we only recorded classes of heights (1/2/3/4/5) rather than actual height in the field, we carried out the average using the midpoints of each height class (1/3.5/7.5/16cm and 25cm for class 5).

For the sake of conciseness, we only show the spatial and temporal variations of total nitrogen, which has been shown to be a key factor in driving the plant species composition along succession in La Crau (Henry, 2009) and is very strongly correlated to current spatial variations in grazing (Average spearman correlation with distance at current sites: -0.90). We report the variations of other soil variables in Appendix 4. It is worth noting that most soil variables are correlated with each other and in particular with the total nitrogen content (average Pearson's $r=0.67 \pm 0.2$ s.d.), thus yielding similar trends in space and time (Appendix 4, Figure 5.13 and 5.14).

ASSOCIATION NETWORKS To obtain the association networks, we computed the total overlap between each species within a pair of transects, then compared this total overlap to what was obtained by randomizing the position of every individual along the transects (and across transects). We retained a positive association when the observed total overlap was within the upper quartile of the null distribution, and a negative one when the total overlap was in the lower quartile (this method is identical to what is described in Chapter 2).

This produced one association network for each pair of transects. We then summarized these association networks into network-level metrics. First, we computed the percentage of positive and negative associations K^+ and K^- (respectively). We then computed a ratio that quantifies the relative importance of positive over negative associations in a network, R , as $(K^+ - K^-)/(K^+ + K^-)$ (Saiz *et al.*, 2017; Alados *et al.*, 2017; Arroyo *et al.*, 2015). This ratio is equal to 1 when all associations are positive, -1 when they are all negative and zero when there is the same number of positive and negative associations in a network.

These three network-level metrics depend on the number of species and their total cover in a given pair of transects. Spatial and temporal variations of these raw numbers may thus reflect these variations in species abundances rather than a true tendency of the community to display a certain type and number of associations (Chapter 3, Box 3.1). To be able to compare these metrics across gradients, we created 199 'null' transects with a randomized position of each individual (allowing the mixing of individuals across the transects in each pair). These 'null' transects have a randomized spatial structure, but the same total cover of each species. For each 'null' pair of transects, we computed the network-level metrics, K^+ , K^- and R , which yielded a distribution of 199 null values for each of these metrics. We then computed the standardized effect size of the observed value, compared to its null expectation as (example given for R):

$$R_{SES} = \frac{R - \mu_{R_{null}}}{\sigma_{R_{null}}} \quad (4.1)$$

where μ is the mean of the null distribution and σ is its standard deviation. We obtained similarly the other network-level metrics K_{SES}^+ and K_{SES}^- . This yields community-level metrics that are broadly independent from the variations of species abundances (Appendix 4, Figure 5.12), and thus allows meaningful comparisons of SES values

along gradients where the species abundance distribution changes. It is worth noting that, in an association network, a link between two species cannot be simultaneously positive and negative. The percentages of negative and positive associations are thus (anti)correlated to some extent (Pearson's $r=-0.63$, $P<0.001$).

4.2.3 Estimation of the spatial variations of vegetation communities

At each site, we documented the spatial variations in the vegetation communities along the general south-east direction (line A-B in Figure 4.3). The change in some property of the community – e. g. species richness – relative to the original "Coussouls" community is expected to be maximal near the entrance of the sheepfold and to decrease with the distance to the entrance (Figure 4.3). As a result, when moving along the general southeast direction, a site where the effect of the past sheep activity is still present should show spatial variations in some properties of the community. For example, a site whose species composition has not completely recovered from the past sheep presence is expected to show spatial variations of the species composition along the south-east direction. Conversely, a site that has fully recovered should show no such spatial variation, i. e. a flat trend along the A-B line: communities close to the sheepfold should be similar to those far from it. The amplitude of the spatial variations of the vegetation community can thus be used as an informative measure of the progress of recovery.

In the following paragraphs, we use y to refer to the property of the community considered, such as species richness, association ratio R_{SES} or the total N measured in a soil sample. We estimated the spatial variations of y at each site by fitting the following saturating function:

$$y \sim \frac{y_0 * d_{1/2} + (y_0 + \Delta y) * d}{d_{1/2} + d} + \epsilon \quad (4.2)$$

where y is the value of the property considered (e. g. species richness) and d the distance to the sheepfold entrance ¹. In this relation-

¹ Why this relationship? Although the evidence is scarce, grazing pressure P (measured in sheep per unit of area and unit of time) seems to be well approximated by a relationship of the form $P = a / (1 + b * d)$ (Figure 5.5), where a and b are constants and d is the distance to the sheepfold. Assuming the property y of the community under study follows a linear relationship with grazing pressure $y = \alpha * P + \beta$, it follows that the relationship between y and d has the form suggested above.

ship, y_0 represents the value of y next to the sheepfold entrance, Δ_y represents the difference between y_0 and the value observed far from the sheepfold (as $d \rightarrow \infty$). $d_{1/2}$ quantifies the distance at which $y = \Delta_y/2$, i. e. the spatial extent of the variations. ϵ represents a normal error of standard deviation σ .

We used a Bayesian framework to fit this model because it allowed us to include prior information about the general shape of the spatial variations of community properties, and thus maintain parameter estimates within realistic bounds. The details of the model fitting procedure are further described in Appendix 4.

We used 'BayesianTools' v0.1.4 in R (R Core Team, 2018) to fit this model (Hartig *et al.*, 2017). We ran 4 chains for each fit with 100,000 iterations each, using a differential evolution markov chain sampler (DE-MCMC, default sampler in BayesianTools, ter Braak & Vrugt, 2008). Convergence was assessed visually and by checking that the Gelman-Rubin criterion (Gelman & Rubin, 1992) was under 1.1.

4.2.4 Description of temporal dynamics

To analyze the recovery of community properties over time, we analyzed how the Δ_y values changed with time of abandonment. The value of Δ_y is the amplitude of spatial variations of a given variable around a site: it is expected to be zero when it shows no variation around a site, i. e. a site has fully recovered from its past use for sheep herding. We modelled the variations of Δ_y as a function of time t using the following exponential decay model:

$$\Delta_y(t) \sim \Delta_{y,\infty} + (\Delta_{y,t_0} - \Delta_{y,\infty}) * \exp\left(-\frac{\log(2)t}{t_{1/2}}\right) + \epsilon \quad (4.3)$$

In this equation Δ_{y,t_0} quantifies the amount of spatial variation observed at current sites, $\Delta_{y,\infty}$ quantifies the long-term spatial variation observed around sheepfolds (it is zero when a site has fully recovered). $t_{1/2}$ characterizes the time required for the observed spatial variation $\Delta_y(t)$ to be equal to half of its value after infinite time has passed, i. e. $(\Delta_{y,t_0} + \Delta_{y,\infty})/2$ – it is thus a measure of the speed of recovery.

We carried out this fit 199 times, using values sampled from the posterior predictive distribution of the previous model. Specifically, we repeated the following process 199 times: for each site, we sam-

pled one Δ_y value from the prediction of the spatial variations model, then used these 15 Δ_y values (one per site) to fit the exponential decay model. This allowed us to take into account the uncertainty on spatial variations of community properties into the estimation of temporal dynamics, and estimate confidence intervals around the overall temporal trajectory.

4.2.5 *Specific patterns in the variations of associations*

Because associations did not show a recovery pattern similar to other aspects of the community, we investigated their variations further. In particular, we investigated two specific patterns: (i) the rapid increase in negative associations close to recently-abandoned sites (abandoned within 9-47.5 years) and (ii) the strong spatial decrease in negative associations in roman sites (1587-1750 years).

We considered the first point by comparing estimates of the percentage of negative associations at the sheepfold (y_0 in equation 4.2) across classes of time after abandonment (current sites, 0-49.5 years, 119-160 years, 1587-1750 years). We then addressed point two by focusing on the spatial variations of the association ratio, the total nitrogen, species richness, total vegetation cover and relative cover of *B. retusum* at roman sites to interpret the long-term trends in plant-plant associations.

4.2.6 *Variations of associations with soil nitrogen content*

Because patterns suggested a close relationship between nutrient content and the SES of the association ratio, we investigated its general relationship with all sites considered at once. We carried out a piecewise linear regression using one breakpoint to investigate changes in the slope of this relationship. The value of the breakpoint and the coefficients of the linear model were estimated using maximum likelihood and the R package 'segmented' v0.5 (Muggeo, 2003).

4.3 RESULTS

4.3.1 *Spatial variations of community characteristics*

The species composition and total nitrogen in the soil showed clear recovery patterns, such that their spatial variations around the sheep-
folds decrease with the number of years after abandonment (Figure 4.5) – i. e. over time, assuming a space-for-time substitution.

The temporal trajectories of the amplitude of spatial variations Δ_y confirmed this trend, with species composition and nitrogen showing convergent trajectories of Δ_y towards zero – i. e. over time, the spatial variation of these properties around the sheepfold decreases (Figure 4.4, a-b). This is a very slow process, however, as even after approximately 1600 years after abandonment, a significant spatial variation in species composition can be still observed.

Associations displayed a very different pattern of spatio-temporal variations. The amplitude of variations around a site (Δ_y) did not converge towards zero, but diverged towards a significant non-zero value (Figure 4.4, c). In other words, the spatial variations of associations followed more complex changes over time than a unidirectional recovery pattern. For example, stronger spatial variations were observed around roman sites than in sites of intermediate abandonment (Figure 4.5, 1).

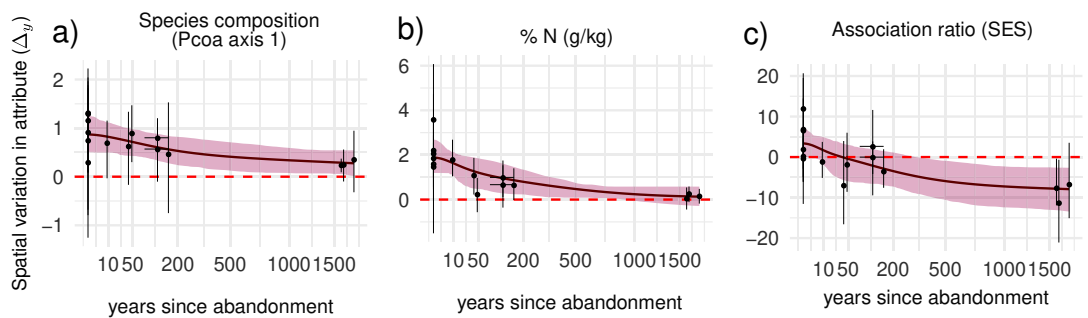


Figure 4.4: Temporal trajectory of the spatial variations of species composition, the soil total Nitrogen and the SES of the association ratio. The trend line corresponds to the exponential decay model described in Equation 4.3, and the ribbon indicate 95% confidence interval around the predicted mean value

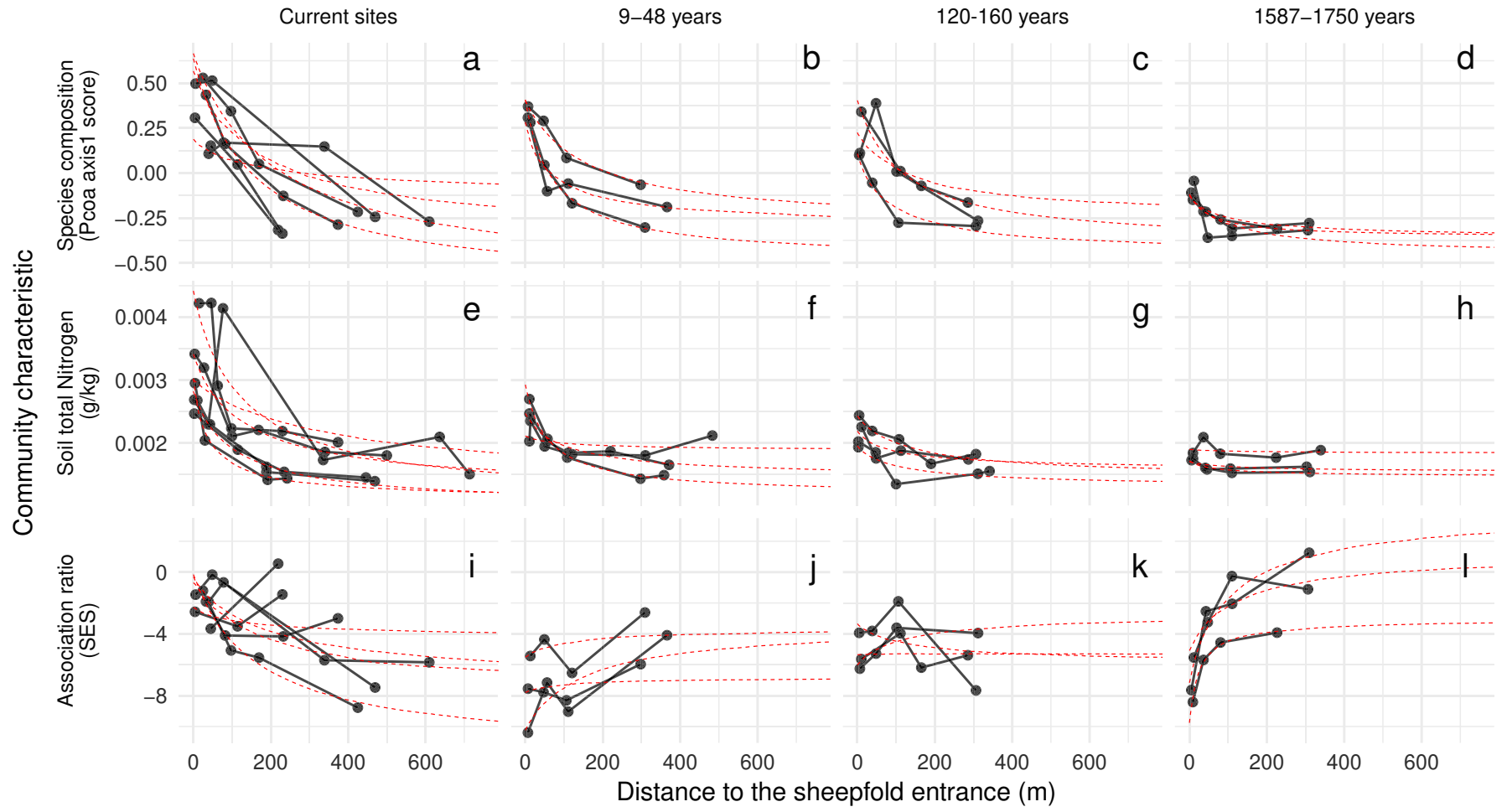


Figure 4.5: Spatial variations of three variables at currently used and abandoned sheepfolds: a proxy of species composition (a-d), the total N in the soil (e-h) and the association ratio (positive when more positive associations are observed than expected from the species composition, i-l). The red dashed line indicates the fit based on the model in equation 4.2. The species composition and the total N show a typical recovery pattern, as the spatial variations progressively flatten (red curves) as time from abandonment increases (left to right). On the other hand, the association ratio displays no such recovery pattern, as spatial variations vary and persist through time.

VARIATION OF ASSOCIATIONS AT RECENTLY-ABANDONED SITES

The spatial variations of associations exhibited rapid changes over time. Most notably, although the association ratio was always negative, its spatial variations around the sheepfold showed a rapid reversal after abandonment (Figure 4.7, a-b). This reversal was the consequence of a strong and significant increase in the dominance of negative associations close to the sheepfold (Figure 4.7, a-b, and Figure 4.6).

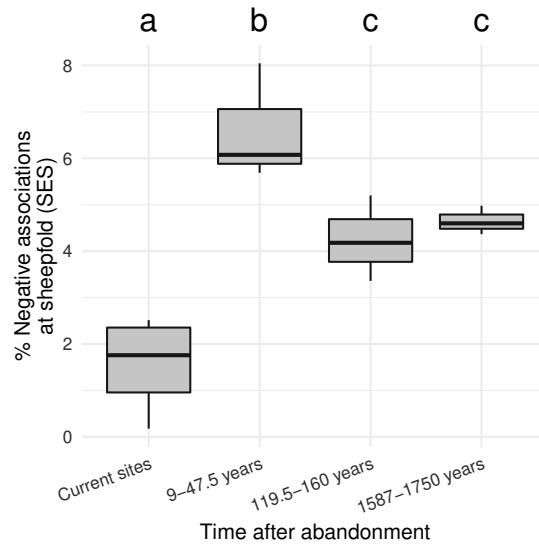


Figure 4.6: Estimate of the SES of the % of negative associations at the sheepfold, for each class of abandonment. Letters on top indicate significantly different groups, based on pairwise Wilcoxon tests and a significance threshold of 0.10.

