Université d’Avignon et des Pays de Vaucluse
École doctorale 536 «Sciences et Agrosciences»

Universidade Federal de Minas Gerais
Programa de Pós-graduação em Ecologia, Conservação e Manejo da Vida Silvestre

TESE

apresentada como requisito para a obtenção do título de Doutor da Universidade Federal de Minas Gerais e da Université d’Avignon et des Pays de Vaucluse (Cotutella)

Composition, phenology and restoration of *campo rupestre* mountain grasslands - Brazil.

Composição, fenologia e restauração dos campos rupestres - Brasil.

Soizig Le Stradic

A tese foi defendida dia 14 de dezembro de 2012 perante a seguinte banca:

William J. Bond	Professor University of Cape Town, South Africa	Relator
Grégory Mahy	Professor Université de Liège Belgium	Relator
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Essa tese foi preparada no Institut Méditerranéen de Biodiversité et d’Écologie e no Laboratório de Ecologia Evolutiva e Biodiversidade

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(Cotutelle)

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Composition, phénologie et restauration de pelouses d’altitude, les *campos rupestres* - Brésil.

Soizig Le Stradic

La thèse a été soutenue le 14 Décembre 2012 devant le jury composé de:

William J. Bond	Professeur University of Cape Town, South Africa	Rapporteur
Grégory Mahy	Professeur Université de Liège Belgium	Rapporteur
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Thèse préparée au sein de l’Institut Méditerranéen de Biodiversité et d’Écologie et du Laboratório de Ecologia Evolutiva e Biodiversidade

A montanha pulverizada

Chego à sacada e vejo a minha serra,
a serra de meu pai e meu avô,
de todos os Andrades que passaram
e passarão, a serra que não passa.

Era coisa dos índios e a tomamos
para enfeitar e presidir a vida
neste vale soturno onde a riqueza
maior é a sua vista a cotemplá-la.

De longe nos revela o perfil grave.
A cada volta de caminho aponta
uma forma de ser, em ferro, eterna,
e sopra eternidade na fluência.

Esta manhã acordo e
não a encontro.
Britada em bilhões de lascas
deslizando em correia transportadora
entupindo 150 vagões
no trem-monstro de 5 locomotivas
- trem maior do mundo, tomem nota -
foge minha serra, vai
deixando no meu corpo a paisagem
mísero pó de ferro, e este não passa.

Carlos Drummond de Andrade.

A mes deux grand-mères,

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Et si j'ai oublié quelqu'un qu'il me pardonne.

General view of *campos rupestres*. Photo credit S. Le Stradic.

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At T0, more graminoids were observed in TSa than in TSt ($p<0.01$, Table 26). Graminoids decreased with time ($p<0.001$), more drastically in TSt than in TSa ($p<0.05$, Table 26). On the contrary, more forbs were observed in TSt than in TSa at

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Introduction

1.Context

In recent decades, the relationship between human society and the environment have been highlighted and have resulted in increasing awareness of the importance of ecosystems in maintaining and improving the collective well-being of humanity, particularly because the world is now changing rapidly. Current economic development and its impact on the environment are unsustainable: degradation of remaining natural habitats is decreasing long-term human welfare in favor of short-term economic gain. Obviously this kind of development does not deliver human benefits in the way that it should: it increases the vulnerability of some of human populations and creates large disparities around the world while the level of poverty remains high (Balmford et al. 2002, MEA 2005, Carpenter et al. 2006). Humans have already greatly altered Earth's surface, especially through land-use changes, which are responsible for about half of terrestrial ecosystem transformations (Daily 1995, Vitousek et al. 1997, Chapin et al. 2000, Klink & Moreira 2002, Sala et al. 2005, Steffen et al. 2007), leading to the current Anthropocene epoch (Steffen et al. 2007, Zalasiewicz et al. 2010).

Ecosystem services are the human benefits provided directly or indirectly by ecosystem functions (i.e., the properties or processes of ecosystems) (Costanza et al. 1997). These services, such as climate stabilisation, drinking water supply, flood alleviation, crop pollination, and recreation opportunities, among others (Osborne & Kovacic 1993, FAO 1998, Chapin et al. 2000, Balmford et al. 2002, MEA 2005, Sala et al. 2005), depend to some extent on biodiversity (Rands et al. 2010) (Figure 1). However, many recent human activities have led to biodiversity erosion (Rands et al. 2010, Barnosky et al. 2011), altering functional diversity and modifying ecosystem properties (Loreau et al. 2001) (Figure 1). The Millennium Ecosystem Assessment (MEA 2005) report indicates that 12–16% of the world's species will be lost over the period of 1970 to 2050 due to habitat loss alone (Sala et al. 2005) and that currently approximately 60% of the ecosystem services are being degraded (MEA 2005). Biodiversity responses to environmental changes (land use and climate changes) are likely to be complex (Chazal & Rounsevell 2009), but it is now widely accepted that these changes in biodiversity also alter ecosystem processes and modify the resilience and resistance of ecosystems to further environmental changes (Chapin et al. 2000, Figure 1). According the stability-diversity hypothesis, biodiversity should promote resistance and resilience to disturbance (McNaughton 1977, Pimm 1984, Tilman & Downing 1994, Chapin et al. 2000, McCann 2000, Loreau et al. 2001). This implies that ecosystem stability depends on the ability of communities to harbor species or functional groups that can respond to disturbances in myriad ways. In this sense, biodiversity provides a kind of "insurance" against environmental fluctuations (Chapin et al. 2000, McCann 2000, Loreau et al. 2001).

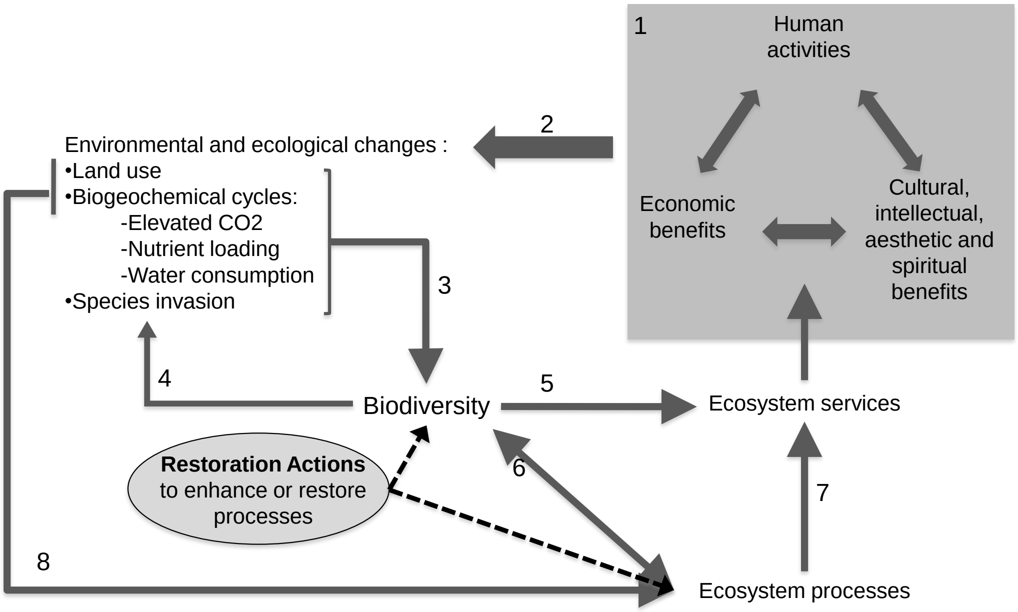

Figure 1: The role of biodiversity and restoration activities in global change. Human activities (1) are now causing environmental and ecological changes of global significance (2). Through a variety of mechanisms, these global changes contribute to changing biodiversity (3), and changing biodiversity feeds back on susceptibility to species invasions (4). Changes in biodiversity, can have direct consequences for ecosystem services impacting human economic and social activities (5). In addition, changes in biodiversity can influence ecosystem processes and feedback to further alter biodiversity (6). Altered ecosystem processes can thereby influence the ecosystem services that benefit humanity (7). Global changes may also directly affect ecosystem processes (8). Restoration actions are represented by dashed lines. (Adapted from Chapin et al. 2000, Palmer & Filoso 2012, Le Stradic unpublished).

Effective conservation of biodiversity is fundamental to maintaining ecosystem processes, but the traditional arguments in support of ecosystem conservation alone are insufficient (Turner & Daily 2008, Rands et al. 2010). Marked economic benefits generated by the conservation of undisturbed natural habitats are an incentive to preserve nature (Balmford et al. 2002, Ring et al. 2010, Nahlik et al. 2012). However conservation in certain locales can be limited because the areas in question are either too small, too few, or too degraded to preserve biological processes and diversity (Anderson 1995; Hobbs & Norton 1996). In this context, ecological restoration can be a viable strategy for enhancing biodiversity and improving ecosystem services (Hilderbrand et al. 2005, Rey-Benayas et al. 2009, Bullock et al. 2011, Schneiders et al. 2012), especially with the development of Payment for Ecosystem Services (PES) schemes, which are designed to compensate actions that maintain, improve, and provide some ecosystem services (Turpie et al. 2008, Farley et al. 2010, Farley & Contanza 2010). The Strategic Plan for Biodiversity specifies that at least 15% of degraded ecosystems must be restored by 2020 (CBD 2011). Roberts et al. (2009) emphasize that “our planet’s future may depend on the maturation of the young discipline of ecological restoration”. However, focusing ecological restoration on ecosystem services should not come at the expense of biodiversity conservation, and damage prevention should always be considered first because restoration possibilities cannot be an excuse for ongoing damage or destruction of ecosystems (Young 2000, Hobbs 2007, Hobbs & Cramer 2008). Young (2000) highlights the important points that 1) restoration can improve conservation efforts but has to remain a secondary resort to the preservation of habitats and 2) the use of *ex-situ* “restoration”, such as mitigation, will never produce an outcome resembling the perfect reversal of habitat and population destruction.