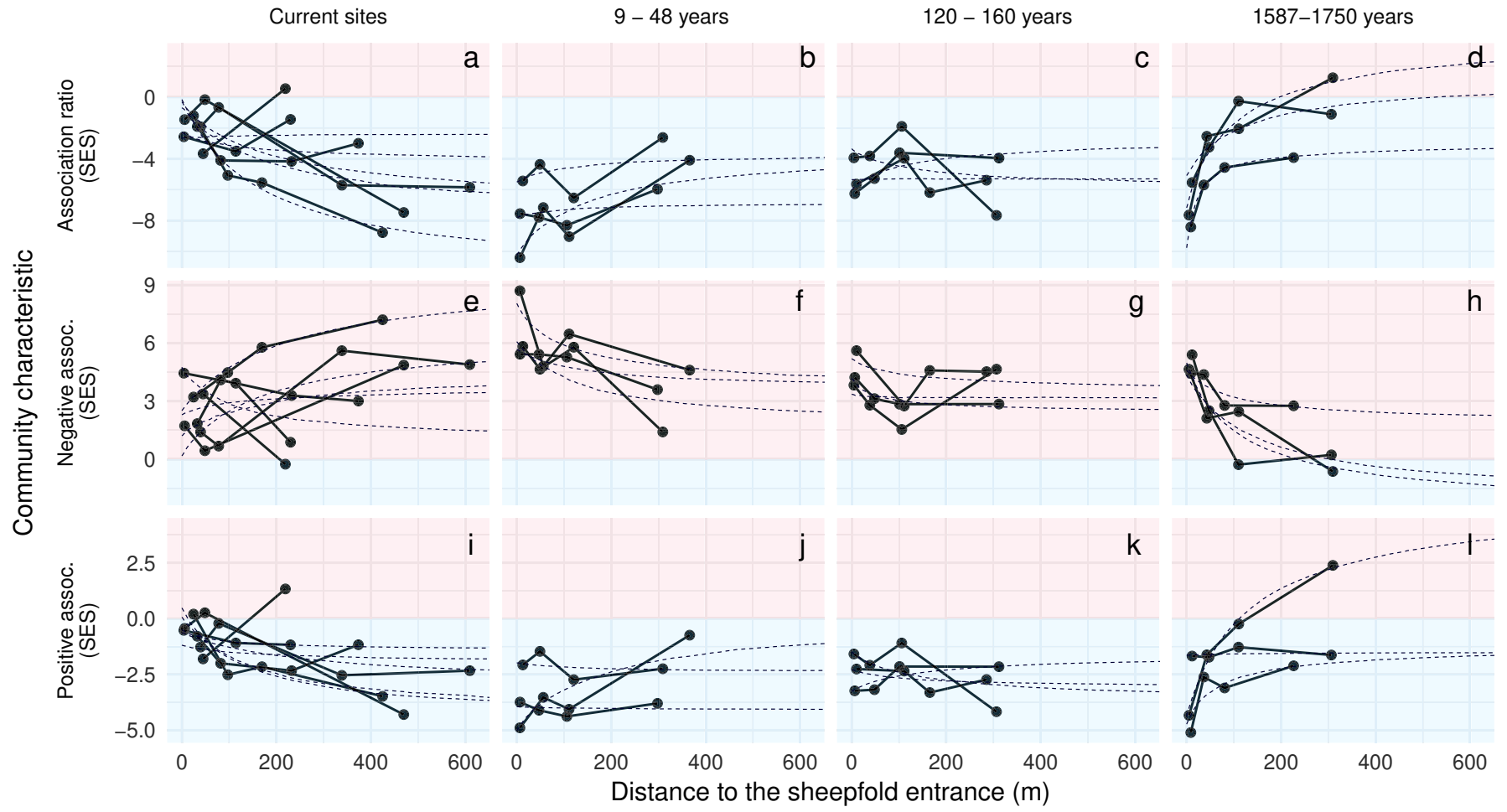


Figure 4.7: Spatial variation of the SES of the percentage of positive and negative associations, and of the association ratio. Colored areas mark the positive (red, value is above its expectation given the species richness and abundances) and negative (blue, value is below its expectation) areas of the SES values.

VARIATION OF ASSOCIATIONS AROUND ROMAN SITES

The strong spatial variations of the association ratio at roman sites ($+8.5 \pm 2.4$ SES values, mean \pm s.d. averaged over the three sites, Figure 4.8) was associated with a slight decrease in total nitrogen (-0.005 ± 0.001 g/kg), and a change of the species composition of the community. In particular, species richness decreased (-10.4 ± 4.6 species), along with the total cover in the transect (-0.11 ± 0.17 % of transect length). This was in favor of an increase of the relative cover of *B. retusum* ($+0.36 \pm 0.23$ %), which underpinned an increase in the total aerial volume taken by plants ($+1164 \pm 277$ cm²).

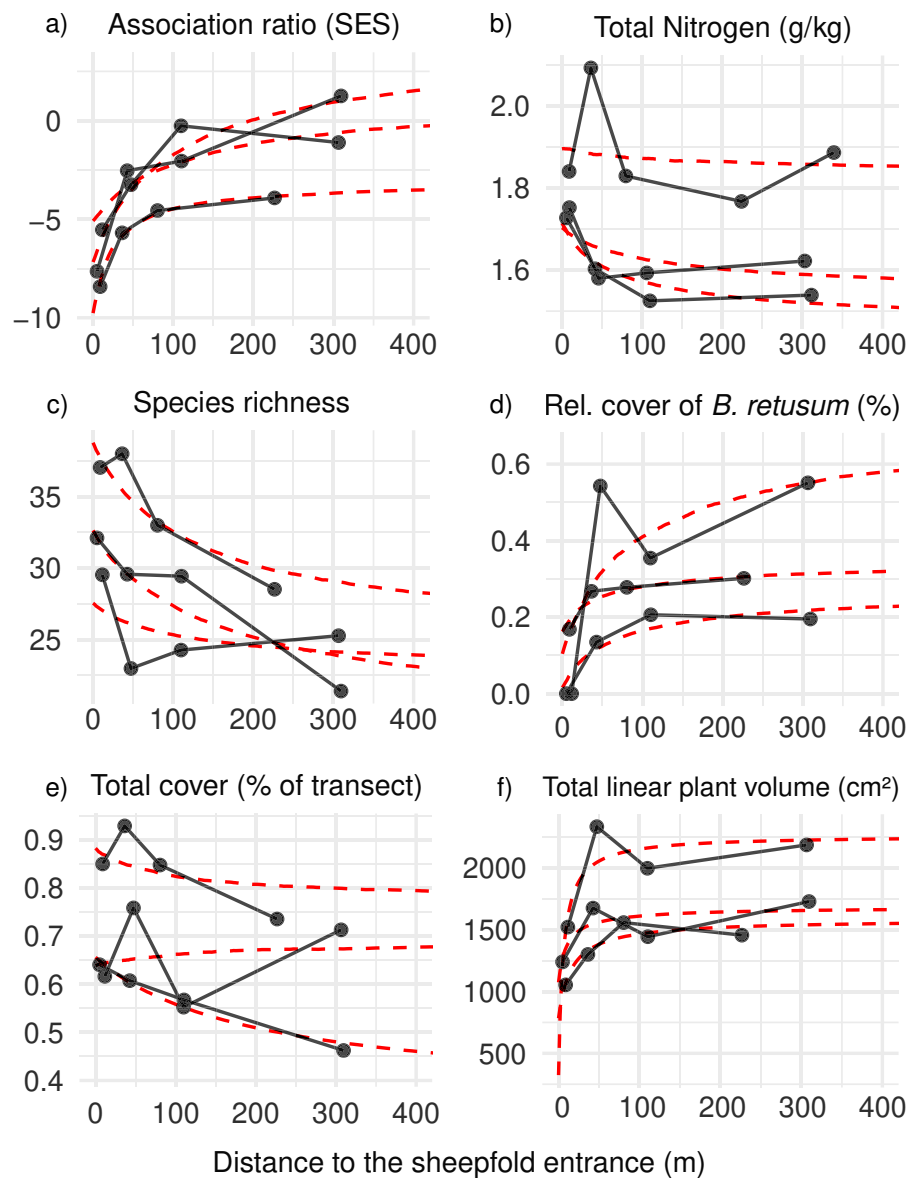


Figure 4.8: Spatial variations, at roman sites, of the association ratio, total nitrogen, species richness, total cover of plants (in % of the transect length), and relative cover of *B. retusum*.

VARIATION OF ASSOCIATIONS WITH NITROGEN LEVELS

The SES of the association ratio was almost always negative regardless of the nitrogen level. However, the piecewise regression identified a turning point (1.83 ± 0.10 , mean \pm s.d., Figure 4.9). For nitrogen levels above this turning point, a decrease in nitrogen yields a decrease in the association ratio (positive slope of 9.8 ± 3.4 SES unit/% Nitrogen). The reverse was found below this turning point, as the decrease in nitrogen was associated with an increase in the association ratio value (negative slope of -7.8 ± 3.3 SES unit/% Nitrogen).

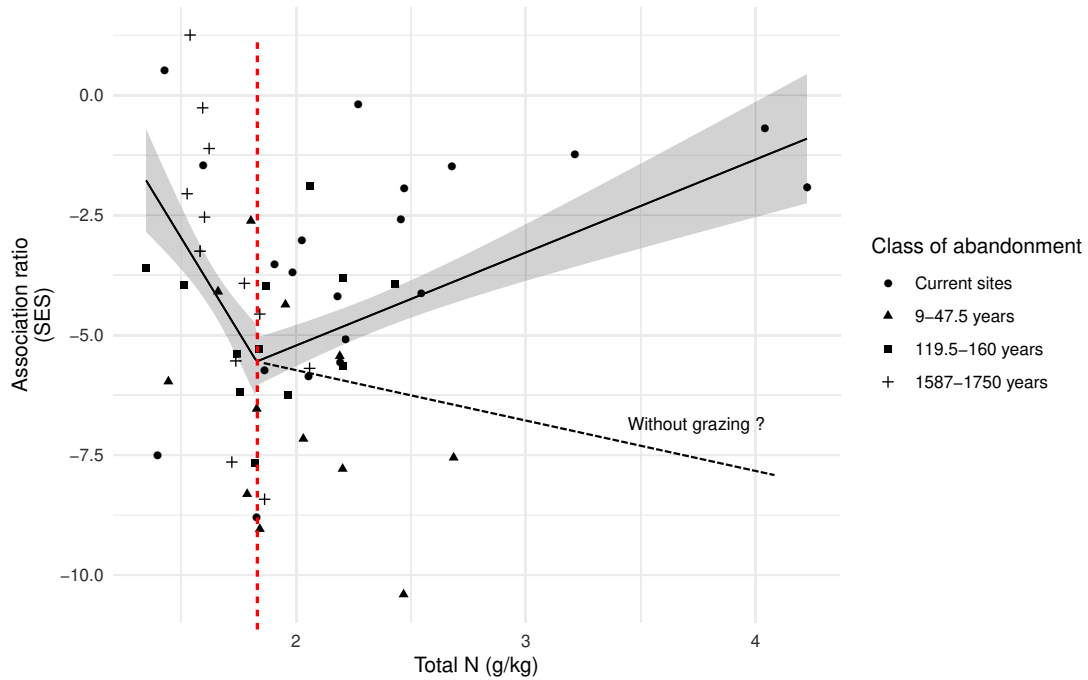


Figure 4.9: Variations of the SES of the association ratio, as a function of total nitrogen. The line and grey ribbons indicate the results of a piecewise regression (ribbons represent confidence intervals). The black, dashed line has been added by hand and shows a possible expectation of the association ratio in the absence of grazing.

4.4 DISCUSSION

Observational data from plant communities in La Crau show that the abiotic conditions as well as the species composition followed a recovery trajectory over time after abandonment, although at a very slow pace: 1,600 years after abandonment, these variables are still significantly different near the sheepfold than in their surroundings. This is consistent with previous studies describing the recovery of vegetation communities in La Crau (Henry, 2009). In contrast, plant-plant associations showed a non-recovery pattern. For example, the spatial variations of associations were stronger at the later stages after abandonment (roman sites) than during more recent time periods. This is in stark contrast with our initial hypothesis of a gradual increase of negative associations with time.

It is noteworthy that the spatial variations of associations were similar across sampled sites and time periods. This supports the fact that associations capture a real, information-rich aspect of the organization of the vegetation communities.

4.4.1 *Short-term and long-term variations of associations*

A first notable pattern captured by associations in the decrease in the association ratio in the early stages after abandonment. This is most likely underpinned by a rebound of competition as grazing is stopped or strongly reduced, while nutrient content remains high. At historical scales however, this is a transient phase and the importance of negative associations stabilizes at a lower level after approx. 100 years (Figure 4.7, g). This rebound of competition reflects fast, possibly annual changes in the organization of vegetation communities. During spring, at current sites, the impact of sheep around sheepfolds is extremely intense and produces a drastic reduction in cover and vegetation height. However, in the first stages after grazing release, nutrient content is high and a strong and rapid regrowth is often observed of ruderal species. A dominance of negative associations would thus certainly be observed during fall season, resulting in likely strong variations of the ratio during the year (Plate 7).

The plant-plant associations displayed strong variations at roman sites. In particular, these sites had a higher negative association ratio near their entrance than in the nearby "Coussoul" community. The latter was characterized by a dominance of *B. retusum*, which – de-

spite being thought as a competitor – was dominant in a community marked by the absence of negative associations.

This apparent contradiction may be resolved when we consider the nitrogen levels, which were at their lowest in this community. These comparatively low nutrient levels may be what drives the absence of negative associations: in less productive environments, the likely dominant origin of negative associations – competition for space – is lacking and thus the association ratio becomes closer to zero or positive. This depletion in nitrogen could be attributable to the sustained grazing since the roman era, which produces a depletion in nutrients of areas far from sheepfolds, in favor of an enrichment of areas close to them. It could also be a consequence of the larger development of *B. retusum*, which may preempt nutrients and thus reduce their accessibility to other plants, but this is poorly supported as there is only a weak correlation between the association ratio and the total aerial volume taken by *B. retusum* (Pearson's $r = 0.10$, $P = 0.58$).

4.4.2 Variations of associations and nutrient levels

Be it at recently-abandoned sites or at roman sites, patterns highlighted the close relationship between the association ratio and the nutrient levels available to the community. This relationship showed dual trends. The decrease from very high nitrogen contents to average is associated with an increase in competition – this is because highly nutrient-rich communities also suffer from very high physical disturbance. Were there no grazing but solely nutrient enrichment, the association ratio would have been probably observed as negative (dashed line in Figure 4.9) – reflecting intense competition for space.

However, below a point in nitrogen levels, the association ratio increases towards zero because of a collapse of negative associations, which may be due to the overall decrease in nutrients available to annual plants. It is in these communities that *B. retusum* increases in biomass, as it may be less affected by the depletion in surface nutrients because of its deeper roots (regularly reaching -40cm). This interpretation remains to be tested, by showing that nutrient limitation is effectively at play in those communities.

4.4.3 Conclusion: the reorganization of communities as identified by associations

To our knowledge, this is the first study applying an association network approach to plant communities outside of arid ecosystems. We show that associations display consistent trends given similar environmental and historical conditions. They may thus be very valuable to measure *in situ* the changes in the organization of plant communities, and complement previous approaches based on traits and/or phylogenetic relatedness to infer the dominant processes present in a community.

Association analyses confirm the peculiarity of the succession in La Crau following the abandonment of sheepfolds, which converges towards late-successional communities impoverished in species and interactions as nutrient availability decreases. This contrasts with our hypothesis of an increase in competition through time, but it is consistent with the prediction of the stress gradient hypothesis that predicts a decrease in the importance of competitive interactions as productivity decreases. We observed very few positive values of the association ratio, suggesting a relative dominance of competitive processes over facilitation at all stages (but see General Discussion). However, in this study, we used community-level metrics (e. g. the total percentage of negative associations), which may hide variations at the species or species-pair level (Sanderson & Pimm, 2015). Future developments of this work could extend the analysis down to these levels, along with confirming that nitrogen levels are low enough to effectively produce nutrient-limitation.

CONCLUSIONS AND PERSPECTIVES

Throughout this thesis, we investigated the link between the structure of interaction networks and the response of ecological communities to perturbations. In this section, we summarize and discuss the results of this thesis, then suggest new research directions that have emerged through the development of this work and the many fruitful discussions with colleagues along these past three PhD years.

5.1 SUMMARY AND DISCUSSION OF RESEARCH QUESTIONS

10 *Can active feedback loops be identified from multimodality in diverse ecological communities ? (Chapter 1)*

In Chapter 1, we asked whether we could identify vegetation communities in which feedbacks were present, using only a single-time snapshot of their state along a main environmental gradient – water content. To do so, we used an extensive dataset documenting the composition of vegetation communities of subalpine meadows. We found bimodal distributions of species composition in two main areas of the dominant water gradient: dry and wet areas. By reviewing local soil conditions and known previous results about vegetation dynamics in meadows, we concluded that possible active feedbacks could impair the resilience of dry areas in meadows, and provided possible mechanisms. In dry areas, a positive feedback between soil nutrients and vegetation growth may thus exist and be responsible for the bimodality observed. This is a valuable result in a conservation context, where the objective is to identify vegetation communities that may be more vulnerable to disturbance. It is, however, insufficient to characterize precisely the type of dynamics at hand in these fragile communities.

According to the theoretical literature, a strong positive feedback may produce alternative stable states. This could mean that dry communities of subalpine meadows, dominated by *Carex filifolia* and with coarser soil could be, in fact, stable and persist in time. This stability could be a consequence of erosion or run-off being strong enough in *C-filifolia* communities to impair the trapping of fine sediments and

the regrowth of a more diverse community. However, this cannot be truly demonstrated based on the multi-modality criterion alone, as the presence of multi-modality is not equivalent to the presence of alternative stable states: continuous but sharp responses along an environmental gradient also show increased multi-modality (Box 1.1).