2.Objectives

This thesis contributes both to 1) an improved theoretical understanding of the functioning of a type of neotropical mountain grasslands, the *campos rupestres* and their dynamics following strong disturbances and 2) novel insights into the implementation of restoration techniques for such environments (Figure 2).

Like all research in restoration ecology and ecological restoration projects, this thesis follows the three steps outlined in the SER primer (SER 2004) (Figure 2):

1) Identify the reference ecosystem & gather information on it (Chap 1, 2 & 4);
2) Identify the disturbance, its effects and assess resilience (Chap 3);
3) Identify which restoration methods can provide an efficient means of initiating the resilience of degraded areas (Chap 3, 4 & 5.

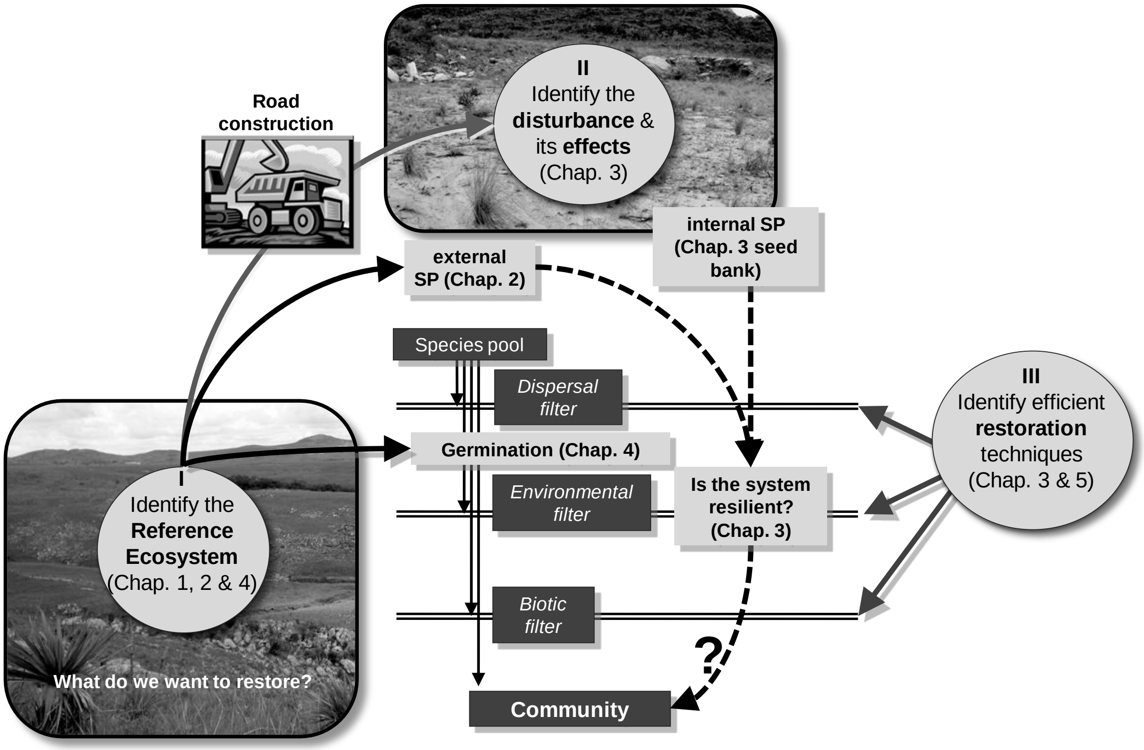

Figure 2: General overview of the organization of this thesis highlighting the steps recommended by the SER primer (SER 2004). Pale grey boxes correspond to the different steps developed in the thesis's chapters, dark grey boxes represent the filters structuring the community (see section 4.5 Assembly rules: How do species assemble into communities?). Full black arrows: studies related to the reference ecosystem; full grey arrow: disturbance which destroyed pristine *campos rupestres*; dashed black arrows: we have assessed if degraded *campos rupestres* are resilient to strong disturbance from the external or internal species pool; dashed grey arrows: restoration techniques we have tested, act on different filters.

As indicated, the first objective of this thesis is to identify and describe the reference ecosystem (Chapters 1, 2 & 4) (Figure 2) and to answer the question, **what do we want to restore?** A clear definition of the restoration target is essential to developing a basis for monitoring progress and for assessing restoration success. Fulfilling this first objective comes down to demonstrating that *campos rupestres* are a mosaic of grasslands with at least two distinct plant communities (i.e. sandy and stony grasslands), each having specific compositional, structural and phenological patterns. One of our goals in performing the phenological study is to define the local species pool, which means assessing global flower and fruit production and determining what species can potentially contribute to recolonisation via their seeds.

The second objective is to identify the main effects of a strong disturbance on soil and seed bank composition and to assess the resilience of *campos rupestres* (Chapter 3) (Figure 2); in other words, **are *campos rupestres* resilient to strong disturbances?** Land-use changes provide an opportunity to study vegetation recovery and community assembly (Prach & Walker 2011). According to theoretical models, three main filters, which, when applied to the global species pool determine the ultimate community structure. These are the dispersal, environmental and biotic filters (Keddy 1992, Lortie et al. 2004) (Figure 2). In order to establish whether restoration is actually necessary, we surveyed plant community characteristics, chemical and physical soil properties, and seed banks, in the areas that were first degraded eight years ago by the harsh but common activity of road construction-related quarrying. Our objective was to determine how this type of degradation modifies soil properties, and whether or not the internal species pool recomposed itself with target species following the degradation. The main questions addressed in the third part of this thesis are (Chapter 3, 4 & 5) (Figure 2): **Can we restore *campos rupestres*?** By using restoration experiments, we identified the factors that limit resilience by acting first on the dispersal filter, then we aimed to overcome the dispersal filter and the germination and to improve environmental conditions, and finally we aimed to overcome the dispersal, the abiotic and part of the biotic filters. Our ultimate aim was to identify efficient techniques for restoring these species-rich grasslands along with, hopefully, some services they once provided. Some evidence has shown that restoration actions that focus on biodiversity are also effective at supporting the increased provision of ecosystem services (Rey-Benayas et al. 2009), even where it is incorrect to assume that restoring biodiversity must inevitably enhance ecosystem services, or vice versa (Bullock et al. 2011).

The ecosystem in the present study is the *campos rupestres*, or tropical mountain grasslands located into the Cerrado domain, or Brazilian savanna. We chose to work with herbaceous species because the herbaceous stratum is the quintessence of these grasslands and regulates fundamental processes, such as post-fire recovery, water balance, annual productivity or mineral cycling (Sarmiento 1984). Moreover, in recent decades, herbaceous ecosystems, which represent more than 31% of world vegetation, have been drastically damaged and fragmented throughout the world (Green 1990, Hoekstra et al. 2005, Gibson 2009). Biodiversity scenarios indicate that grassland ecosystems, and tropical ecosystems in general, are expected to be the most strongly impacted by land-use changes in the future (Chapin et al. 2000, Sala et al. 2000, 2005); in this context, the Cerrado has already been classified as a priority area for conservation due to the anthropogenic pressures that it faces (Myers et al. 2000, Mittermeier et al. 2004, Hoekstra et al. 2005). It is therefore important to preserve and restore diverse grasslands since it can aim at conserving both biodiversity and locally important ecosystem services, and this is particularly true of mountain grasslands (CBD 2004, MEA 2005).

Having discussed the background and objectives of this study, we now turn to the main relevant theoretical concepts as well a good general overview of the field.

3.Restoration ecology

3.1. Definitions

Ecological restoration is the practice of restoring ecosystems and **restoration ecology** is the science upon which this practice is based (SER 2004). Restoration ecology is intended to offer clear concepts, models, methodologies and tools for practitioners. As will be discussed later, restoration ecology also plays an important role in ecological theory.

Ecological restoration is also the process of intentionally aiding in the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004). **Ecological restoration *sensu stricto***, is an intentional activity that initiates or accelerates ecosystem recovery in order to re-establish all of the attributes of the reference ecosystem: its biotic integrity in terms of species composition and community structure, its functional processes, its sustainability in terms of overall resilience and resistance to disturbances, its productivity, and its services (SER 2004, Clewell et al. 2005) (Figure 3). This objective is theoretical and often unrealistic: it is very difficult to achieve complete restoration of an ecosystem back to its original state (Lockwood and Pimm 1999, Palmer et al. 2006, Choi et al. 2008, Hobbs et al. 2011). Alternative, less ideal ecological restoration activities can also be carried out, and these usually fall under the designation **ecological restoration *sensu lato*** (SER 2004). Examples include such activities as **rehabilitation** or **reclamation** (SER 2004) (Figure 3). **Rehabilitation**, in which pre-existing ecosystems are also taken as models, places its emphasis on the re-establishment of some function, ecosystem processes, productivity, or services, and this may involve only partial re-establishment of the original ecosystem attributes (SER 2004) (Figure 3). Clearly this can be said of a majority of restoration projects.

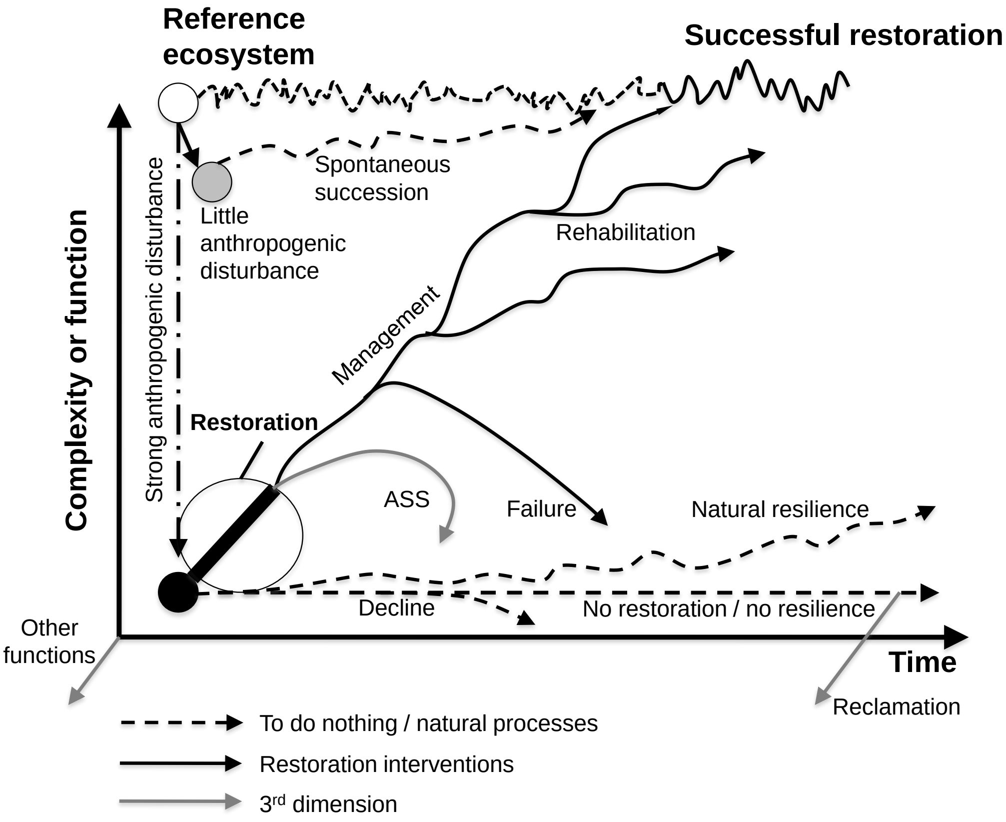

Figure 3: Schematic representation of the trajectory of a natural or semi-natural ecosystem over time. Full lines correspond to trajectories resulting from restoration interventions (reference ecosystem trajectory, rehabilitation or failure); dashed lines represent natural processes, or trajectories observed without interventions, and grey lines, the functions evolving in a third dimension, ASS (Alternative stable state). (Modified from Hobbs & Norton 1996, Prach & Hobbs 2008, Buisson 2011).

3.2. Goals & Reference Ecosystem

In each restoration project, the fundamental starting point is to define realistic and achievable goals based on a reference ecosystem, and to plan the restoration process and measure its success accordingly (SER 2004, Hobbs 2004, Hobbs & Cramer 2008). In setting goals and deciding what type of intervention, if any, is required, it is essential to identify a reference ecosystem i.e. to establish what we want to restore, and to understand exactly how the reference works (Hobbs 2004, Hobbs & Cramer 2008). It is possible to use the pre-disturbance state as reference ecosystem, but only if enough is known about historical conditions and/or if large areas of the pre-disturbance state are still found in the landscapes (Choi et al. 2008, Buisson 2011). The reference can also be defined as whatever state is expected to arise out of the natural progression of the ecosystem's historical trajectory (Aronson et al. 1995, Clewell et al. 2005). To be realistic and reachable, goals should include multiple endpoints of functional or structural equivalence (Hilderbrand et al. 2005). Indeed, if reference ecosystems are dynamically resilient to stresses or endogenous disturbances, they may occur in a number of alternative states (Aronson et al. 1995, Suding & Hobbs 2009). Restoration therefore attempts to bring an ecosystem to its reference trajectory so that it may evolve normally along its appropriate successional pathway, and this allows it to synchronize with any potential variations of the natural ecosystem (Figure 3).

Restoration goals are obviously subjective because they are determined by humans, although there may be significant reference to nature (Choi et al. 2008). Setting restoration goals involves a set of values, including the ethical and philosophical bases for our actions, concepts of “good” restoration, humanity’s place in nature, the influence of indigenous peoples on the environment, and local popular support, which is often closely linked with socio-economic sustainable development (Hobbs 2004, Aronson et al. 2006, Hobbs 2007, Choi et al. 2008). Finally, economic feasibility will determine the level and extent of intervention that can be considered (Hobbs 2007).

3.3. Type of intervention

The assessment of current, degraded conditions, relative to the reference ecosystem, is followed by considerations of which intervention possibilities are likely to improve the situation (Hobbs & Cramer 2008). There are three approaches to restoring a disturbed site: (1) to rely completely upon spontaneous succession: the “do nothing” approach, (2) to exclusively adopt technical measures: interventionist approaches, and (3) to combine both previous approaches by manipulating spontaneous succession toward a target (Hobbs & Cramer 2008, Prach & Hobbs 2008, Hobbs et al. 2011). The “do nothing” approach could be as simple as removing of the cause of disturbance (Palmer et al. 2006, Hobbs & Cramer 2008), and is most effective in cases where the disturbance intensity is low to moderate, e.g. in traditional land-use abandonment (Prach & Hobbs 2008). In case of harsh to extreme disturbances, intervention is often necessary: the recovery through natural processes either does not occur or does so too slowly (Palmer et al. 2006, Hobbs & Cramer 2008, Prach & Hobbs 2008, Hobbs et al. 2011). It is therefore important to determine whether active restoration is required, and this involves the identification of restoration thresholds, which are essentially barriers (arising from either abiotic or biotic factors) to recovery of degraded systems (Hobbs 2007, Hobbs & Cramer 2008, Suding & Hobbs 2009).

3.4. Legislation

Among the most drastic disturbances, quarrying and mining activities cause major soil damage, leading to uncontrolled soil erosion and water quality alteration (Pimentel et al. 1995, Valentin et al. 2005). As a result, many countries have passed laws that require the reclamation, rehabilitation, or restoration of quarries and mines once exploitation is over. Examples of such legislation include, in the US, the Surface Mining Control and Reclamation Act of 1977; in Australia, the National Environment Protection Measures Act; in Canada, the Law for environment quality (L.R.Q., c. Q-2, a. 20, 22, 23, 31, 46, 70 & 87); in France, Décret n° 77-1133 du 21/09/77 pris pour l'application de la loi n° 76-663 relative aux ICPE; and in Brazil, Law 9605/1998, Law 9985 18/07/2000 (linked to article 225, § 1°, paragraphs I, II, III and VII of the Federal Constitution (1988)), article 19 of Law 4771/65, the technical standard ABNT 13030, SMA 08/2008 legislation (Aronson et al. 2011)).

3.5. Restoration Ecology & Community Ecology

The study of ecological theory and the science of restoration are mutually beneficial. This is because ecological restoration allows the implementation of restoration ecology experiments, which can form the basis of important experimental tests of ecological theory (Young 2005, Palmer et al. 2006). Bradshaw (1987) has even described restoration a kind of acid test of our ecological understanding (Figure 4). To paraphrase, if the processes at work in an ecosystem are not understood, then reconstructing the ecosystem is unlikely. Theoretical ecology thus provides fundamental knowledge that can serve as helpful guidance for restoration ecology. Conversely, restoration ecology results and outcomes can help us to comprehend how natural communities work and can reveal the deficiencies in our theoretical understanding of such systems (Palmer et al. 1997, 2006) (Figure 4).

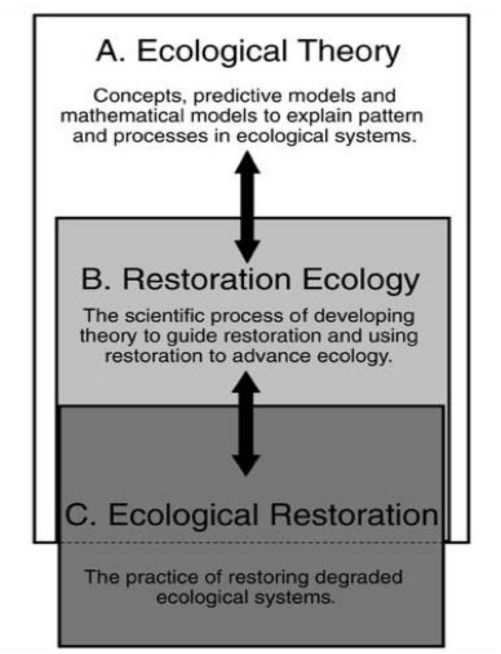

Figure 4: The relationship between ecological theory, restoration ecology, and ecological restoration can be viewed in a hierarchical fashion (Palmer et al. 2006).

Central questions in community ecology are: How do species coexist? What factors govern the composition and abundance of species in communities? These questions are also central to ecological restoration because they can be applied to the reference ecosystem, and thereby serve to frame the discussion on how exactly to reach the restoration goals. Land use changes and ecological restoration provide a good opportunity to study community assembly, since restoration tends to initiate or accelerate species assembly (Prach & Walker 2011).