To go further and truly understand the processes behind the bimodal pattern, the most direct way would be to collect temporal data or perform disturbance experiments (Petraitis, 2013). However, other correlative approaches may also provide valuable information, such as the analysis of spatial patterns, either through indicators (Chapter 2) or associations (Chapter 3). These spatial patterns help understand the interactions at play in a given community, and could thus also be used to confirm the presence of a feedback in vegetation communities.

15 *How does biotic stress alter plant-plant associations ? (Chapter 3)*

We described in Chapter 3 the variations of plant-plant association networks along gradients of biotic stress (grazing). In particular, we focused on an important structural patterns of plant-plant association networks: the number of positive and negative associations, and the ratio between the two. We found a consistent deficit of positive associations, and thus a consistently negative association ratio. This suggests that competition (most likely for space) is the dominant interaction type in these grasslands. This is generally consistent with the fact that the majority of the species surveyed are annuals (55% of the total cover in the dataset), which tend to engage less in specific plant-plant interactions (e. g. allelopathy), other than through the preemption of resources. It is worth noting that this pattern may change in other ecosystems, especially where there may be several different height classes in plants, e. g. where a shrub layer coexist with a lower herbaceous stratum. In previous studies focusing on arid systems (Saiz *et al.*, 2014), *Brachypodium retusum* engages mostly in positive associations with other plants and higher shrubs in particular. However, it was mostly present in negative associations in the fully-herbaceous communities of La Crau, highlighting a very different behavior of the same species in two different plant communities.

Biotic stress, and more specifically sheep trampling and grazing, reduced the strength and number of associations between species. Interpreting this in terms of interactions, it suggests that under high

levels of stress, the dynamics of the plants are governed by the resistance to stress rather than by the interactions they may have with each other. We did not observe any community-level importance of positive interactions such as associative protection, although the latter has
5 been observed in the field (Plate 5). It could play a bigger role in other ecosystems, where differences in palatability between plants are more important, and where grazing levels are not as intense (e. g. (Graff & Aguiar, 2011; Saiz & Alados, 2012)). This may also be due to the fact that this type of interaction is relatively rare compared to competitive
10 interactions, and thus may be poorly-detectable when considering community-level metrics – such as the association ratio – that average species-specific variations. Extensions of this work would benefit from analyzing these finer-grained variations of associations along the stress gradient, e. g. at the species level or the species-pair level.

15 More generally, we looked at a single, specific aspect of the association networks we built: the ratio between positive and negative associations. A more thorough analysis of the structure of networks, possibly including the analysis of modularity, nestedness or other structural patterns would probably reveal interesting changes in these
20 patterns.

How resilient are plant-plant association networks ? How do their temporal dynamics compare to other facets of the community ? (Chapter 4)

In Chapter 4, we considered the temporal variations of association networks, using abandoned sites as different snapshots of a given system's recovery process. In terms of network description, we focused
25 on the temporal variations of the balance between negative and positive associations. Interestingly, it proved to be very variable over long time scales and did not show a simple, unidirectional recovery trend such as others properties of the community (e. g. species composition). The resilience of association networks thus does not exhibit a
30 simple, direct return-to-equilibrium response, but rather shows complex variations after a perturbation. These variations were nonetheless consistent across sites of similar historical and environmental condition. This shows that associations describe a real pattern of ecological communities, and contain a lot of information to understand
35 what governs the temporal dynamics of a vegetation community, and in particular the importance of biotic interactions. The association ratio was always mostly negative, highlighting that competition for

space was present at every stage of the pseudo-succession. However, variations in this ratio highlighted key phases in the dynamics of the vegetation community – a rebound in competition in the first stages after abandonment, and a decrease of competition in the late successional stages. A general relationship was found between the association ratio and the nutrient levels in the soil. This relationship highlighted a critical nutrient level below which the association ratio becomes closer to zero – i.e. the importance of positive and negative associations is equivalent. At low nutrient levels, competition for space has a reduced importance in structuring the community. This is well in line with predictions from the stress gradient hypothesis (Chapter 3, Bertness & Callaway, 1994; Callaway *et al.*, 2002), which suggests a decrease of the importance of competition relative to facilitation in less productive environments. This interpretation requires further work to be confirmed. In particular, it may be that these levels of nutrients are low for our dataset, yet not low enough to produce nutrient-limitation in plants.

Plant-plant associations have been mostly used in arid ecosystems. In these areas, spatial patterns can sometimes be so evident that no statistical analysis is required (e.g. Verdú & Valiente-Banuet, 2008), and associations correlate with the already-known importance of facilitation (Saiz & Alados, 2011, 2012; Saiz *et al.*, 2018). For this case, using associations as good proxies for interactions is apparently well-founded – or at least well-received in the literature.

A major contribution of this PhD is the demonstration that associations also show coherent variations in more mesic communities, where facilitation may be less prevalent (Chapter 3 and 4). As such, they appear as a valuable tool to investigate biotic interactions in many vegetation communities. Despite this optimism, it is worth noting that their use is only at its early stages and much work remains to be done to properly understand exactly the information plant-plant spatial associations bring.

5.2 PERSPECTIVES

5.2.1 *Towards a better link between interactions and plant-plant associations*

The use of plant-plant associations is still in its infancy, as manifested
 5 by the low number of publications on plant-plant association networks¹. A clear upcoming challenge for association-based studies is the lack of a well-established understanding of the link between associations and interactions. While the intuitive equivalence between positive (resp. negative) interactions and spatial aggregation (resp.
 10 segregation) seems well-founded, it still requires a 'leap of faith' at the time of interpreting patterns.

A possibly way forward could be to use independent data such as measurement of traits to make sure the interpretation is correct. For example, species with competitive strategies could tend to engage more frequently in negative interactions. Some other interactions such as associative protection depend on a specific trait: low palatability, which could correlate with a tendency to produce positive associations. Verifying such hypotheses in the field could guide the interpretation of associations.

20 Another, more methodological line of research could be to improve the way we compute associations: at this time, they do not take into account many of the complexities found in real-world systems. For example, co-occurrence can only imperfectly detect aggregation. Here, we considered that two individuals overlapped when they occupied
 25 the same point along a linear transect (i.e. carrying out the continuous equivalent of point-intersect sampling). In fact, the zone of influence of many plants extends beyond their exact location in space and some plants can be spatially aggregated yet never totally overlap (Figure 5.1). For example, a plant can provide shade and improve
 30 local conditions for another one, yet never occur at the same exact position in space (Valiente-Banuet & Ezcurra, 1991): by using only point co-occurrence, this type of interaction is missed. On the other hand, other positive interactions such as protection against herbivory should lead to an increase in point co-occurrence only, because facilitated plants have to occur below the canopy of the facilitator.
 35

¹ It is striking that most contributions on plant-plant association networks come from a single author: Saiz & Alados (2011, 2012); Saiz *et al.* (2018, 2017), and only focus on arid ecosystems

These two examples highlight that interactions may have an effect at different scales and distances to an individual. As a result, point co-occurrence is a too simplistic measure of spatial association, and probably misses interactions between plants. In particular, it may capture better spatial segregation due to competition for space compared to other interactions, which may partially explain the dominance of negative associations in the results presented in this thesis. A possible solution would be to increase the scale of sampling, and consider that co-occurrence happens between two plants when they are closer than a certain target distance (instead of counting co-occurrences only when they overlap). However, this only moves the problem to the choice of this cutoff distance, which is known to affect the results of the analysis (Araujo & Rozenfeld, 2013; McNickle *et al.*, 2017). A better method to infer plant-plant interactions should solve this problem and describe aggregation at different scales – e.g. by using the O-ring statistic at different distances. In the next paragraphs, I discuss a possible way to infer better interaction coefficients from the spatial structure of plants.

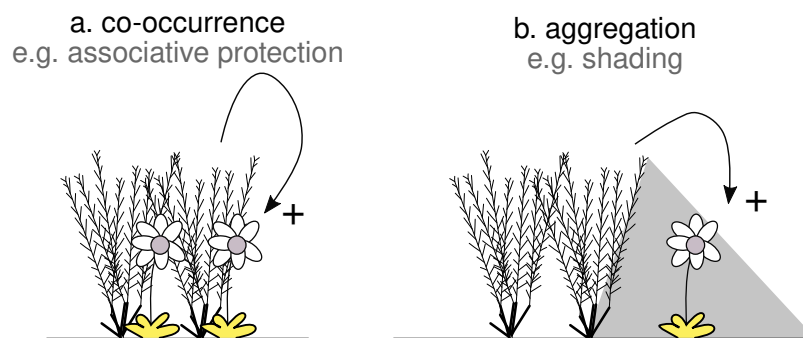


Figure 5.1: Co-occurrence occurs where two plants are located at the same exact vertical point. A positive interaction can also give rise to two plants being close to each other more often than expected by chance – aggregation, yet never co-occur at the same position in space. In this case, however, the positive interaction cannot be inferred using only point co-occurrence.

By measuring the spatial distribution of plants, we can compute the probability of observing an individual of a given species, at a given distance from another individual with whom it interacts². This probability is the net result of multiple interaction types: preemption for space, shading, competition for resources, etc. (Figure 5.2). The statistical problem is to infer the magnitude and spatial scale of these

² In fact, this is a simplification as individuals in the field are always under the influence of several other individuals and not only one

interactions – in other words, infer the shape of curves b, c, d from curve e in Figure 5.2.

A possible approach could come from individual-based modelling. We built an individual-based model based on the zone-of-influence principles presented in Figure 5.2 (Appendix 3). This model can produce spatial distributions of plant individuals, given known interaction coefficients between plant species (see also Box 3.2). By ‘fitting’ this model to data, we could obtain the interaction coefficients (that define curves b, c, d in Figure 5.2) that best reproduce the observed patterns. This is typically done using Approximate Bayesian Computation (ABC) methods (Csilléry *et al.*, 2010; Hartig *et al.*, 2011, 2012). Such an approach has been applied to derive realistic parameters for individual-based forest models (Hartig *et al.*, 2014), but it could be as useful for herbaceous communities. Finally, it is worth keeping in mind that inferring interactions is likely to be a "messy business", involving a synthesis of spatial patterns, trait data and ecological intuition. Bayesian methods have the advantage of explicitly allowing the use of prior, external knowledge, but more likely than not, sound interaction estimations will require combining multiple, correlative and experimental approaches.

5.2.2 *Structural patterns in plant-plant interaction networks and the stability of plant communities*

A rich body of literature has focused on the structural patterns that determine the stability properties of a community. For example, much work supports – although rarely by experimental means – that nestedness increases the stability of mutualistic networks and modularity that of antagonistic networks³ (Thebault & Fontaine, 2010). Plant-plant interactions networks, as inferred through associations, contain by nature positive and negative links. As a result, it is yet unknown how the structure of networks relates to the dynamics and stability of the ecological community, as most network descriptors such as nestedness and modularity are not directly applicable to signed networks. Other specific structural patterns, could show interesting patterns (e. g. structural balance, Saiz *et al.* 2018), but this has very scarcely been explored so far in the ecological literature.

Beyond the sole theoretical interest, monitoring changes in interactions in plant communities could be used as a useful indicator of

³ networks where links represent negative interactions, e. g. host-parasites networks

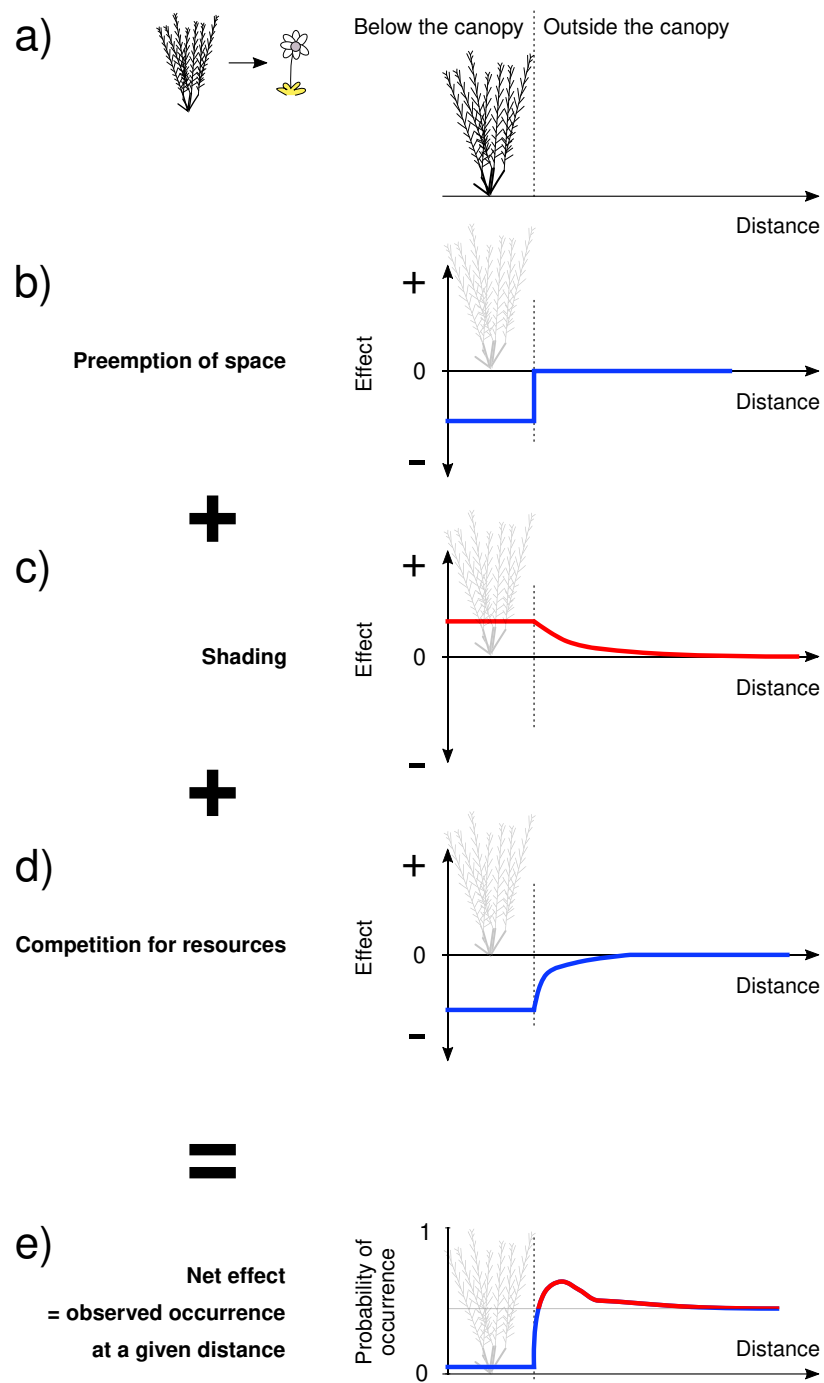


Figure 5.2: The observed pattern of occurrence of a given species, at a given distance from another individual depends on multiple, super-imposed mechanisms of interaction. Some of these mechanisms such as preemption of space only occur below the canopy of the individual (b), while others may have an effect that extends further (c, d). The net effect of these interactions is reflected in the probability of occurrence of the target species (e) – which can be measured on data.

reorganization, and possibly degradation. In Chapter 2 of this work (Génin *et al.*, 2018a), we focused on indicators of ecosystem degradation. These often rely on the measurement of some kind of aggregation pattern (e. g. spatial autocorrelation), or the size and distribution
 5 of vegetation patch sizes, which arise in plant communities because of facilitation (Génin *et al.*, 2018b; Schneider & Kéfi, 2016). In other words, the spatial association of plants is the basis for indicators of degradation. There is thus a natural connection between these indicators and the use of plant-plant associations. So far, the indicators
 10 only consider a binary state (vegetated or not vegetated) and do not use species data. Typically, a single value of vegetation aggregation is derived from the data (e. g. the Moran's I). Association networks could be a way to describe species-specific aggregation in a given landscape. Because pairs of species may react differently to stress,
 15 describing the aggregation of species at the species pair level could lead to a more precise and useful indicator of degradation (Dakos & Bascompte, 2014; Holmgren & Scheffer, 2010).

More generally, interaction networks are seldom used as practical management tools, yet they may be very information-rich to identify
 20 reorganizations of a community, beyond the sole changes in species composition (Memmott, 2009; Gray *et al.*, 2014). They remain still costly to obtain and complex to analyze, which may be why research has focused more on aggregated properties (biomass, total cover, etc.), yet future research and developments could lower the cost of entry
 25 to mapping interactions in empirical communities and increase their use.

5.2.3 *The conservation of complex communities*

Multiple authors have called for a more holistic vision of what defines an ecological community, that includes not only species but also their
 30 interactions (e. g., Tylianakis *et al.*, 2010; Memmott *et al.*, 2007a; Gray *et al.*, 2014) – it is the definition we adopted in this thesis (Figure 0.1). However, the use of interaction networks in general remains limited: while common in plant-pollinator studies and food-webs, many other types of interactions lag behind – probably because of the high cost
 35 of mapping them. The use of interactions as a unit of description is thus still far from having permeated ecological research.