4. Community Theory

4.1. Ecological community

At the beginning of the 20th century, two contrasting perceptions of communities were proposed. Clements (1916) favored a holistic conceptualization, and considered the different species in a community to be tightly integrated and interdependent, essentially assimilating into a kind of super-organism. In contrast, Gleason (1926) adopted more of an individualistic notion of plant association noting that “an association is not an organism, scarcely even a vegetational unit, but merely a coincidence”.

The formal definition of community is an assemblage of organisms of multiple species living in a specified place and time (Vellend 2010). Conceptually, it would be useful when describing a community to take into account the spatial context of local communities within the region, and to consider the role of historical events in driving the relevant ecological patterns and processes (Agrawal et al. 2007, Ricklefs 2008).

Patterns of species composition and diversity, observed on a local scale, are the outcomes of disturbance, succession, and filter models within the broader community (Young et al. 2001, White & Jentsch 2004, Weiher et al. 2011) This represents a convergence of concepts from diverse areas coming together to provide ideas relevant to ecological restoration (Hobbs et al. 2007a): the succession theory comes from plant biology, and assembly rules come from the study of animal, rather than plant communities (Young et al. 2001)

4.2. Community ecology

Community ecology is the study of a set of species co-existing at a given time and place. It deals with patterns in the diversity, abundance, and composition of species within communities, and of the processes underlying these patterns. There has been considerable debate surrounding the ability of community ecology to provide useful guiding principles, given the complex nature of communities themselves. There are vast numbers of processes, each system appears unique (Lawton 1999, Simberloff 2004), and this amounts to a perfect storm in which well-constructed models fail to provide general rules about many species communities. In addition, Ricklefs (2008) questions the degree to which ecological communities are sufficiently coherent for objective study.

To address this, Vellend (2010) provides a conceptual synthesis of community ecology and points out that in the most general sense, patterns in the composition and diversity of species are influenced by four classes of processes: selection (deterministic fitness difference between individuals of different species), drift (random changes in species' relative abundance), speciation (the creation of new species), and dispersal (the movement of organisms across space) (Figure 5). McGill et al. (2006) assert that community ecology should be re-built using general traits, as opposed to specific species, to create a more quantitative and predictive science, bringing general patterns to community ecology.

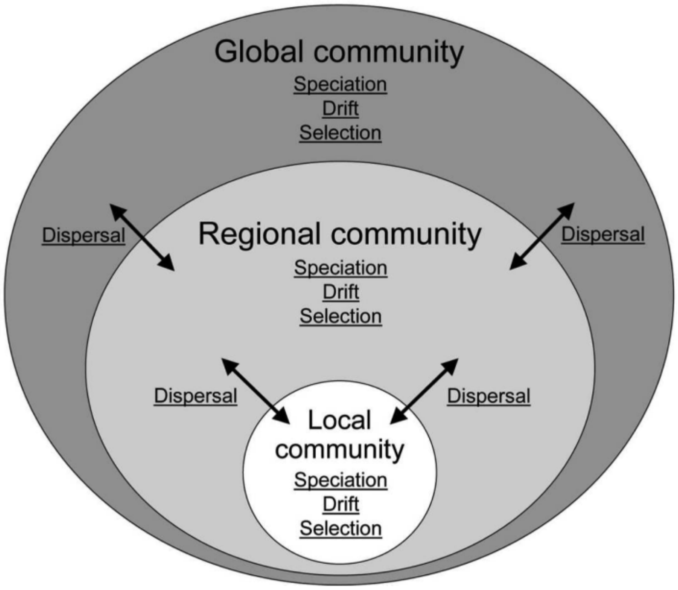

Figure 5: The theory of community ecology (from Vellend 2010)

Community ecology is currently crucial to understanding why and how the environment affects communities across space, which helps to predict the ecological impact of global changes (Simberloff 2004, McGill et al. 2006).

4.3. Disturbance & Resilience

A **disturbance** is a relatively discrete event in time that disrupts an ecosystem, community, or population structure, changing resource availability along with the underlying substrate or physical environment regardless of whether these are perceived as “normal” for the given system (White & Pickett 1985). Disturbances have a wide range of effects, which may depend upon the state of the communities prior to the disturbance, among other biotic and physical factors (White & Pickett 1985, White & Jentsch 2001). Disturbances occur on a wide range of spatial and temporal scales, affecting all levels of organization (White & Jentsch 2004). Disturbances usually produce heterogeneous and patchy effects (White & Pickett 1985), which alter competition and impact the structure of communities (Temperton & Zirr 2004).

Disturbance can have a variety of quantitative and qualitative causes; they can be exogenous or endogenous. Exogenous disturbances are those in which the force originates outside the ecosystem; endogenous disturbances are those in which the force originates either within the ecosystem or as a byproduct of its successional development (White & Jentsch 2004). Disturbance descriptors, such as temporal and spatial characteristic, magnitude, specificity, and synergism are used to describe disturbance regimes. Disturbances vary greatly in severity, and so do their consequences, producing a large variation in potential succession, which ranges from primary to secondary (see 4.4 for definitions) (White & Jentsch 2004).

The type of intervention required for restoration depends greatly on the type and extent of the damage to the ecosystem (Hobbs 2007). Before launching a restoration project, one must therefore first identify the processes that led to the degradation and determine whether restoration is actually necessary (Clewell et al. 2005). By evaluating the resilience and resistance of an ecosystem, one can assess the impact of disturbances. **Resistance** (also called ecological resilience, Beisner et al. 2003, van Nes & Scheffer 2007) is defined as the ability of ecosystems to withstand the disturbance (it is commonly associated with the width of the basin of attraction, representing the amount of disturbance necessary to change the system's state); while **resilience** (also called recovery rate or engineering resilience, Beisner et al. 2003, van Nes & Scheffer 2007) is the process/rate/time of recovery for ecosystems returning to equilibrium following a disturbance or period of stress (usually connected with the slope of the basin of attraction) (Leps et al. 1982, Lockwood 1997, Mitchell et al. 2000, Beisner et al. 2003, van Nes & Scheffer 2007). Hysteresis appears when a parameter is changed, resulting in landscape changes, and leading to a change in the position of the equilibrium point; following a perturbation, the return trajectory leads the community to a different state (i.e. alternative stable state (ASS)), from which it is difficult to return to the original state (Beisner et al. 2003).

The alternative stable state model suggests that while communities are structured and restricted to some extent, they can also end up in any of a number of possible ASS. This is because an element of randomness is inherent in all ecosystems (Beisner et al. 2003, Temperton & Hobbs 2004). If communities/ecosystems follow this model, their recovery from degradation will follow one of several possible trajectories, depending on their particular histories, the availability and order of arrival of organisms, and some element of randomness (Lockwood & Samuels 2004, Temperton & Hobbs 2004). With this in mind, a restoration effort should aim at placing the resilience of the degraded system on a desirable trajectory. However, since alternative states exist, restoration can result in unexpected trajectories (Lockwood & Samuels 2004; Temperton & Hobbs 2004).

Although disturbance does play a role in community structure, restoration efforts cannot simply reintroduce species. Rather one must consider using and/or restoring natural disturbances and assess how they influence the sustainability of the restored community (Palmer et al. 1997). Moreover, disturbance management can be a useful tool in ecological restoration, especially if the degraded community is locked in an undesirable state, because it makes it possible to move the community to a more desirable state (Hobbs & Norton 1996, Temperton & Zirr 2004).

4.4. Succession: How do ecosystems change following a disturbance?

According to Clements (1916), ecological succession is the sequential replacement of species following a disturbance. Succession deals with the overall changes in substrates and the associated species turnover, and deals with such issues as facilitation, competition, herbivory, invasive species, priority effects, biodiversity loss, climate change, and plant-soil interaction in both the short and long term (Walker et al. 2007, Walker & Del Moral 2009, Prach & Walker 2011). Today, the notion of community climax is used far less frequently because stable succession end points are too simplistic of an idea. However, the fact remains that some terrestrial communities do tend to return to pre-disturbance states in a more or less predictable way (Young et al. 2001), especially if the disturbance is endogenous. Primary succession involves species change on substrates with little or no biological legacy following severe disturbances (e.g. lava flows, landslides and mine wastes). Secondary succession begins with some biological legacy (i.e. internal species pool) following a disturbance, such as fire or abandonment of agricultural lands (Walker & Del Moral 2003). Both types of succession can take place after natural or anthropogenic disturbances (Walker & Del Moral 2003).

In case of extreme disturbances, such as volcano eruptions, urban clearances, and mine and quarry exploitations, regeneration processes resulting from primary succession are usually dependent on the availability of propagule sources in the surrounding areas because seed banks are usually destroyed (Bakker & Berendse 1999, Bradshaw 2000, Shu et al. 2005). Succession in terrestrial communities involves the arrival of plants and their establishment, along with changes in the physical environment and the nature of the resources generated by the community itself (Bradshaw 2000, White & Jentsch

2004). Spontaneous vegetation succession can be determined by both landscape (i.e. proximity of seed sources) and local site factors (Rehounková & Prach 2006).

Ecological restoration can attempt to initiate, accelerate, improve, slow down, turn back, or mimic successional sequences (Palmer & al. 1997, Walker et al. 2007, Prach & Walker 2011). Understanding the possible role of site factors and external forces in driving succession is essential for predicting, and possibly even manipulating, further succession (Young et al. 2001, Walker & del Moral 2003, Del Moral et al. 2007, Walker & del Moral 2009, Prach & Walker 2011). Both success and failure can be important factors in improving restoration practices and the development of theoretical concepts concerning succession (Hobbs et al. 2007b).