An interesting lead for interaction research is their use in conservation. In a moving and widely-quoted article, Janzen (1974) expressed

the problem of the extinction of ecological interactions after deforestation:

« What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions. Many of the remaining participants of these interactions will probably hold on for many years, but they constitute little more than a haphazard, semi-self sustaining zoo and botanical garden. Their complex behaviors, morphologies and physiologies seem unnecessarily complex, even maladaptive in the defaunated fencerow-pasture-field habitats they now occupy. »

Decades after this call for the conservation of complex communities rather than just species lists, ecologists are now revisiting central topics and tools of conservation research, but now including interactions as a unit of study; e. g. diversity-area scaling (Valiente-Banuet *et al.*, 2015), biotic homogenization (Laliberté & Tylianakis, 2010), beta-diversity (Poisot *et al.*, 2012), restoration (Kaiser-Bunbury *et al.*, 2017). However, this mostly concerns plant-pollinator interactions and much work remains to be done for other types of interactions – such as plant-plant interactions. Yet as this work shows, these vary in space and time and some rare and desirable interactions may occur in some places, while the species themselves may not be a conservation target. For example, in La Crau, *Brachypodium retusum* plays a very original role akin to an "engineering species", yet the species itself is a common and widespread grass, and thus not a conservation target in general. A more interaction-focused conservation could help us not miss the protection of this important, if not essential, facet of ecological communities.

Part III

PLATES & APPENDICES

PLATES



Plate 1: General view of the landscape in La Crau, with a sheepfold in the background.



Plate 2: Grazed vegetation in La Crau, with a sheep herd in the background.



Plate 3: A large sheep flock gathering near the sheepfold in the evening (Peau de Meau).



Plate 4: Typical *Coussoul* community, which is present in less-grazed areas and dominated by the grass *Brachypodium retusum*.



Plate 5: Close-up view of an individual of *Onopordum illyricum* displaying a protective effect on a diverse set of annual species growing under its canopy.



Plate 6: Typical state of vegetation during the grazing season in front of a sheepfold (Peau de Meau); only few stress-tolerant species persist through the intense trampling.



Plate 7: Ruderal species close to the sheepfold (La Grosse du Couchant) display a strong regrowth soon after the grazing pressure is released around sheepfolds (compare with Plate 6).



Plate 8: The remaining foundations of a roman sheepfold (Vergières). The white line materializes the walls of the past sheepfold.



Plate 9: Ruling tape used to measure the length over which plant individuals (or parts of them) intersect the transect. In this picture, the grass *Brachypodium retusum* and *Carlina hispanica* intersect the tape, interspersed with leaves of *Dactylis glomerata*. Here, a leaf of *C. hispanica* would be recorded as overlapping the transect from 44.0 cm to 46.5 cm (white arrows).

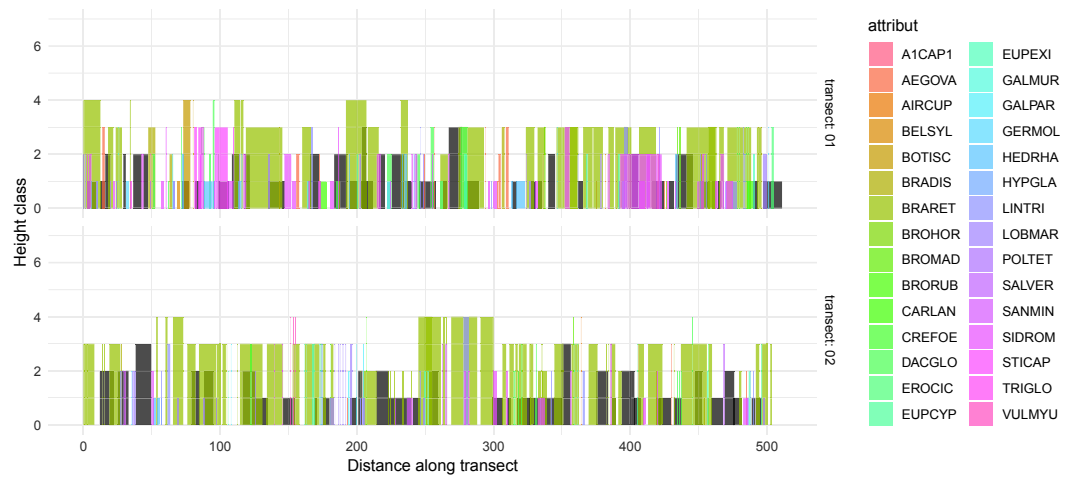


Plate 10: Schematic representation of a pair of transects sampled in the field (Peau de Meau, Coussoul-type vegetation). Each rectangle materializes one individual with its height class, and the color represents the species (pebbles are in black). Full names of species are given in Appendix 1.

APPENDIX 1: SPECIES CODES USED IN THIS WORK

Species code	Species name	Species code	Species name
1	AEGNEG	74	LINSTR
2	AEGGOVA	75	LINTRI
3	AEGTRI	76	LOBMAR
4	AIRCUP	77	LOLPER
5	AJUIVA	78	LOLRIG
6	ALYSIM	79	LYSARV
7	ANAGSP	80	LYSFOE
8	ANCARV	81	LYSLIN
9	ANTARV	82	MALSYL
10	*ASPAYA	83	MARVUL
11	ASPCYN	84	MEDCOR
12	AVEBAR	85	MEDMIN
13	BELSYL	86	MEDMON
14	BOTISC	87	MEDRIG
15	BRADIS	88	MEDTRU
16	*BRARET	89	NEAAPU
17	BROHOR	90	*ONOILL
18	BROMAD	91	PETPRO
19	BRORUB	92	PHLYC
20	BROSTE	93	PLABEL
21	BUFTEN	94	PLACOR
22	*CAMMON	95	PLALAG
23	CAPBUR	96	PLALAN
24	CARATA	97	PLASUB
25	*CARHIS	98	POAANN
26	CARLAN	99	POABUL
27	CARNIG	100	POLTET
28	CARTEN	101	PSIINC
29	CATRIG	102	RANPAL
30	CERPUM	103	REIPIC
31	CHEALB	104	RESPHY
32	CHEMUR	105	ROSCRI
33	CHEVUL	106	RUMPUL
34	CLINEP	107	RUTMON
35	CONCAN	108	SAGAPE
36	CRATIL	109	SALVER
37	CREBUR	110	SANMIN
38	CREFOE	111	SCAATR
39	CREPSP	112	SCAAUS
40	CRESAN	113	SCOLAC
41	CRUANG	114	SENVUL
42	CYNDAC	115	SHEARV
43	CYNECH	116	SIDROM
44	DACGLO	117	SILGAL
45	DIPTEN	118	SONASP
46	ECHASP	119	SONOLE
47	EROCIC	120	STEMED
48	ERYCAM	121	*STICAP
49	EUPCYP	122	*SYLMAR
50	EUPEXI	123	TAECAP
51	EUPFAL	124	TARAUT
52	EUPSEG	125	TEUCHA
53	FILGAL	126	THYVUL
54	FILGER	127	TOLBAR
55	FILMIN	128	TORNOD
56	FILPYG	129	TRAPOR
57	FILPYR	130	TRIANG
58	GALMUR	131	TRICAM
59	GALPAR	132	TRICHE
60	GASVEN	133	TRIGLA
61	GERMOL	134	TRIGLO
62	GERRROT	135	TRISCA
63	HEDRHA	136	TRISTE
64	HELBRO	137	*TRISUB
65	HIRINC	138	TRISUF
66	HORMUR	139	TRITOM
67	HYPGLA	140	TYRLEU
68	LAMAMP	141	URODAL
69	LEOTUB	142	*URTURE
70	*LEPGRA	143	VERARV
71	LINARV	144	VERSIN
72	LINPEL	145	VULCIL
73	LINRIG	146	VULMYU
			Linum strictum
			Linum trigynum
			Lobularia maritima
			Lolium perenne
			Lolium rigidum
			Lysimachia arvensis
			Lysimachia foemina
			Lysimachia linum-stellatum
			Malva sylvestris
			Marrubium vulgare
			Medicago coronata
			Medicago minima
			Medicago monspeliaca
			Medicago rigidula
			Medicago truncatula
			Neatostema apulum
			Onopordium illyricum
			Petrorhagia prolifera
			Phlomis lychnitis
			Plantago bellardii
			Plantago coronopus
			Plantago lagopus
			Plantago lanceolata
			Plantago subulata
			Poa annua
			Poa bulbosa
			Polycarpon tetraphyllum
			Psilurus incurvus
			Ranunculus paludosus
			Reichardia picroides
			Reseda phyteuma
			Rostraria cristata
			Rumex pulcher
			Ruta montana
			Sagina apetala
			Salvia verbenaca
			Sanguisorba minor
			Scabiosa atropurpurea
			Scandix australis
			Scorzonera laciniata
			Senecio vulgaris
			Sherardia arvensis
			Sideritis romana
			Silene gallica
			Sonchus asper
			Sonchus oleraceus
			Stellaria media
			Stipa capillata
			Syllibium marianum
			Taeniatherum caput-medusae
			Taraxacum autumnale
			Teucrium chamaedrys
			Thymus vulgaris
			Tolpis barbata
			Torilis nodosa
			Tragopogon porrifolius
			Trifolium angustifolium
			Trifolium campestre
			Trifolium cherleri
			Trinia glauca
			Trifolium glomeratum
			Trifolium scabrum
			Trifolium stellatum
			Trifolium subterraneum
			Trifolium suffocatum
			Trifolium tomentosum
			Tyrimnus leucographus
			Urospermum dalechampii
			Urtica urens
			Veronica arvensis
			Verbascum sinuatum
			Vulpia ciliata
			Vulpia myuros

APPENDIX 2: DESCRIPTION OF LA CRAU AND THE SURVEY PROTOCOL

The plain of the Crau is located in the south of France, and its main area is comprised in a triangle between Arles, Salon and Marseille (Bouches-du-Rhône, 5.3). The Crau area is characterized by a flat landscape where vegetation is dominated by herbaceous species. For this reason, it is often referred to as a steppe (Figure 1), despite not being as arid (average annual rainfall of 540 mm/year) as true steppe biomes. The maintenance of such a landscape is due to the combination of several local factors that reduce water availability and encroachment by ligneous species.

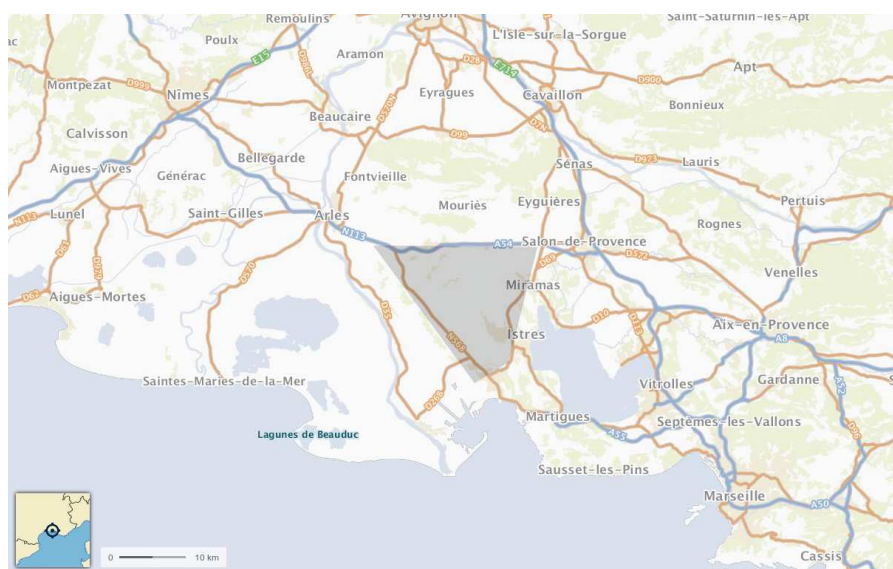


Figure 5.3: General situation of the Crau. The main area is located within the dark triangle.

Most recent areas of La Crau appeared as the result of the accumulation of pebbles in the former Durance river delta (now an affluent of the Rhône river). Cementing of the pebbles produced a conglomerate layer (puddingstone) that limits the groundwater accessibility by plants to the first 50 centimeters of soil (Tatin *et al.*, 2013). This contributes, along with strong and recurrent winds (the *Mistral*) and a warm Mediterranean climate, to a local increased aridity compared to surrounding areas.

In addition, the openness of the area is maintained by a long history of grazing. Dozens of documented roman settlements comprising sheepfolds, along with a rich artifactual and literary evidence supports the presence of a vibrant economy based on sheep herding around La Crau during the roman era (Badan *et al.*, 1995; Motz, 2012). Charcoal analyses suggest that sheep herding was already active during the Late Neolithic/Bronze Age (approx. -2,000 B.C., Henry *et al.*, 2010) and remains of enclosures dating from 3,000 B.C. have been found (Tatin *et al.*, 2013). This use of the area for extensive herding persists to this day, but because of historical changes in the sheep-herding practices and sheep races, archeological evidence of grazing practices is sparse for some historical periods. Remains of sheepfolds with known abandonment times mostly date from the late roman empire period (100-350 A.D. Badan *et al.*, 1995), and the XIXth and XXth centurie) (Henry, 2009). Grazing during the middle ages is thought to be the product of a less-specialized economy based on unimproved sheep races that did not require permanent structures (Henry *et al.*, 2010).

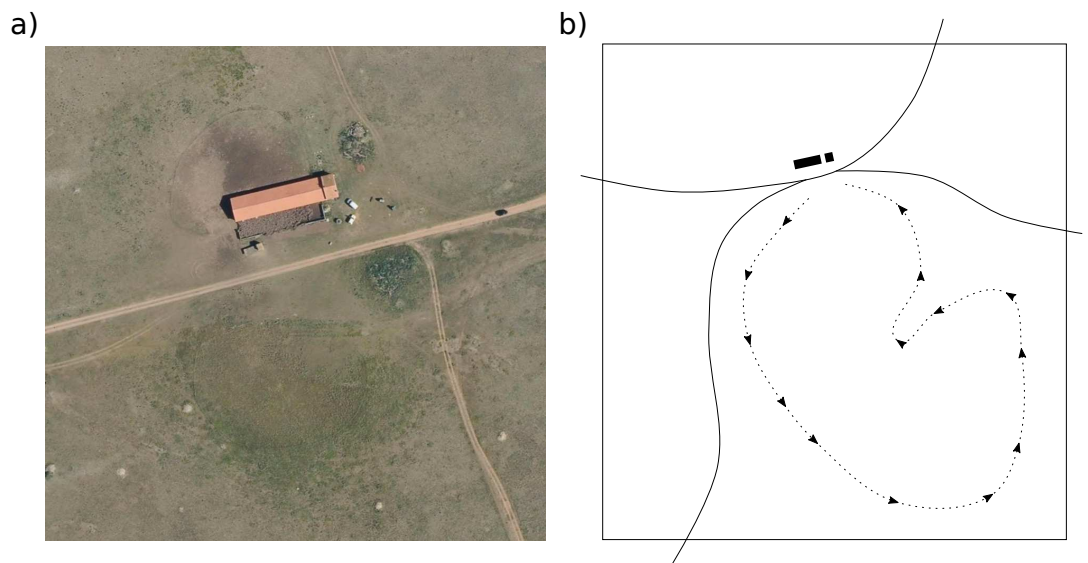


Figure 5.4: (a) Aerial view of a sheepfold (Nouveau-Carton); (b) schematical illustration of the sheepfold within a grazing zone (b, continuous lines indicate roads). Sheep station at night in enclosures laid by the sheepfold (dark green patch in the aerial view), and driven within the zone during the day by the shepherd (b, dotted lines).

In La Crau, flocks of sheep are not confined but driven by shepherds within delimited extensive zones ("Coussouls") of large size (most of them above 70 ha, with a maximum of 540 ha, Tatin *et al.*, 2013). Most of these zones include a sheepfold built next to a shelter for the

shepherd. Sheep are gathered in the sheepfold at night or, because of the large size of the herds (typically 1,600 individuals Tatin *et al.*, 2013), in temporary enclosures next to it. As a result, sheep spend more time near the sheepfold than elsewhere in the area, resulting in

5 a natural gradient of grazing pressure and other impacts related to the presence of sheep (e. g. nutrient enrichment through dung deposition or trampling). This gradient has the greater length towards the south-east, which is the main direction of dominant winds.

Vegetation communities respond to this grazing gradient, resulting

10 in a strong species turnover with ruderal, nitrophilous communities near the sheepfold, and typical "Coussouls"-type communities (dominated by *Brachypodium retusum* and *Asphodelus ayardii*) where grazing is at its lowest (Figure 5.9, Molinier & Tallon, 1950; Gomila, 1987). Two other vegetation types (sometimes referred to as "belts"), corresponding to intermediate levels of grazing have been described, one

15 defined by the presence of *Onopordum illyricum*, and another by the dominance of *Trifolium subterraneum*. In the absence of accurate measurement of the grazing pressure (but see Figure 5.5), we reused these known vegetation types to guide our surveys and ensure that we docu-

20 mented a large range of grazing pressures.