4.5. Assembly rules: How do species assemble into communities?

The concept of pool–filter–subset underlies the main approach in community assembly theory (Weiher et al. 2011). Local assemblages are non-random and viewed as subsets of the regional species pool determined by assembly rules that are a set of abiotic and biotic filters (Keddy 1992, Weiher & Keddy 1995, Gotelli & McCabe 2002, Temperton & Hobbs 2004, Temperton & Zirr 2004, Weiher et al. 2011). Contrary to succession, assembly theory focuses mainly on the final community composition (White & Jentsch 2004). A hierarchical filter model was adapted by Lortie et al. (2004) (Figure 6) to include abiotic filters that determine whether a species would colonize, establish and persist in a given habitat through (i) stochastic processes (i.e. the dispersal filter); (ii) specific tolerances of species to the site local abiotic conditions (i.e. the environmental filter); (iii) a set of biotic filters that are imposed by positive and negative direct and indirect interactions among plants; and (iv) direct interactions with other organisms (both are biotic filters) (see also Fattorini & Halle 2004, Weiher et al. 2011) (Figure 6). New species may come in from the surroundings via dispersal (i.e. from the external seed pool), from the seed bank, or from surviving individuals (i.e. the internal seed pool) (Fattorini & Halle 2004) (Figure 6). The relative importance of each process varies in space and time (Lortie et al. 2004), and their dependence on each other arises from feedback loops (Belyea 2004; Fattorini & Halle 2004). White & Jentsch (2004) suggested adding a disturbance filter that acts acts on survival, reproduction, colonizing ability and adaptations. Ecosystem degradation may affect some or all processes (Belyea 2004) and lead to a reduced species pool at the degraded site (Figure 6).

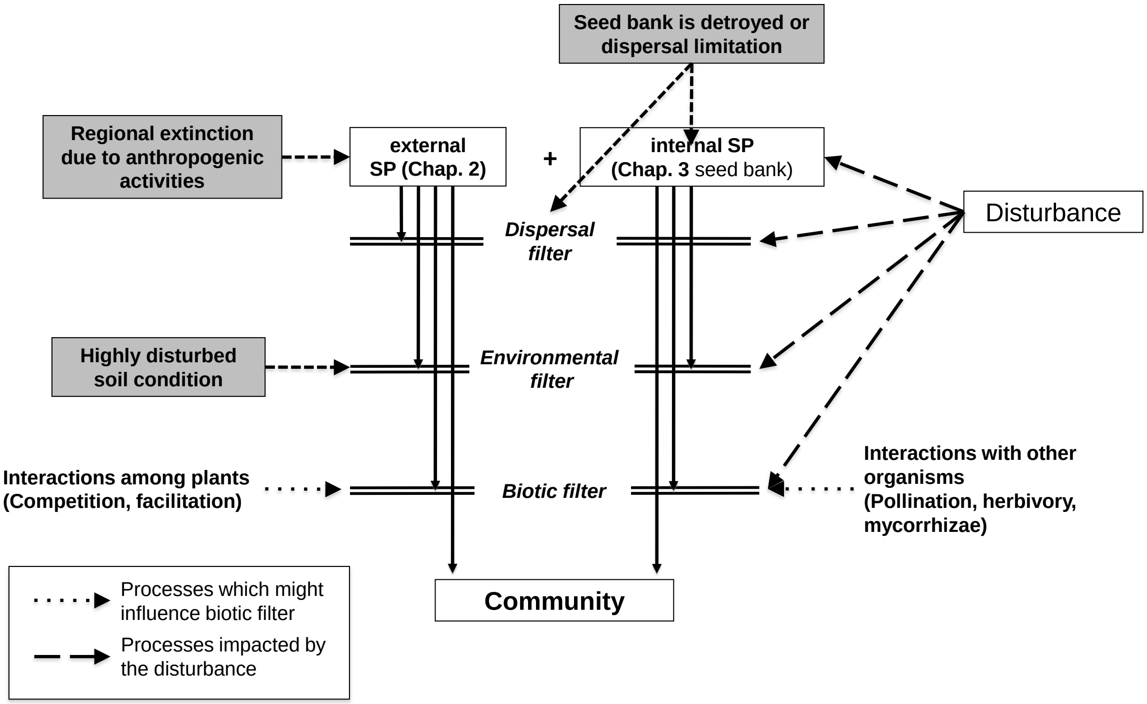

Figure 6: The main processes / filters that structure a plant community. Each process/filter is represented by a pair of horizontal lines. Solid arrows depict the movement of species through the filters. Grey boxes indicate how ecosystem degradation may affect the different levels (inspired by Lortie et al. 2004, Fattorini & Halle 2004, Belyea 2004, Buisson 2011, Le Stradic unpublished).

The inherent goal in many restoration activities is to bypass dispersal and environmental constraints, thereby allowing desired species to arrive and to establish (Belyea 2004). From this it follows that every restoration project involves asking the following implied questions (Menninger & Palmer 2006):

1. How do regional processes determine species composition?
2. What environmental conditions and habitat characteristics favor species survival and influence community structure?
3. How do biotic interactions shape community structure?

Filter models can be very useful at the beginning of a project for determining what constrains the arrival of species to a system (Temperton & Hobbs 2004, Belyea 2004). Once the constraining mechanisms are identified, remedial action can be taken to by-pass them. Restoration interventions are designed to act on the different filters and modify one or all of them in order to reach a reference community. However, due to the stochasticity inherent in all ecosystems, it is a myth to think that only controlling initial species composition and succession is sufficient to achieve the desired end point (Temperton & Hobbs 2004, Belyea 2004, Hilderbrand et al. 2005). Understanding assembly is fundamental to determining the most relevant management that allows direct succession to the desired state, since the order of arrival of different species (priority effects) can drastically change the development trajectory of a community (Bradshaw 1996, Young et al. 2001, Temperton & Hobbs 2004, del Moral 2007).

5.Biological model

5.1. Savanna ecosystems

5.1.1.Definition

The word *sabana* is of Amerindian origin and is currently used in ordinary Spanish. Originally, savanna designated a flat, grassy landscape that may or may not have isolated shrubs and trees in addition to the other the vegetation that characterizes this landscape (Bourlière & Hadley 1970, Sarmiento 1984). However, this original meaning has been lost (Sarmiento 1984). Richards (1976) notes that the definition of savanna is complex because savannas represent a considerable heterogeneity of physiognomies, of ecological status, and of floristic composition throughout the world. Walter (2006) also underlines the multitude of definitions and concepts. Working definitions were originally based on the physiognomy (i.e. vegetation structure), and later on the environmental conditions that led to savannas (i.e. climate, soil, hydrography or geomorphology). As a follow-on to this analysis, Eiten (1972) points out that floristic composition is also an important consideration.

In this thesis, we consider the following definition, which refers to the savanna's most important ecological and physiognomic characteristics: we think of savanna as a heterogeneous formation in time and space, which can be defined as a **tropical formation** where the **grass stratum** is dominant, continuous, and occasionally interrupted by **trees and shrubs**, where the stratum is **burnt from time to time**, and where the main growth patterns are closely associated with **alternating wet and dry seasons** (Bourlière & Hadley 1970, 1983, Sarmiento 1984). The contribution of trees to the structure of the savanna (i.e. cover or density) determines to a large extent the physiognomy of the savanna (for more details, see section 5.2 Cerrado). Sarmiento (1984) adds to this definition the notion that tropical savannas are to be found in warm, lowland tropics, but Colinsson (1988) notes that savannas can also be found in warm-climate highlands.

5.1.2.Geographic distribution

Because of the difficulties presented by the lack of a standardized definition of savanna (Walter 2006), the exact geographic distribution of savannas is not particularly well established. Tropical savannas cover some 20% of the world's land surface and occur in Central and South America, India, southeastern Asia, northern Australia and occupy a large part of the African continent (Bourlière 1983, Collinsson 1988, Osborne 2000) (Figure 7). Yet there are major differences among the savannas of the various continents. The soils of the American savannas are considerably less fertile than the others (Sarmiento 1992). Additionally, because of the large mammal extinction connected with a sharp decrease in open vegetation during the mid-Holocene epoch (De Vivo & Carmignotto 2004), large herbivores do not play a key role in the function and vegetation structure of Neotropical savannas (Central and South America), in stark contrast to Paleotropical savannas (African, Asiatic and Australian savannas) (Sarmiento 1992). Fire, which is a characteristic of all savannas, has many analogies with mammal herbivory because it "consumes" the above-ground herbaceous biomass and greatly impacts the overall vegetation, structure and function (Bond & Keeley 2005) of the savanna. Fire regime is defined according to its intensity, its severity, its frequency, its seasonality, and also its fuel consumption and spread pattern (Bond & Keeley 2005). Fire alters the soil water regime along with the carbon and nutrient fluxes (Cochrane 2009). It also acts as a selective force, having at different times a neutral, positive, or negative impact on plant demography and phenology by affecting plant growth, recruitment, and sexual or vegetative reproduction (Hoffman 1998, Miranda et al. 2002, 2009, Pausas et al. 2004).