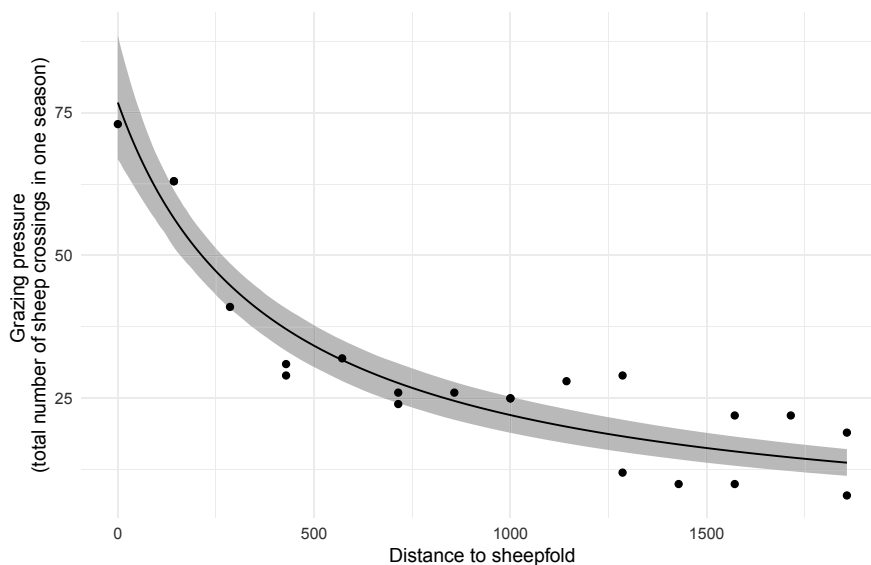


Figure 5.5: Grazing pressure as a function of distance to the sheepfold in the S-E direction. Values are extracted from Dureau (1997) for his study of the "Coussouls de l'Opéra". With the exception of this study, the spatial distribution of grazing pressure within grazing areas remains (to my knowledge) undocumented. The fit is a function of the form $y = a / (1 + b * x)$.

The chapters presented in this thesis are based on a sampling program that spanned three years (2016-2018). Surveys were carried out during spring which is the period where sheep are present (typically from March to June Tatin *et al.*, 2013), and when 80% of plants can be identified to the species level (Bourrely *et al.*, 1983). The surveys comprised three different methods in order to document different aspects of plant communities along the direction of maximum extension of the grazing gradient (south-east). This direction had to be adjusted for some sites, where evidence of disturbance was present in the south-east direction (e.g. abandoned fields).

We documented 16 sites spread out in La Crau: 6 which are currently in use, 4 that were abandoned in the second half on the XXth century, 3 that were abandoned during the first half of the XXth century or XIXth century and 3 roman sites (Table 5.1). Abandonment dates were taken from Henry (2009) and Badan *et al.* (1995). Vegetation communities change in structure and taxonomic composition as spring passes because of the effect of grazing and of the completion of plant life cycles. To make sure this effect was not correlated with any other characteristic of the sites, we randomized during spring the date of survey of each site.

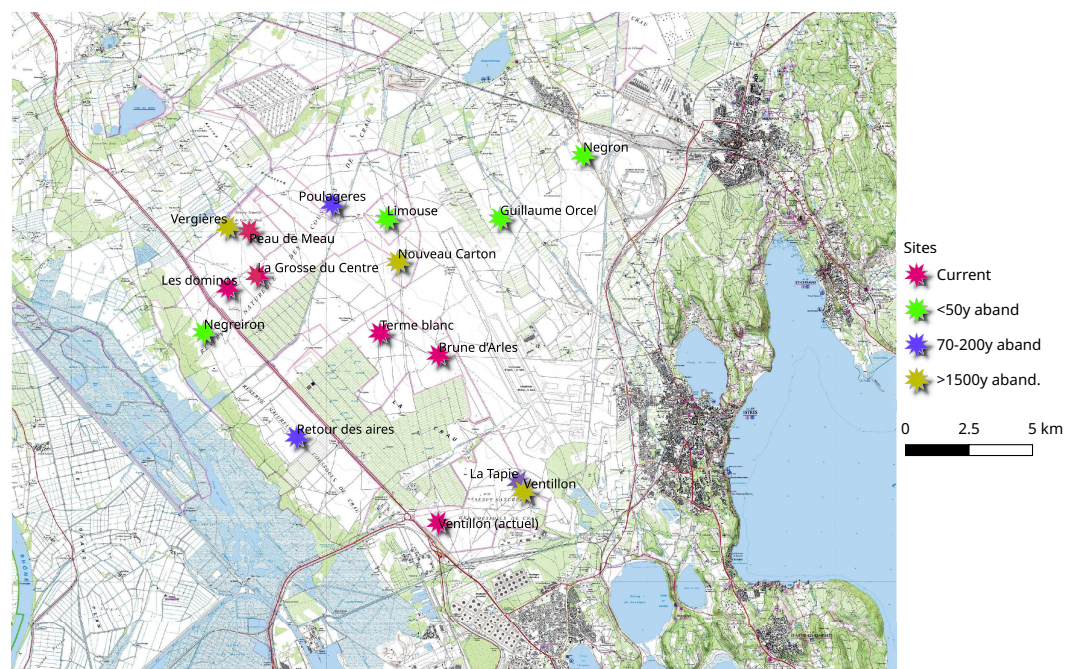


Figure 5.6: Geographical distribution of the sampled sites in the Crau area.

Site	Year of usage starting	Year of aband.
Peau de Meau	-	Currently used
La Grosse du Centre	-	Currently used
La Grosse du couchant (ou Les dominos)	-	Currently used
Terme blanc	-	Currently used
Ventillon (current)	-	Currently used
Brune d'Arles	-	Currently used
Negreiron	-	2008
Limouse	-	2008 (but enclosures are still set up near the entrance)
Guillaume Orcel	<1857	1968-1971
Négron	1857	1975-1978
Poulagères	1780	1857-1944
Retour des aires	1780	1857-1944
La Tapie	1780	1857-1944
Vergières	88	267
Nouveau Carton	60	400
Ventillon (roman)	220	430

Table 5.1: Table of the surveyed sites, with abandonment dates. Most abandonment dates were extracted from Henry (2009) and some others from Badan *et al.* (1995). When a date range is provided, it means that the real date is within the bounds. Dashes indicate unknown dates. Note that Limouse, despite being abandoned in 2008 is still being used to set up enclosures, and was thus removed from the analyses of Chapter 4.

We first carried a quadrat-based survey and recorded the presence/absence of all species in a grid of 5 by 5 20x20 cm subquadrats (resulting in a quadrat size of 1m², Figure 5.8). The first quadrat was placed as close as possible to the sheepfold entrance. The spacing
5 between quadrats then followed a geometric series, i. e. the second quadrat was placed at $d_2=2m$ from the first, then subsequent quadrats were placed such that $d_{n+1} = b * d_n$ where b was between 1.2 and 1.5. Adjustments to this spacing rule were made to avoid local disturbances unrelated to grazing (Figure 5.7 and 5.9). We also recorded an
10 ocular estimate of vegetation cover and height within each quadrat.

Around each 1m² quadrats, we recorded in a 3x6 m area the presence of indicator species (Figure 5.8), which were known to be indicators of the four identified vegetation communities (Molinier & Tallon, 1950; Gomila, 1987). These indicator species were then used to ensure
15 that we documented all vegetation types, hence a large range of grazing pressures, and were used to stop the survey once we reached the "Coussouls"-type community.

We recorded the spatial structure of the vegetation, which is required to compute species associations, using 5 meter-long continuous
20 transects. For current sites, we placed a pair of transects in each of the four vegetation types identified by indicator species. Transects were separated by at least 10m but no more than 75 m (to ensure grazing pressure was similar for the two transects, Figure 5.9). This resulted in 8 transects (4 pairs) per site, except when vegetation types
25 could not be observed, resulting in possible missing pairs of transects. We computed the average distance to the sheepfold for each pair of transect, and used this number to place pairs of transects in abandoned sites.

The start and direction of each transect was decided based on a pen
30 throw, avoiding local disturbances such as dirt roads. We then laid out a measuring tape and recorded the length and position of overlap of each part of plant individual on the transect, along with an index of height ranging from one to five (classes bounds of 0/2/5/10/20/>20 cm, Plate 9 and Figure 10). We also recorded the intersection of pebbles
35 along these transects as they can affect the distribution of plant individuals in space.

It is worthy of note that we recorded the change in species composition along gradients twice: with 1m² quadrats, then with transects. In this thesis, we did not use the quadrat data, because transects were

found to detect more species and thus document more exhaustively the species composition of vegetation communities.

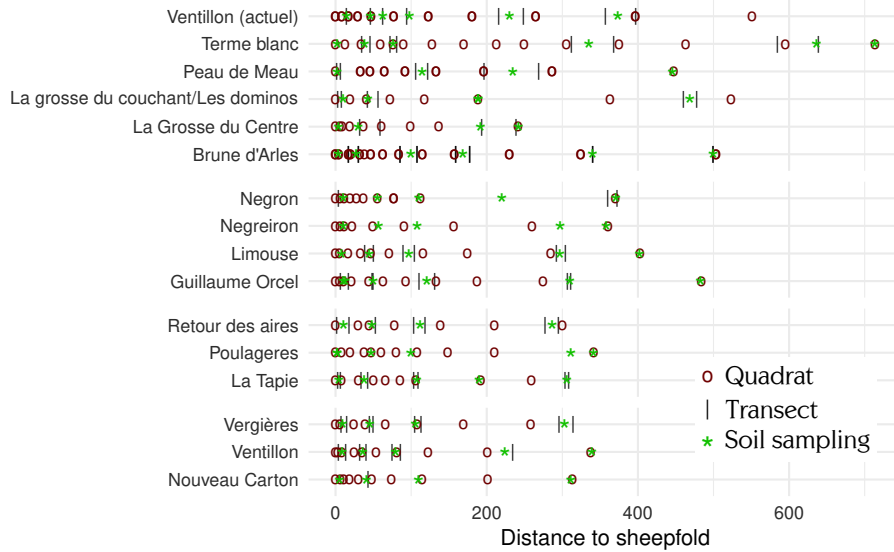


Figure 5.7: Distances of sampling for quadrats, transects and soil samples for each site.

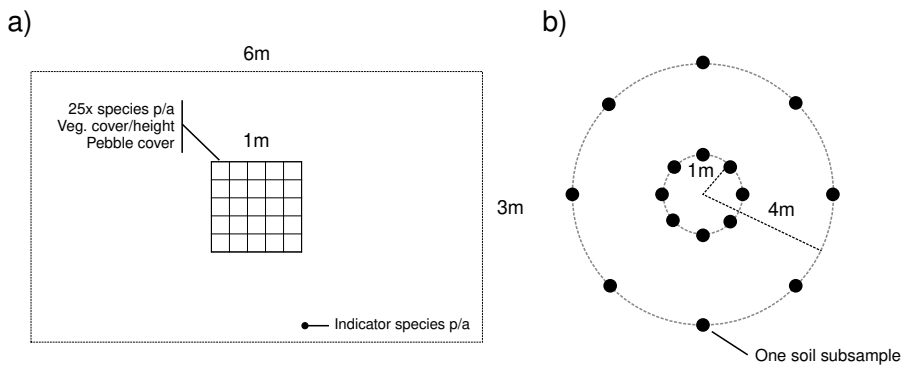


Figure 5.8: (a) Information recorded around each quadrat (p/a stands for presence/absence) (b) Spatial distribution of the 16 sub-samples for soil sampling.

In addition to quadrat and transects, soil samples were taken between Oct. 16 and Oct. 31 2017. One sample was taken at the average distance of each transect pair, and complemented by samples placed at quadrat positions. This resulted in 4 to 6 soil samples per site.

Each soil sample was taken by mixing 16 sub-samples regularly spaced around two circles with radii of 1 m and 4 m around a center point (Figure 5.8). All surface litter was scraped and approximately 125 cL of soil ⁴ was sampled at each point between 0 and 10cm. All subsamples were mixed in a bowl and a compound sample of 400g

⁴ the volume of an individual portion of yogurt

was then taken from the mixed subsamples. This sample was dried for at least 72h at 40°C, sieved to 2mm and sent for analyses (Laboratoire Teyssier⁵). Soil analyses included pH (in water), cation total exchange capacity (Metson method), total CaCO₃, total organic matter, total phosphorus (Olsen method), exchangeable K, Mg, Ca and Na and total Nitrogen.

⁵ route des Junchas - 26460 Bourdeaux, France

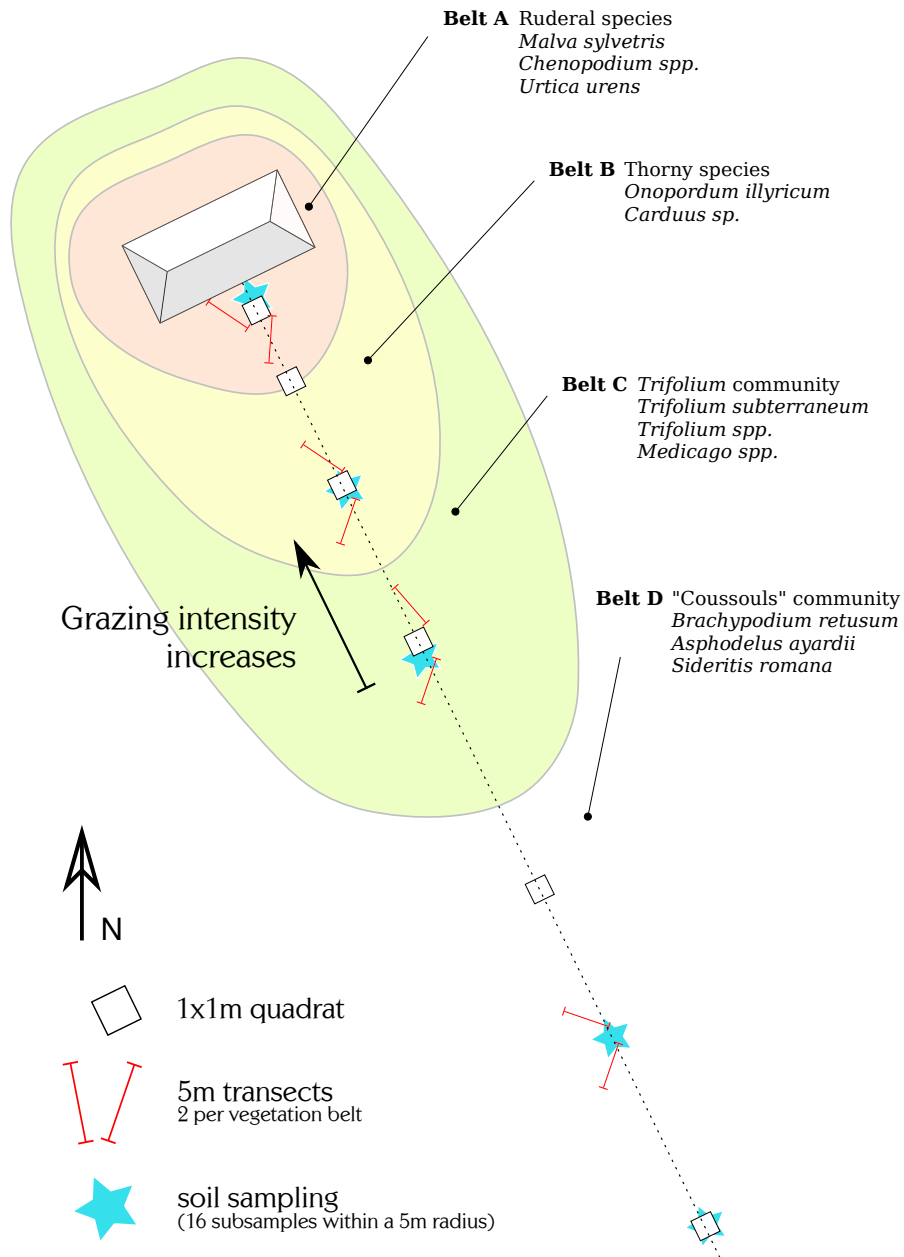


Figure 5.9: Graphical summary of surveys carried out for a given site. Four vegetation belts have been identified based on a set of indicator species, as indicated by colors and labels. Labels indicate notable species present in each belt. Quadrats were carried out at different distances from the sheepfold entrance. In each belt, a pair of 5m transects was laid out to measure the spatial distribution of species individuals. Soil was also sampled at least four times at the average distance of each pair of transects.

APPENDIX 3: UNDERSTANDING PLANT-PLANT ASSOCIATIONS: A MODELLING APPROACH.

To investigate the link between interactions and spatial associations, and to more specifically study the effect of space preemption on that relationship (Box 3.2), we used a spatially explicit, individual-based model.

In this model, plant individuals are represented as discs on a two-dimensional square surface of size $S \times S$. An individual k is defined by the species it belongs to, s_k , its size (radius) r_k and its position in space x_k, y_k . Individuals interact with their neighborhood by affecting the recruitment of new individuals and the mortality of nearby individuals.

Interactions are defined at the species level i.e. all individuals of the same species have the same effect on their neighborhood. An interaction function $\beta_{i \rightarrow j}(d)$ describes the effect of species i on species j at a distance d from the center of the individual of species i .

This function is defined as follows:

$\beta_{i \rightarrow j}(d) = a_{ij}$ if $d < r_i$ (the center of the target individual of the interaction is under the canopy of the interactor) or
 $\beta_{i \rightarrow j}(d) = a_{ij} * \exp(\frac{r_i - d}{\delta})$ if $d > r_i$ i.e. the center of the target individual is outside the canopy.

δ here characterizes the distance at which interactions have an effect. The coefficients a_{ij} describe the strength of the interaction between a pair of species and thus define a species-level interaction network. These interactions are directional, i.e. there is no assumption that a_{ij} is equal to a_{ji} , and intra-specific interactions a_{ii} can be included.

In what follows, we use the subscripts r and m on the $\beta_{i \rightarrow j}$ and a_{ij} to denote that an interaction affects recruitment (r) or mortality (m).

Temporal dynamics

The model is based on discrete time steps. At time step t , the number and position of newly recruited individuals is determined, as well as the number of dying individuals (removed from the system). The changes are then applied to obtain the system state at time step $t + 1$.

MORTALITY At each time step, each individual j has a probability of dying $P(M_j)$ (being removed from the system) that is affected by its interactions with all the N other individuals present in the system:

$$P(M_j) = \text{logit}^{-1} \left(1 + \exp \left(\beta_0^m + \sum_{\substack{k=1 \\ k \neq j}}^N \beta_{s_k \rightarrow s_j}^m (d_{jk}) \right) \right) \quad (5.1)$$

where β_0^m is the log-odds ratio of the base probability p_0^m of dying, $\log(p_0^m / (1 - p_0^m))$. The β_0^m the $\beta_{s_k \rightarrow s_j}^m (d_{jk})$ represent the effect of individual k (of species s_k) on the mortality of individual j at distance d_{jk} .

RECRUITMENT OF NEW INDIVIDUALS At each time step, each individual spreads f propagules randomly in the whole system. Because plants take physical space the recruitment process is divided in two steps: (i) physical access of the propagule to the ground and (ii) successful establishment of the new individual.

For each propagule spread by existing individuals, a random point x, y in the system is chosen and the probability $P(A_{x,y})$ of the propagule reaching the ground is computed. This probability depends on the k individuals whose canopy intersects the chosen point, and the 'permeability' α_{s_k} of those individuals:

$$P(A_{x,y}) = \prod_k \alpha_{s_k} \quad (5.2)$$

α_{s_k} , the permeability, is a coefficient between zero and one that characterize the probability of a propagule going through the canopy of a given species s_k . A higher permeability means that propagule can more easily go through the plant and access the ground. $P(A_{x,y})$ effectively quantifies the probability that a propagules goes through all the canopies that intersect the position x, y – and thus access the ground.

If the propagule accesses the ground at location x, y , its probability of growing there $P(R_j|A_{x,y})$ depends on a base probability p_0 and is

modulated by all the N individuals already present in the system at distance d_k from the propagule landing point:

$$P(R_j|A_{x,y}) = \text{logit}^{-1} \left(1 + \exp(\beta_0^r + \sum_{\substack{k=1 \\ k \neq j}}^N \beta_{s_k \rightarrow s_j}^r(d_k)) \right) \quad (5.3)$$

where β_0^r is the log-odds ratio of the base probability p_0^r of recruitment, $\log(p_0^r/(1 - p_0^r))$.

5 To model the fact that plants compete for resources in addition to space, we introduced a density-dependence on the successful recruitment of new individuals. Each propagule trying to grow in the system has this probability $P(R_j|A_{x,y})$ further reduced depending of the density d_{s_j} (observed cover of species s_j) of the species to which it
 10 belongs:

$$P(R'_j|R_j, A_{x,y}) = P(R_j|A_{x,y})(1 - d_{s_j}) \quad (5.4)$$

A random uniform number is taken between 0 and 1. If it is below the probability $P(R'_j|R_j, A_{x,y})$ then a successful recruitment event takes place (a new individual of species j is added into the system at position x, y).

<i>Parameter</i>	No permeability effect	With perm. effect	Description
S	50	50	Side length of the considered space
r_k	1 for all k	1 for all k	Size (radius) of individual k
a_{ij}^r	0	0	Effect of species j on the recruitment of species j
a_{ij}^m	0	0	Effect of species j on the mortality of species j
p_0^m	0.25	0.25	Base probability of individual mortality
p_0^r	0.5	0.5	Base probability of propagule recruitment
α_{s_k}	1 for all species	0 for all species	Permeability of species s_k
δ	0.001	0.001	Spatial range of interactions.

Table 5.2: Parameters used in the model simulations

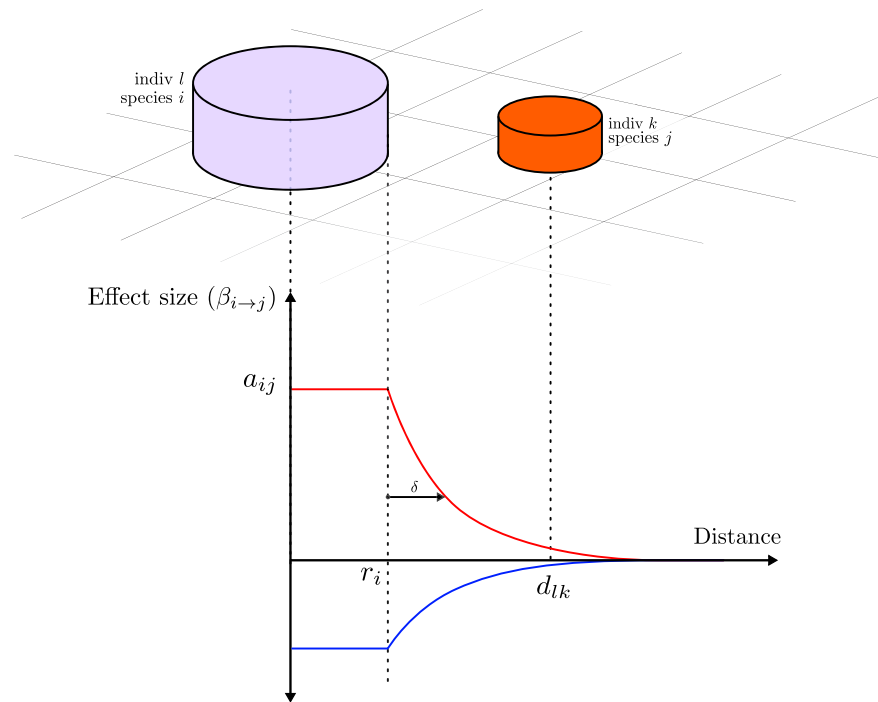


Figure 5.10: Geometric representation of interactions between plants. An interaction between two individuals is defined by a function $\beta_{i \rightarrow j}$ between the pair of species that depend on a pairwise coefficient a_{ij} , the distance between the two individuals d_{kl} and δ that characterizes the distance of interaction. The interaction can increase locally the focal process (mortality or recruitment, red) or a decrease it (blue).

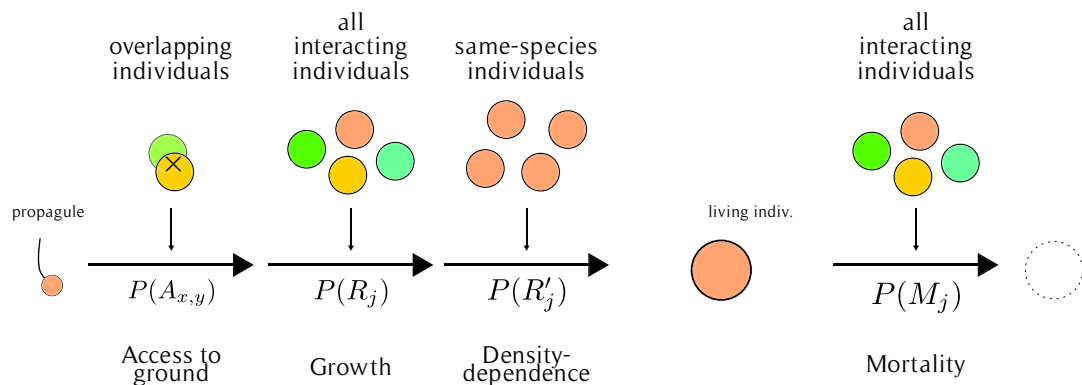


Figure 5.11: Life cycle of a model individual and interactions at play in the model.

Simulations

At the start of the simulations, individuals of each species were randomly added in the system until the density of each species reached $1/S$ (where S is the number of species). At each time step, the variation of species densities were computed by regressing the density of each species against time, using the last 1000 time steps. Simulations were stopped when no species had a temporal variation of its density above 10^{-4} .

For the results presented in Box 3.1, we considered two situations. First, we modelled a situation with no interaction, i. e. all a_{ij} were set to zero. We then considered another situation, but with the physical space occupied by plants taken into account, by setting the permeability of all species α_j to zero (where j is the species, Table 5.2).

APPENDIX 4: ADDITIONAL MATERIAL FOR
CHAPTER 3 AND 4

5.3 CORRELATIONS BETWEEN SES OF ASSOCIATIONS AND TRAN-
SECT COVER/RICHNESS

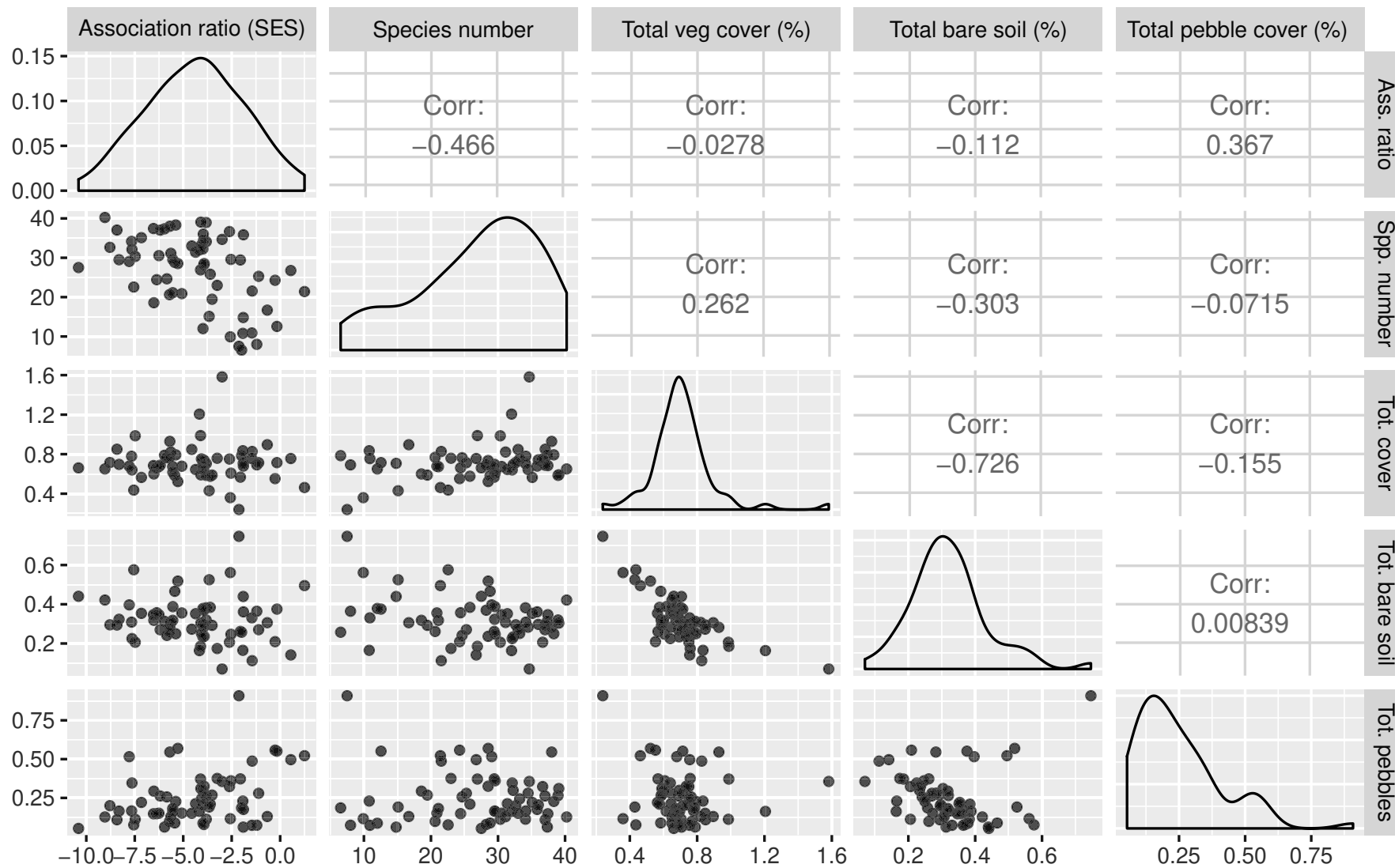


Figure 5.12: Pair plot of the SES of association ratio with vegetation species richness, total cover of vegetation, bare ground and cover pebble. The total cover of vegetation is given in in % of the length of the transect, and can be above 1 as individuals can overlap.