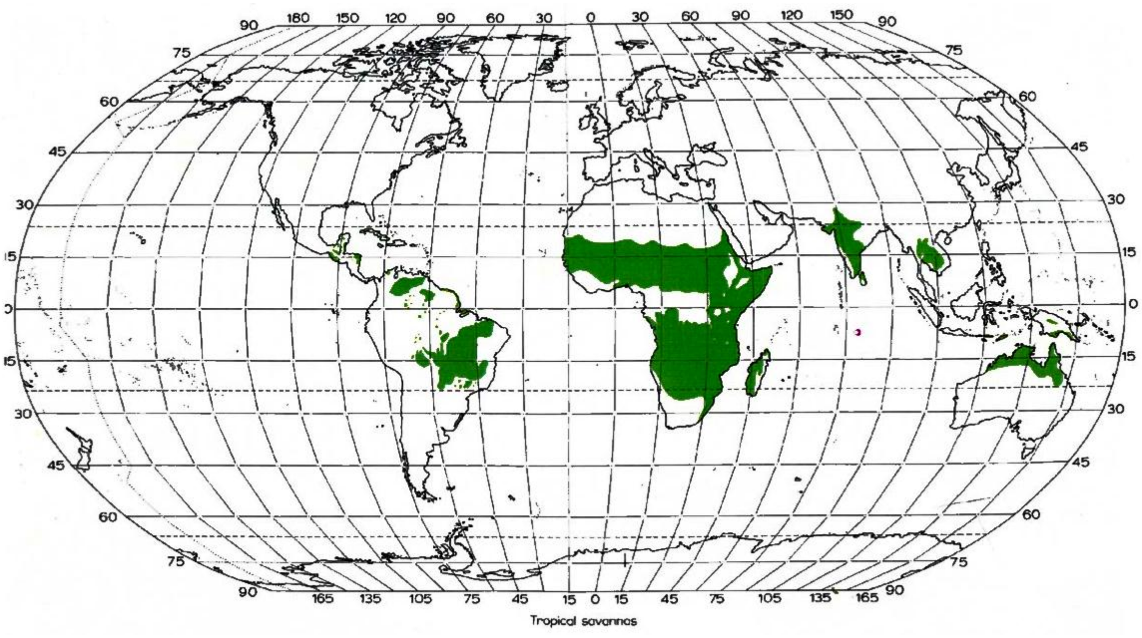

Figure 7: Map of the tropical savannas according Bourlière 1983

5.1.3.Main processes controlling savannas

At the beginning of the 20th century, the climatic theory (i.e. the presence of a dry season during winter as a driver for savanna formation) was a popular explanation for the origin of savannas (Beard 1953). More recently, various alternative hypotheses have been proposed, with current debate seeming fall under two main schools of thought: one favoring a bottom-up model (formation and regulation by, e.g., water and soil nutrients); and the other, top-down (formation and regulation principally through fire and herbivory) (Bourlière et Hadley 1970, Sarmiento 1984, Collinson 1988, Mistry 2000, Van Langevelde et al. 2003, Bond & Keeley 2005, Scanlon et al. 2005, Bond 2008, Midgley et al. 2010) (Figure 8). The details of, and some of the problems with, the main competing hypothesis can be summarized as follows:

1) Climate: Savannas only occur in climates characterized by the alternation of wet and dry seasons. On the contrary, we now know that savannas are found in climates capable of supporting forests.
2) Edaphic factors (i.e. nutrient and water availability): savannas occur on soils too nutrient-poor to allow forest establishment.
3) Fires and herbivory: fires prevent forest re-establishment and grazing activity by large herbivores serves to maintain open vegetation.

4) Human activity: savannas are an anthropogenic artifact created by clearing and burning forests. This particular point is controversial because there is now evidence that savannas are ancient and actually pre-date the earliest human populations.

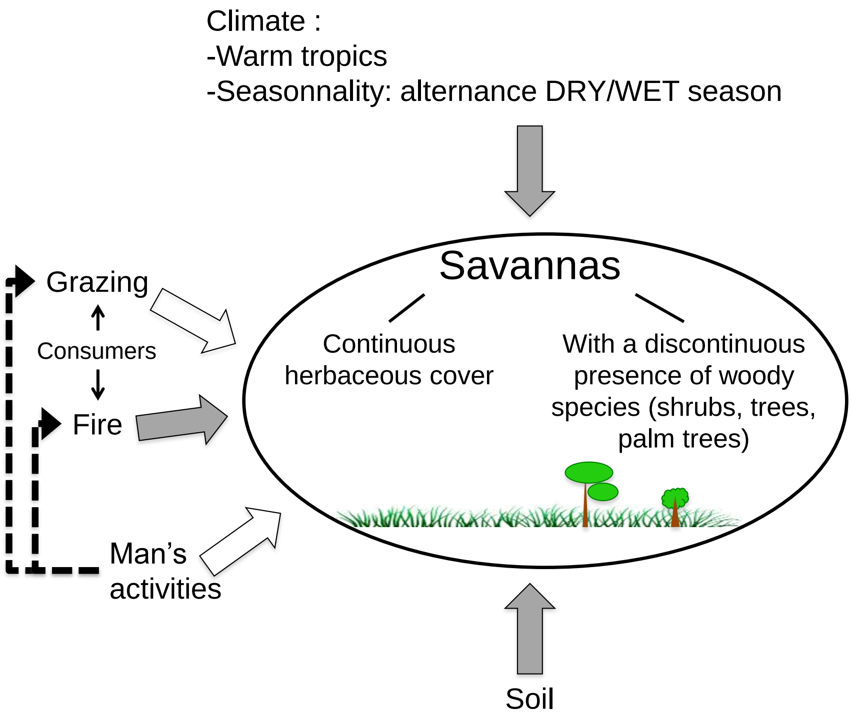

Figure 8: The main processes affecting savanna functioning. Grey arrows: factors occurring in all savannas. White arrows: factors occurring in some savannas at particular times (Le Stradic unpublished).

In tropical America, dry savannas do not exist; rather, tropical American semi-arid areas contain woodlands or shrub-lands that do not have a continuous layer of perennial graminoids (Sarmiento 1992). Neotropical savannas can be classified into the following three categories based on the degree of seasonal variation in water availability in their soils (Sarmiento 1984, 1992): seasonal, hyper-seasonal and semi-seasonal. Seasonal savannas have a well-marked dry season (3 to 7 months); hyper-seasonal savannas alternately exhibit periods of water shortage, water availability, and water excess in an annual cycle, with topsoil becoming water-saturated (such as on bottomlands and areas with poor drainage) during water excess; semi-seasonal savannas lack extended dry periods, so the soil remains water-saturated for several months.

5.2. Cerrado

5.2.1. What is the Cerrado?

The Cerrado domain (Cerrado *sensu lato*) covers approximately 2 million km^2 of Central Brazil, representing about 23% of the land surface of the country (Furley & Ratter 1988, Ratter et al 1997) (Figure 9). In terms of areal coverage, it is the second most important vegetation formation in Brazil (Furley & Ratter 1988, Ratter et al 1997). Cerrado has the richest flora among the world's savannas (>7,000 species) (Mendonça et al. 1998, Furley 1999, Castro et al. 1999, Klink & Machado 2005).

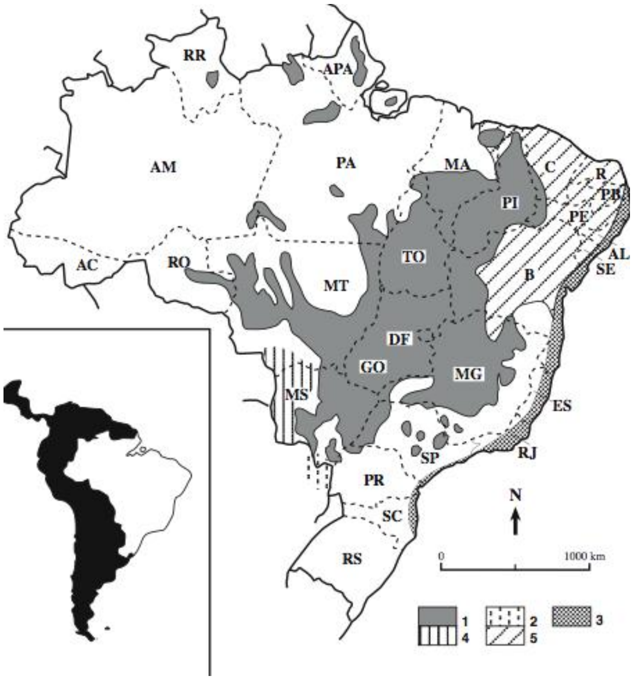

Figure 9. The distribution of cerrado and associated vegetation formations in Brazil. 1, cerrado; 2, chaco; 3, Atlantic forest; 4, Pantanal (wetlands); 5, caatinga. Letters refer to Brazilian states: B=Bahia; DF=Federal District; GO=Goias; MA= Maranhão; MG=Minas Gerais; MS=Mato Grosso do Sul; MT=Mato Grosso; PA=Pará; PI=Piaui; RO=Rondônia; SP= SãoPaulo; TO=Tocantins. From Furley (1999).

Like other tropical savannas[1], the Cerrado is not uniform in physiognomy; its various physiognomies are primarily differentiated by their degree of woody strata cover

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[1] I define the Cerrado as a savanna according to Rizzini (1997) and Coutinho (2006), but a debate still exists (see the next paragraph and Batalha (2011)).

(Goodland 1971, Sarmiento 1984). Indeed, loosely speaking, the Cerrado category encompasses a gradient of physiognomies ranging from grassland (*campo limpo*) to dense-canopy woodland (*cerradão*), with many others that are intermediate (*campo sujo, campo cerrado, cerrado sensu stricto*) (Coutinho 1978) (Figure 10). Several reasons have been proposed as explanations for the varying physiognomies (Oliveira-Filho & Ratter 2002); examples of which include the availability of nutrients and water (Askew et al 1970, Goodland & Pollard 1973, Haridasan 2000, Marimon & Haridasan 2005), the nature of the associated fire regimes (Coutinho 1990, Miranda et al 2002), and the distribution of aluminium content (Haridasan 1982) (Figure 10).

5.2.2.The controversial Cerrado

Like the definition of savanna, the definition of Cerrado is also controversial: *Is Cerrado a savanna? Is Cerrado a biome?* Indeed, the cerrado has been variously referred to as a biome (Oliveira-Filho & Ratter 2002), as the Brazilian savanna vegetation (Ratter et al 1997), as a complex of biomes (Coutinho 2006, Batalha 2011), or as a unique entity (Eiten 1972) (Figure 10). Eiten (1968, 1972), who has published several influential articles about the Cerrado, points out that the Cerrado is a unique entity, and cannot be considered a true savanna because its floristic richness greatly differentiates it from typical tropical savannas. He defines the Cerrado as a mix of xeromorphic woodland, scrub, savannah, and grassland vegetation in central Brazil (Eiten 1968). The cerrado forms a vegetational and floristic province in an intermediate-rainfall region with a definite dry season (Eiten 1972). The Cerrado cannot be uniquely classified as savanna because of its rich variety of physiognomies (Coutinho 1978). Coutinho (1978), in his "forest-ecotone-grassland" concept, states that the Cerrado is a complex of oreadic[2] formations, representing savanna-intermediary formations (*campo sujo, campo cerrado, cerrado sensu stricto*) and two extreme formations: a forest formation (*cerradão*) and a grassland formation (*campo limpo*). He concludes that the Cerrado is a mosaic of three biomes (see also Walter (2006) and Batalha (2011)). Coutinho (2006) later reviews the concept of the biome, strengthening his prior definition (Coutinho 1978) while noting that all tropical savannas have a physiognomic complexity, which leads to a kind of mosaic that manifests as a gradient of communities. At the same time, he also acknowledges the fact that savannas are considered biomes by the majority of authors. Olson et al.

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[2] The term oreadic refers to a floristic province recognized by Martius (1840-1906) in Flora Brasiliensis

(2001) include the Cerrado in the ecoregion[3] of “tropical & subtropical grasslands, savannas and shrublands,” underlining a certain unicity between the Cerrado and other savanna formations.

Recent work, by such authors as Ratter et al. (1997), Silva & Bates (2002) and Oliveira & Marquis (2002), considers the entire Cerrado, in which the *cerradão* is explicitly included (Figure 10), a savanna. On the other hand, Coutinho (2006) concludes that the Cerrado is a savanna biome, and because the *Cerradão* is actually a distinct seasonal forest, he considers it separately (see also Rizzini 1997 and Walter 2006) (Figure 10). Finally Batalha (2011) corroborates the “forest-ecotone-grassland” concept of Coutinho (1978) and emphasizes that Cerrado is not a biome but a complex of biomes (Figure 10).

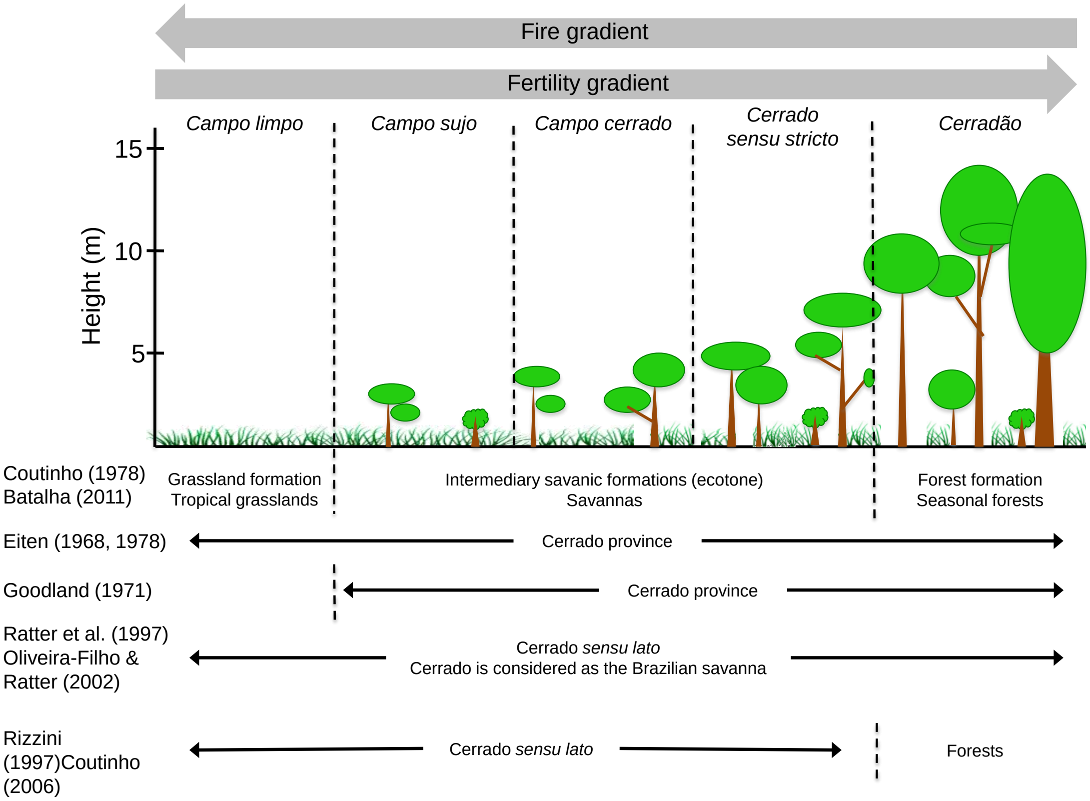

Figure 10: Simplified structural gradient of Cerrado ecosystems (modified from Coutinho 1978) and representation of the ideology developed by some authors on the concept of Cerrado (Le Stradic unpublished).

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[3] The author defines ecoregions as “relatively large units of land containing a distinct assemblage of natural communities and species, with boundaries that approximate the original extent of natural communities prior to major land-use changes”.

5.2.3.Brief history of the evolution of the Cerrado

During the Cretaceous epoch, angiosperm was spread, creating a (Crane & Lidgard 1989, Lupia et al. 1999, McElwain et al. 2006) new fire regime by increasing fuel availability (Bond & Scott 2010). The savanna's origin, marked by the expansion and the predominance of C4 grasses, is estimated to have occurred during the Miocene epoch some 8 million years ago, and is thought to have been the result of environmental pressures associated with intense light levels, high temperature, low CO_2, and fire (Keeley & Rundel 2005, Bond et al. 2005, Beerling & Osborne 2006, Edward et al. 2010). Fire played an important role in promoting the spread of grasslands and savannas at that time, accelerating forest loss (by slowing the recovery rates of tree species following destruction by fire), and generating positive feedback loops which promoted drought and more fire (Bond et al. 2003, Beerling & Osborne 2006).

Neotropical vegetation was structured by four major events (Burnham & Graham 1999, Safford 1999, Fiaschi & Pirani 2009): (1) isolation (break-up of West Gondwana and separation of South America from Africa), (2) the uplift of the Andes and changing drainage systems, (3) the closure of the Isthmus of Panama, and (4) quaternary climate fluctuations. Vuilleumier (1971) highlights the evidence for climatic events that occurred during the last million or so years and have affected the biota of South America. The last glacial period was wetter than the Holocene epoch (90 000 to 21 000 Years Before Present) (Van Der Hammen 1974). However, during the Last Glacial Maximum (LGM) (20,000 to 18,000 YBP, late Pleistocene) there was a decrease in precipitation and a very dry period (drier than the Holocene), associated with lower temperatures and lower atmospheric humidity (due to the slight recession of glaciers) (Van Der Hammen 1974, Ledru 2002). Werneck et al. (2012) demonstrates that the LGM and LIG (Last Interglacial, 120 000 YBP) were the periods of narrowest and widest Cerrado distributions, respectively. During the LMG, climatic conditions did not allow for the development of the Cerrado (Ledru 2002, Werneck 2012). The late Pleistocene was marked by the extinction of the South American megafauna, and the mid-Holocene, by the loss of other large-mammal lineages due to the reduction of open formations in South America (De Vivo & Carmignotto 2004). The increase in seasonality beginning ca. 7 000 YBP was necessary for Cerrado vegetation to grow on the Central Plateau and to eventually result in the physiognomy of the Cerrado we know today (Ledru 2002, Ledru et al. 2006).

Cerrado lineages began to diversify less than 10 Million years (MY) ago, with most lineages diversifying 4 MY ago or more recently, coinciding with the expansion of the savanna biome worldwide (Simon et al. 2009: the near-synchronous expansion of C4 grasses around the world dating back to 8 MY ago marked the origin of the modern savanna biome (late Miocene) (Beerling & Osborne 2006, Edward et al. 2010). Simon et al. (2009) also show that the Cerrado formed *in situ* via recent and frequent adaptive shifts to resist fire, rather than via the dispersal of lineages already adapted to fire.