5.4 CORRELATIONS BETWEEN SOIL VARIABLES

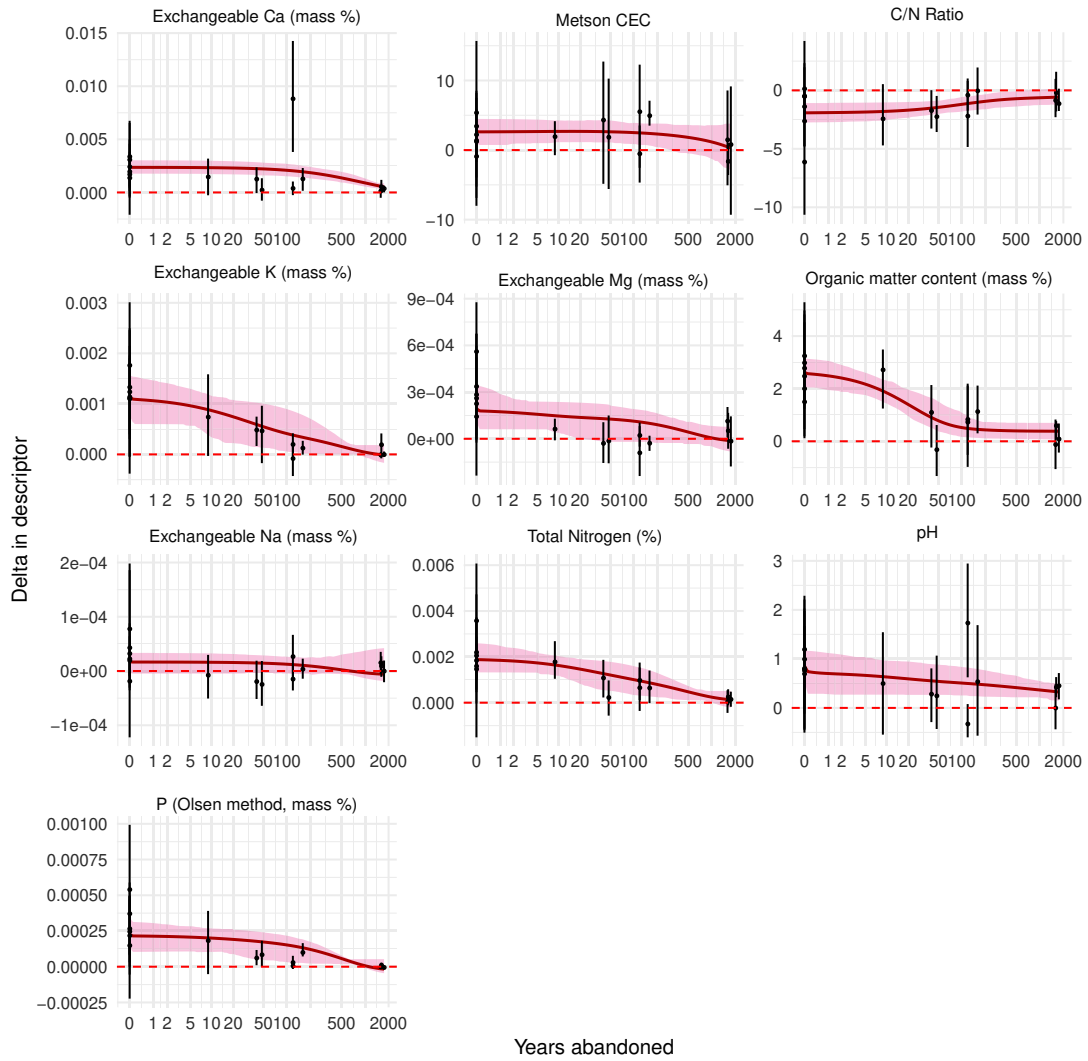


Figure 5.13: Temporal variations of soil spatial change around sites

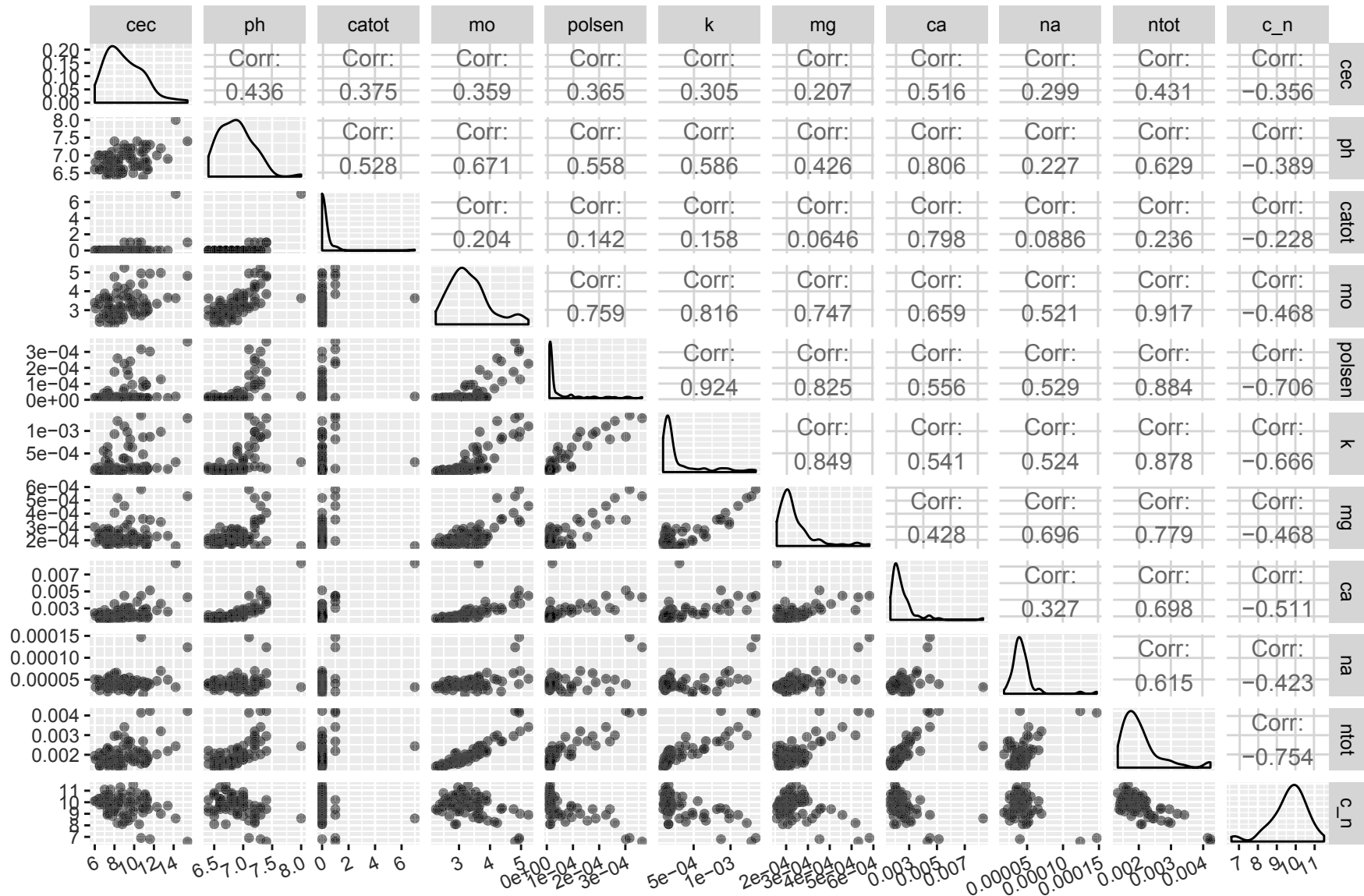


Figure 5.14: Pair plot of relationships and correlation between soil variables

5.5 RATIONALE FOR THE CHOICE OF PRIORS IN CHAPTER 4

To estimate the amplitude of spatial variations at each site of community characteristics (e.g. species richness), we fitted a model of the form

$$y \sim \frac{y_0 * d_{1/2} + (y_0 + \Delta y) * d}{d_{1/2} + d} + \epsilon \quad (5.5)$$

5 To avoid overfitting and keep the parameters y_0 , $d_{1/2}$ and Δy , we used a Bayesian framework with weakly informative priors. Because each different community property has different units, the priors could not be set using absolute values, but were set depending on the observed y values at each site.

10 For each site, sampling yielded a set of values $y_1 \dots y_n$, corresponding to distances $d_1 \dots d_n$ to the sheepfold (n is the number of samples taken at a site, typically 2-4 for transects and 4-6 for soil samples). From this set of points, we extracted y_1 , y_n and σ_y (the standard deviation of y values). We computed the distance at which the y values
15 are closest to their median $x_{1/2}$, and the average value of y at distances greater than this midpoint y_{inf} . A graphical summary of these variables is present in Figure 5.15.

The priors were then set as follow for the parameters:

$$\begin{aligned} \Delta y &\sim \mathcal{N}(y_{inf} - y_1, 3\sigma_y) \\ 20 \quad y_0 &\sim \mathcal{N}(y_1, 3\sigma_y) \\ d_{1/2} &\sim \mathcal{N}(x_{1/2}, 200) \text{ (truncated between 0 and } d_n) \\ \epsilon &\sim \mathcal{N}(0, 3\sigma_y) \end{aligned}$$

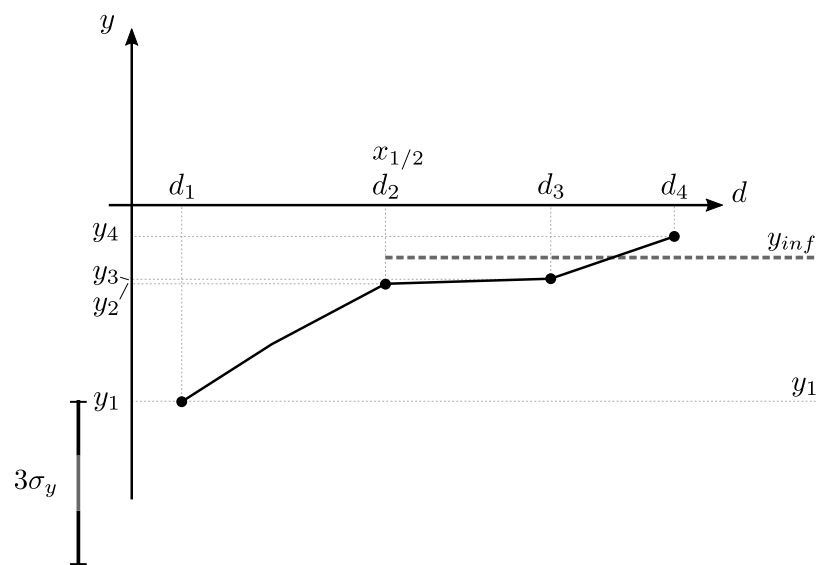


Figure 5.15: Graphical representation of the parameters used for priors. Here, y represents the variable under study (e.g. species richness) and d represents the distance to the sheepfold.

Les changements globaux vont nécessairement produire une réorganisation importante des systèmes écologiques. L'aire de distribution de nombreuses espèces va changer, et le fonctionnement de nombreuses communautés écologiques sera bouleversé. Prédire les conséquences de ces changements, tant à l'échelle biogéographique qu'à l'échelle d'une communauté est donc devenu une question centrale en écologie (Mouquet *et al.*, 2015).

Si l'on peut raisonnablement identifier les changements d'aire de répartition de chaque espèce à partir de ses besoins abiotiques (e.g. (Devictor *et al.*, 2008)), il est difficile de prédire l'effet de perturbations à l'échelle des communautés. En effet, de nombreux systèmes écologiques ne répondent pas linéairement aux perturbations et changements de conditions environnementales, mais peuvent au contraire se réorganiser brutalement, avec parfois des conséquences importantes sur les populations qui dépendent de ces systèmes (Scheffer *et al.*, 2003; Ellis *et al.*, 2011; Estes *et al.*, 2011; Vasilakopoulos & Marshall, 2015; Lever *et al.*, 2014).

Ce type de réponses émerge du fait que les communautés écologiques ne sont pas simples mais complexes, au sens qu'elles sont composées de nombreux éléments en interactions. Les espèces composant une communauté écologique sont liées entre elles par des interactions, qui peuvent parfois être extrêmement nombreuses et diverses. Cette diversité d'interactions rend très difficile la prédiction des effets des perturbations dans les communautés écologiques: par exemple, il est très complexe de prédire les conséquences de l'arrivée d'une nouvelle espèce, comme l'atteste les nombreux "dommages collatéraux" de l'introduction d'espèces dans la lutte contre les ravageurs (e.g., Carvalheiro *et al.*, 2008).

Malgré cette complexité, les réseaux d'interactions écologiques présentent des patrons structurels qui déterminent la réponse de la communauté entière à des perturbations. Par exemple, certains réseaux d'interactions peuvent présenter des boucles de rétroactions, qui amplifient l'effet des perturbations (Wilson & Agnew, 1992). Il a été montré que dans les écosystèmes arides, les interactions facilitatrices entre plantes peuvent conduire à des réorganisations abruptes suite à un changement d'aridité, même faible (Kéfi *et al.*, 2007; Rietkerk *et al.*,

2004). Dans ces systèmes, les plantes poussent en îlots (patch), ce qui permet de maintenir une certaine disponibilité en ressources localement. Lorsque le stress augmente, la présence des interactions facilitatrices et la structure en patch permet d'absorber l'augmentation du stress, jusqu'à un certain point critique où la communauté se dégrade et devient désertique.

Les interactions présentes dans les systèmes écologiques ne conduisent pas toujours à de telles réorganisations abruptes. D'autres études montrent également que la structure de nombreux réseaux d'interactions entre espèces aurait tendance à augmenter la stabilité de la communauté (Lever *et al.*, 2014; Verdú & Valiente-Banuet, 2008; Memmott *et al.*, 2004; Stouffer & Bascompte, 2011; Thebault & Fontaine, 2010).

De nombreux travaux ont donc été dédiés à l'identification de la capacité d'une communauté à répondre aux perturbations. Une première approche, basée sur l'usage d'indicateurs, a été utilisée pour identifier les communautés susceptibles de répondre brutalement à un changement de condition environnementale. Cependant, cette approche n'est applicable que lorsqu'un patron particulier est présent dans le système écologique – une boucle de rétroaction. Dans la plupart des cas, les interactions entre les espèces sont peu connues et il est donc nécessaire de les documenter afin de comprendre comment elles peuvent affecter la stabilité de la communauté. Depuis le début des années 2000 et le développement d'outils permettant l'analyse de réseaux (Morales-Castilla *et al.*, 2015; van Borkulo *et al.*, 2015; Poisot *et al.*, 2012; Delmas *et al.*, 2017), de nombreuses études cherchent à cartographier les interactions entre espèces dans les communautés et de comprendre comment leur structure détermine la résilience du système en entier.

Cette vision unidirectionnelle d'interactions données et fixes, déterminant la stabilité et la résilience d'une communauté écologique, a été cependant critiquée (de Ruiter, 2005). De fait, les interactions entre espèces sont variables, et affectées par les perturbations elles-mêmes. Les nombreux travaux portant sur les réseaux d'interactions plantes-pollinisateurs ont montré que leur structure déterminait la réponse de la communauté aux perturbations (Memmott *et al.*, 2004), mais l'intensité des interactions elles-mêmes était également affectée par les perturbations (Memmott *et al.*, 2007b). Pour décrire la dynamique d'une communauté suite à une perturbation, il est donc nécessaire

de s'intéresser aux variations d'abondances des espèces, mais aussi à celles des interactions.

Il existe donc une relation à double sens entre la réponse d'une communauté aux perturbations, et la structure des interactions qui la composent (Figure 5.16). Le travail présenté ici s'attache à contribuer à ces deux aspects.

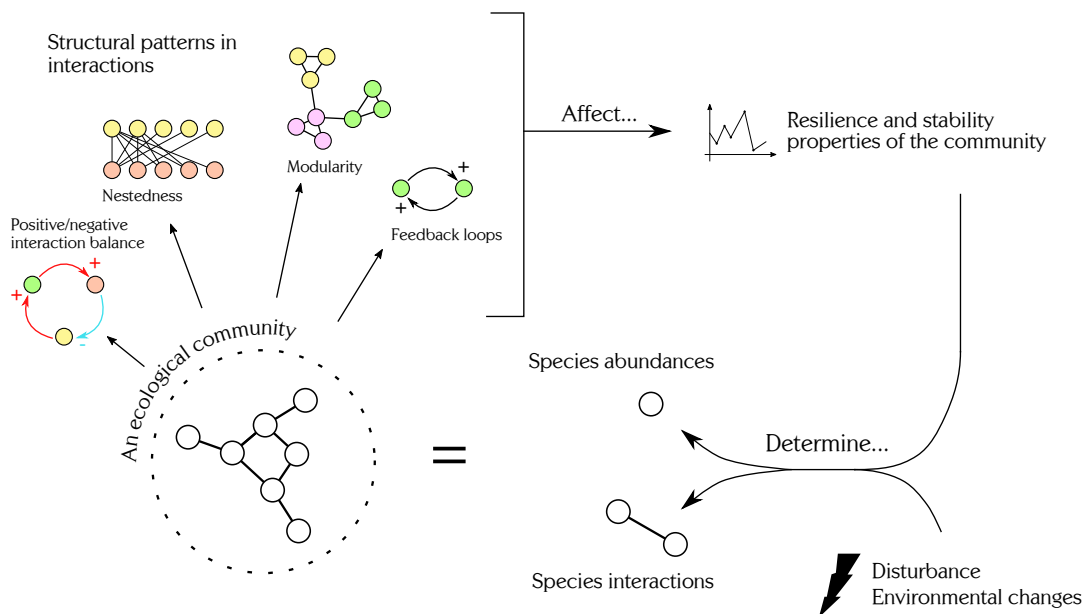


Figure 5.16: Un communauté écologique est définie par un ensemble d'espèces et leurs interactions. Ces interactions peuvent présenter certains patrons structurels (par ex. des boucles de rétroaction) qui détermine la résilience et la stabilité de la communauté – autrement dit sa réponse au perturbations. Cette dernière, combinée avec les caractéristiques effectives des d'une perturbation affecte en retour les abondances et les intensités d'interaction entre espèces

5.6 OBJECTIFS DE LA THÈSE

Ce travail de thèse contribue à lier interactions écologiques et réponse aux perturbations des systèmes écologiques, en utilisant les communautés végétales comme modèles d'étude.

Les deux premiers chapitres sont centrés sur un patron d'interaction spécifique: les boucles de rétroactions. Quand elles sont présentes, la communauté écologique est susceptible de répondre de manière abrupte à des changements environnementaux.

Plus spécifiquement, le premier Chapitre pose la question suivante: *peut-on identifier des boucles de rétroactions à partir de patrons de multi-*

*modalité*⁶?. Ce travail est basé sur des approches dites d'"analyse de potentiel", et révèle, dans un écosystème subalpin protégé, certaines communautés où des boucles de rétroactions pourraient produire des réorganisations importantes et potentiellement abrupte des communautés végétales à des perturbation à venir.

Le deuxième Chapitre représente un effort de synthèse de l'état de l'art concernant les indicateurs de faible résilience (en anglais *early-warning signals*) au sein d'un paquet R. Le but de ce travail est de permettre une dissémination plus ample de ce type de méthode afin de tester leur pertinence dans des systèmes empiriques.

Les deux derniers chapitres sont centrés sur les variations des interactions au sein des communautés végétales le long de gradient de perturbation. Ils se basent sur un jeu de données collecté au cours des trois ans de doctorat en plaine de Crau (Bouches-du-Rhône, France).

Le chapitre trois décrit l'effet du pâturage sur les variations des réseaux d'associations autour de sites actuellement utilisés. En particulier, il pose la question de savoir *quel est l'effet d'un stress biotique sur l'importance relative des interactions positives et négatives dans les communautés végétales ?*.

Le quatrième et dernier chapitre adopte une perspective temporelle et étudie la dynamique temporelle des réseaux d'associations plante-plante. En particulier, il pose la question suivante: *quelle est la résilience des réseaux d'associations ? Comment se compare-t-elle à d'autres aspects de la communauté ?* Pour ce faire, une approche par chronoséquence est adoptée, en documentant les variations des réseaux d'associations plante-plante autour de sites abandonnés à des dates connues.

⁶ La multimodalité fait référence au fait que des observations peuvent être distribuées en "paquets", produisant une distribution à plusieurs modes

5.7 PRINCIPAUX RÉSULTATS ET DISCUSSION

5.7.1 *Peut-on identifier des boucles de rétroactions à partir de patrons de multimodalité ?*

Dans le premier chapitre, nous avons identifié des zones où une
5 boucle de rétroaction est potentiellement présente, sur la base d'une multimodalité dans les observations de composition spécifique des communautés végétales. En utilisant des données décrivant les conditions environnementales locales ainsi que des résultats connus de la littérature, nous avons pu identifier des mécanismes potentiels qui
10 sous-tendraient la présence d'une boucle de rétroaction. En particulier, dans les zones sèches des clairières sub-alpines, il est possible qu'une boucle de rétroaction positive entre végétation et qualité du sol puisse diminuer la résilience de ces communautés aux perturbations (Figure 5.17). Ce résultat est précieux dans le cadre de la conservation de ces espaces, mais il ne permet pas d'identifier complètement la réponse possible des ces communautés à une perturbation.
15

Lorsqu'une boucle de rétroaction positive est présente dans un système, elle peut produire des états stables alternatifs. Dans le cas des zones sèches des clairières, les communautés dominées par *C. filifolia*
20 pourraient persister indéfiniment dans cet état s'il correspondait effectivement à un état stable. Or, ceci ne peut être démontré sur la base de la multi-modalité seule, celle-ci pouvant aussi émerger de situations sans états stables alternatifs (Encadré 1.1).

La manière la plus directe de tester le type de dynamique présente
25 dans ces communautés serait via l'acquisition de données temporelles ou expérimentales (Petraitis, 2013). Cependant, d'autres approches corrélatives telles que celles proposées par les indicateurs de résilience (Chapitre 2) ou l'utilisation d'associations plante-plante pourraient être envisagées.

30 5.7.2 *Quel est l'effet d'un stress biotique sur l'importance relative des interactions positives et négatives dans les communautés végétales ?*

Dans le Chapitre 3, nous avons décrit les variations des interactions plante-plante le long de gradients de stress biotique. L'étude s'est concentrée sur un patron structurel important des réseaux plante-
35 plante: le ratio entre associations positive et négative. Ce patron est fortement lié à la manière dont les communautés de plantes peuvent

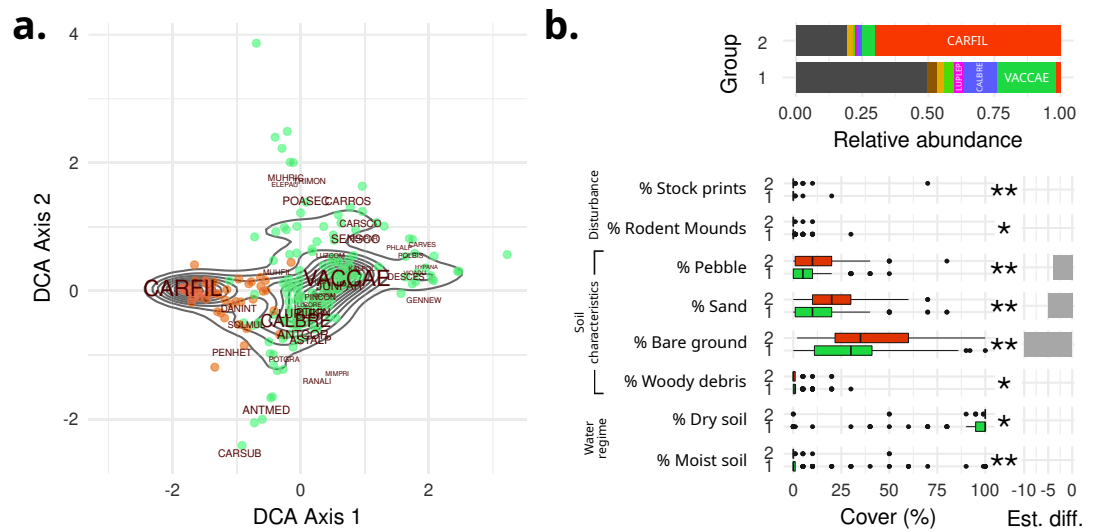


Figure 5.17: La composition spécifique des communautés des zones sèches des clairières subalpine est bimodale (a), avec une communauté dominée par *C. filifolia* (2) contrastant avec une communauté plus diverse (1). Ces deux groupes diffèrent principalement en terme de granulométrie du sol (Gravier - *pebble* - et sable - *sand*) et de pourcentage de sol nu (*Bare ground*). La présence d'une bimodalité dans la composition spécifique à des niveaux hydriques similaires, et son lien avec la qualité du sol pourraient suggérer une boucle de rétroaction positive entre végétation et qualité du sol.

répondre aux perturbations. Une dominance de la facilitation entre plante à l'échelle de la communauté peut potentiellement produire des boucles de rétroactions (Kéfi *et al.*, 2016), ou encore permettre à un nombre plus grand d'espèces de coexister (Saiz *et al.*, 2018).

5 Les communautés végétales étudiées présentent un déficit d'associations positives, et par conséquent un ratio entre associations positives et négatives toujours négatif. Cela suggère que la compétition est le mécanisme le plus structurant dans ces communautés de plante. Le stress biotique, et plus spécifiquement le pâturage et le piétinement
10 par les moutons diminue la force et le nombre des associations entre espèces (Figure 5.18). Sous des niveaux importants de stress, les interactions entre espèces jouent un rôle vraisemblablement mineur sur la dynamique de la communauté végétale.

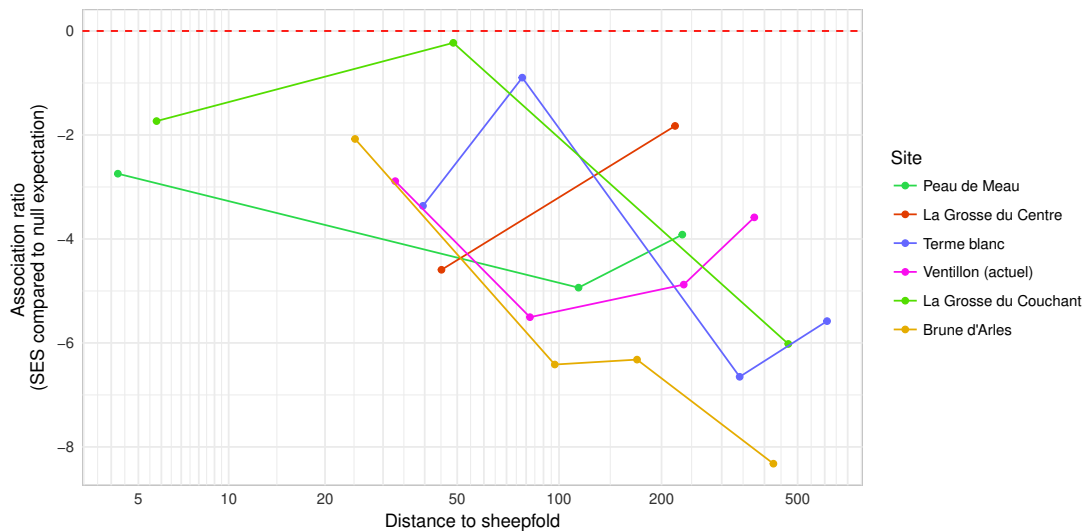


Figure 5.18: Variations du ratio d'association (taille d'effet comparé à l'attendu aléatoire) en fonction de la distance à la bergerie. Le ratio est proche de l'attendu aléatoire proche de la bergerie, ce qui marque une diminution de l'importance des associations dans la structuration de la communauté dans ces zones à forte perturbation (pâturage très important). Ce ratio devient plus négatif à mesure que le pâturage diminue (la distance augmente), mettant en évidence une importance accrue de processus de compétition entre espèces.

15 L'étude plus en détail de la tendance de chaque espèce à réaliser des associations négative ou positive révèle que celle-ci est corrélée principalement à son abondance totale dans un transect et non à la hauteur moyenne de la plante. Cela suggère que la ressource en compétition est l'espace et non la lumière (Figure 5.19).

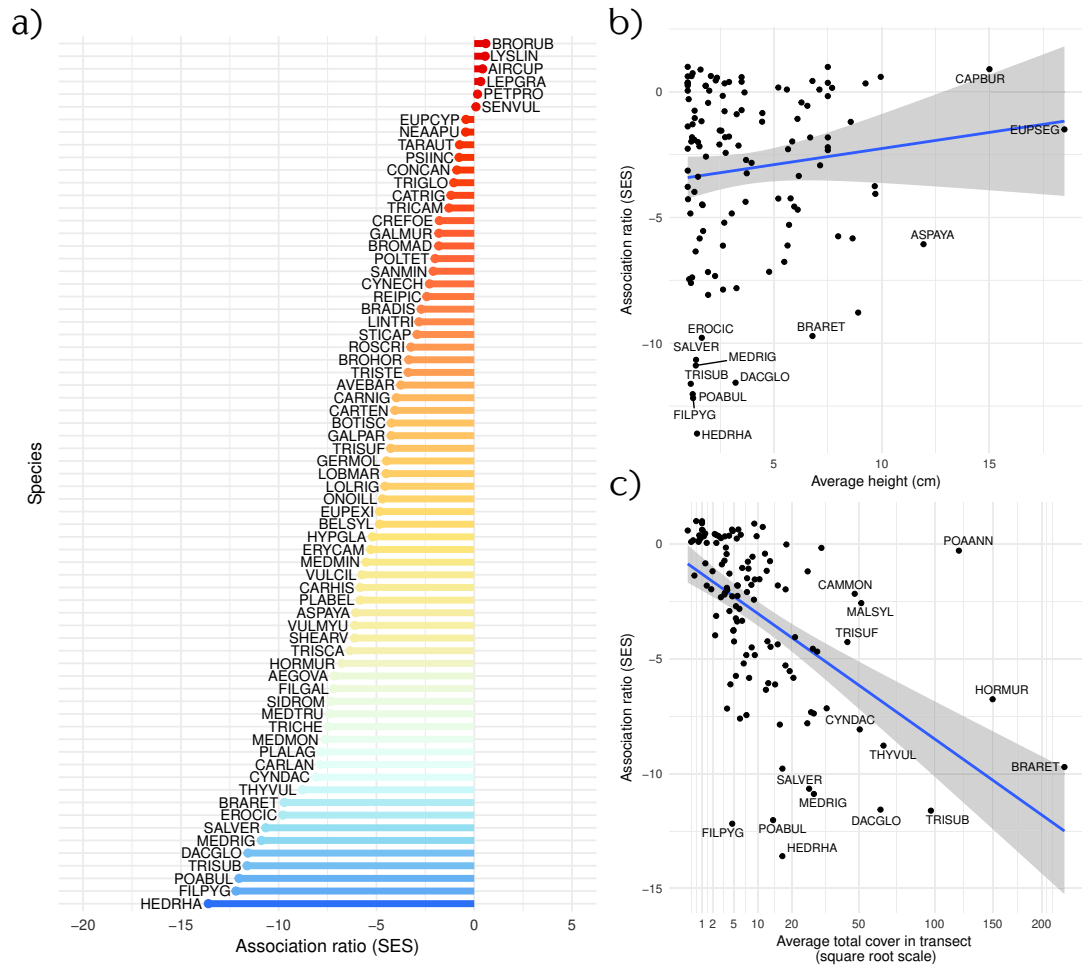


Figure 5.19: (a) Taille d'effet comparée à l'attendu aléatoire du ratio d'association pour chaque espèce (seulement les espèces avec au moins 200 associations potentielles sont incluses dans ce graphe). (b,c) Relation entre la taille d'effet du ratio d'association et la hauteur moyenne de la plante (b) ou la couverture totale de la plante dans les transects où elle est présente (c).

5.7.3 *Quelle est la résilience des réseaux d'associations plante-plante ?
Comment se compare t'elle à celle d'autres aspects de la communauté ?*

Les réseaux d'association plante-plante montrent des variations importantes dans le temps, mais ces variations sont corrélées entre sites. Cela suggère que les associations entre espèces dans une communauté végétale contiennent beaucoup d'information sur les processus qui déterminent sa dynamique temporelle. Le ratio d'associations (importance des associations positive par rapport aux associations négatives) est, dans le temps comme dans l'espace, principalement négatif, suggérant que la compétition pour l'espace est le mécanisme dominant à tous les stades de la pseudo-succession. Des variations plus fines sont cependant présentes dans ce ratio, correspondant à des phases clés de la dynamique végétale. Les valeurs de ratios d'associations les plus faibles ont été observées pour les bergeries récemment abandonnées, suggérant un rebond de compétition pour l'espace lorsque les conditions abiotiques sont toujours favorables (abondance en nutriments), mais que la pression de pâturage est relâchée. Les sites romains montrent également des variations importantes de valeurs d'associations, avec une augmentation de ce ratio dans les communautés les plus éloignées de la bergerie.

Ces variations du ratio d'associations s'inscrivent dans un schéma de variation plus général avec la quantité de nutriments présents dans le sol (Figure 5.20), avec un changement de signe de la relation entre variation en nutriments et variation en ratio d'associations. En dessous de cette valeur seuil, une diminution de la quantité d'azote produit une diminution de l'importance des associations négatives, suggérant une diminution de l'importance des interactions avec la diminution de productivité. Cette constatation est en accord avec l'hypothèse du gradient de stress (Stress Gradient Hypothesis, SGH, Callaway *et al.* 2002), mais il serait intéressant de confirmer que la limitation en nutriment a bien lieu dans les communautés de plantes pauvres en azote.

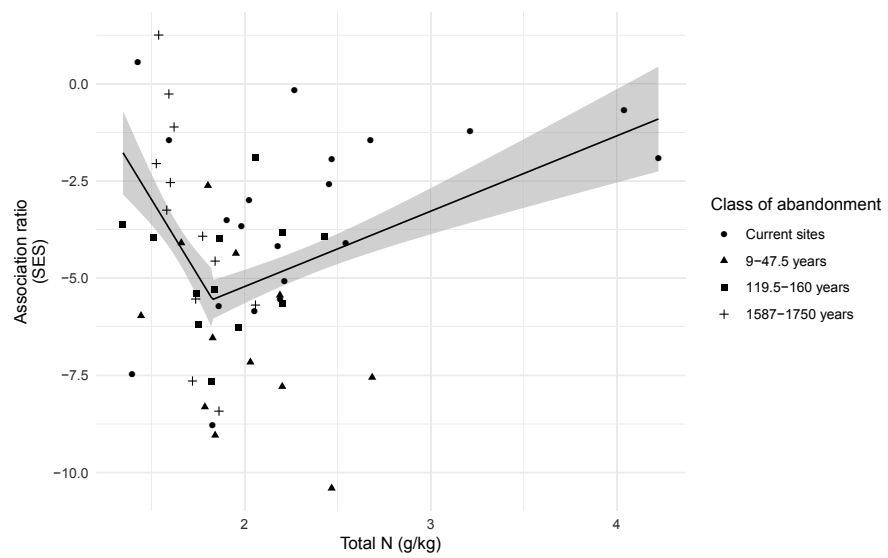


Figure 5.20: Variation du ratio d'association en fonction de la quantité d'azote total du sol. Les droites de régression correspondent à une régression par segments (*piecewise regression*).

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ABSTRACT

Ecological systems are not simple but composed of many different elements (species, for example) interacting with each other. These networks of interactions exhibit structural properties that determine ecological systems' ability to absorb and recover from perturbations. Mapping interactions along with their changes in time and space is therefore key to understand and predict empirical communities' response to global changes. In this thesis, we used plant communities as model systems (i) to explore how spatial patterns may help identify feedback loops which make communities more fragile to upcoming changes and (ii) to map species interactions in empirical communities and describe how they change along stress gradients and recover from perturbations. To do so, we used two datasets documenting plant communities in subalpine meadows (USA) and Mediterranean grasslands (France). Our results show that feedback loops can be inferred to some extent from the spatial patterns of plant communities and hence help identify communities that may respond more abruptly to perturbations. Going to a more detailed level of description, plant-plant interactions (as measured through spatial associations) were shown to respond strongly and consistently to stress but exhibited a weak resilience to disturbances. This work shows that plant-plant interactions – which are linked to the response of the community to perturbations – can be uncovered using spatial patterns. It paves the way towards a better understanding and a better anticipation capacity of how ecological communities might reorganize when subject to disturbances.

RÉSUMÉ

Les systèmes écologiques sont complexes car composés d'une multitude d'éléments en interaction. Ces interactions, entre espèces par exemple, forment des réseaux qui présentent des propriétés structurelles déterminantes pour la réponse du système écologique entier aux perturbations. Pour mieux identifier cette réponse, il est donc important de cartographier les interactions présentes dans les communautés écologiques et de comprendre leurs variations dans le temps et l'espace. Dans ce travail, nous avons utilisé les communautés de plantes comme systèmes écologiques modèles afin (i) d'identifier à partir de patrons spatiaux certains motifs présents dans les réseaux d'interaction écologiques (les boucles de rétroaction) et (ii) de cartographier les réseaux d'interactions (tels que mesurés par les associations spatiales entre plantes) le long de gradients de stress. Pour ce faire, nous avons utilisé deux jeux de données documentant des communautés de plantes de clairières subalpines (Etats-Unis) et méditerranéennes (La Crau, France). Nos résultats montrent que les boucles de rétroaction peuvent être inférées à partir des patrons spatiaux présents dans les communautés de plantes, permettant ainsi d'identifier des communautés pouvant répondre de manière abrupte aux perturbations. Les interactions entre plantes (déduites de leurs associations spatiales) dépendent fortement du stress appliqué à la communauté, et présentent une résilience faible aux événements de perturbation. Ce travail montre que les interactions entre plantes peuvent être cartographiées in situ à partir des associations spatiales. Il ouvre la voie vers une meilleure compréhension et capacité d'anticipation de la réponse des communautés écologiques face aux perturbations.