5.3. Campos rupestres

5.3.1.Definition

Campos rupestres, one physiognomy of the Cerrado, are a mosaic of grasslands found at altitudes of between 800m and 2000m and covering around 130 000 km^2 of total area (according to potential distribution models Barbosa 2012) (Figure 11). They are especially found along the Espinhaço Range, although some isolated *campos rupestres* occur also in the state of Goiás (Romero 2002). They have been defined as a more or less continuous herbaceous stratum with sclerophyllous evergreen shrubs and sub-shrubs growing between rocky outcrops (Giulietti et al. 1997). Eiten (1978) notes that "whereas cerrado woody plants cannot grow on bare rock (except where it can find a deep crack), *campo rupestre* woody plants, may form groves of open or even closed scrub over outcropping hard bedrock, so that not all this upland vegetation is really 'campo'" (i.e., grassland). Barbosa (2012) has shown that they are stable ecosystems and points out that there was no significant expansion of *campos rupestres* during the middle Holocene and during the last glacial maximum, probably due to the strong edaphic specificity of this ecosystem.

5.3.2.Espinhaço range

Excluding the Andean vegetation, there are three main highland vegetation formations in South America: *Tepuis* on the Guayana shield, *campos de altitudes* (i.e. *Brazilian páramos*) in southeast Brazil, and *campos rupestres*, principally along the Espinhaço Range in eastern Brazil but also in the state of Goias. Although they have strong physiognomy similarities, each of the three is characterized by a unique flora comprising a large number of endemic and vicarious species (Maguire 1970, Giulietti et al. 1997, Safford 1999, Alves & Kolbek 2010). As previously discussed, Cerrado woody lineages span from the late Miocene to the Pliocene (during the tertiary) (Simon et al. 2009), but the floristic composition of these mountain formations were also impacted by the quaternary climatic and vegetation fluctuations (Vuilleumier 1970, Van Der Hammen 1974, Fiaschi and Pirani 2009, Werneck et al 2012).

The Espinhaço range or *Serra do Espinhaço* in portuguese ("Backbone Range"), is one of the most important biogeographic regions in Brazil, located in the states of Minas Gerais and Bahia (eastern Brazil). The Espinhaço range corresponds to the watershed between the Atlantic Ocean and the São Francisco River Basin (Derby 1906). The Espinhaço range is oriented north-south and covers an area about 1,000km long by 50 to 100km kilometers wide, with a mean elevation of over 1,000m and occasional peaks reaching 1,800-2,100 m. It is divided in various massifs, such as the Serra da Piedade, Serra do Caraça, Serra do Cipó (in which the present studies were carried out), Diamantina plateau, Serra do Cabral, Serra do Grão-Mogol, Chapada Diamantina (Pico das Almas, Mucugê), Morro do Chapéu, Serra da Jacobina (Giulietti et al. 1997) (Figure 12).

Although the mean elevation is only 1,000m, the local relief has rugged topographic features. Schistose rocks make up the predominant formations, and these consist in particular of precambrian quartzites, sandstones subject to metamorphism, and ferruginous schists (Derby 1906). The present form of the range is the result of a combination of long erosive processes and more recent tectonic (tertiary) processes (Giulietti et al. 1987). The soils are in general shallow and sandy, highly acidic, and extremely nutrient poor as a result of the aforementioned erosion processes (Giulietti et al. 1997, Benites et al. 2007). In 2005, the Espinhaço Range was designated a Biosphere Reserve by UNESCO (UNESCO 2005), and it now includes 16 protected areas (National Parks, State Parks, State Ecological Stations and Municipal Natural Parks) (Figure 12).

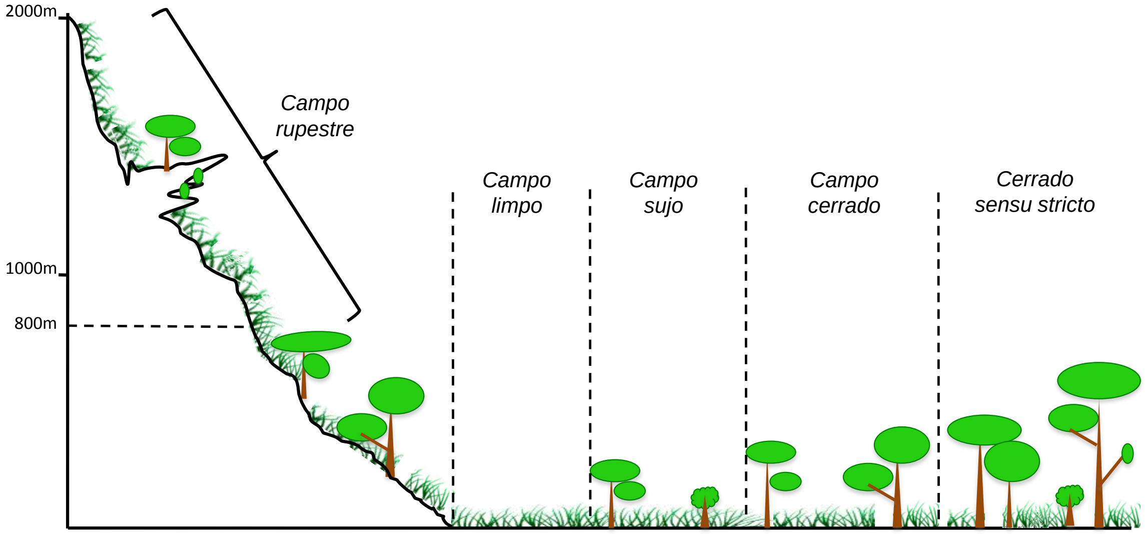

Figure 11: *Campos rupestres* considered as a physiognomy of the Cerrado (Le Stradic unpublished)

5.3.3.Characteristics of the *campos rupestres*

The presence of quartzitic rocky outcrops is a fundamental property of *campos rupestres* as well as the associated coarse texture and shallow sandy soil, with high Al^{3+} and low nutrient contents (Benites *et al.* 2003, 2007). In contrast to the Cerrado, *campos rupestres* are almost all well-drained dry grasslands (with the notable exception of the peat bog physiognomy) (Eiten 1978). The local drainage systems, together with the heterogeneity of the topography, create humid and arid sites that are often separated from each other by just a few centimeters (Vitta 1995, Alves & Kolbek 2010). *Campos rupestres* are subjected to stressful climatic conditions, such as high daily temperature oscillations, intense irradiation (UV), strong winds, and a marked dry season.

Alves et al. (2007) defined *campos rupestres* as “a species-rich, extrazonal vegetation complex bound to Precambrian quartzite outcrops which emerge as a mosaic surrounded mainly by cerrado and caatinga”. They are composed of many distinct plant communities (Giulietti et al. 1987, Meguro et al. 1994, Queiroz et al. 1996, Conceição & Pirani 2005, Conceição et al. 2007c) and this makes it difficult to define *campos rupestres* as a floristic unit (Alves & Kolbek 2010), a problem rendered even more difficult by the high level of endemism (Giulietti et al. 1987, 1997, Alves & Kolbek 1994, Pereira 1994, Pirani et al. 1994, Harley 1995, Vitta 1995, Rizzini 1997, Conceição & Pirani 2007). Just as in the *Tepuis* formation (Venezuela), the *campos rupestres* is a center of diversity for Xyridaceae and Eriocaulaceae. Distant *campos rupestres* can share many similar families and genera that confer a certain unicity on the ecosystem. Examples include Eriocaulaceae (*Leiothrix, Paepalanthus, Syngonanthus*), Velloziaceae (*Vellozia, Barbacenia*), Xyridaceae (*Xyris*), Melastomataceae (*Cambessedesia, Marcetia*) Asteracae (*Lychnophora*) or Lythraceae (*Cuphea, Diplusodon*), and so on (Giulietti et al. 1997). Because of the high level of endemism, the combination of species is not equipped to circumscribe *campos rupestres* (Alves & Kolbek 2010). The combination of the topography, the nature of the substrate and, the peculiar climatic conditions are generally identified as the reason for the speciation and adaptation phenomena that have brought about an extraordinary biodiversity. *Campos rupestres* support more than 4,000 plant species (Giulietti et al. 1997) and 1,590 plant species in the Serra do Cipó (Giulietti et al. 1987) with one of the highest level of endemism in Brazil as previously noted.

Botanical collection in *campos rupestres* began in the 19th century (Saint-Hilaire 1833), but it was only the later decades that saw growing interest in understanding the structure and functioning of *campo rupestre* communities. We have identified, within the present bibliography, some floristic survey studies dealing with granitic, quartzic, or ironstone outcrops (Pereira 1994, Vincent 2004, Conceição et al. 2007c, Jacobi et al. 2007, Ribeiro et al. 2007, Scarano 2007), *campos rupestres* located in Bahia (Queiroz et al. 1996, Conceição & Pirani 2005, 2007, Conceição et al. 2007a, b, c), *campos rupestres* associated with an iron substrate (i.e. canga) (Vincent 2004, Viana & Lombardi 2007, Mourão & Stehmann 2007, Messias et al. 2012), and *campos de altitude* (Caifa & Silva 2005, Ribeiro et al. 2007).

Most of these studies deal with the shrubby physiognomy occurring on rocky outcrops while very few studies address physiognomies dominated by grasses, and these represent the matrix, and therefore the quintessence, of *campos rupestres* (Conceição and Pirani 2005, Viana and Lombardi 2007, Borges et al. 2011, Messias et al. 2012). We have thus a knowledge gap concerning the composition and structure of the herbaceous components of *campos rupestres*. The direct consequence of this is that it is currently quite difficult to set up tailored conservation and restoration efforts, because the reference ecosystem is poorly understood.

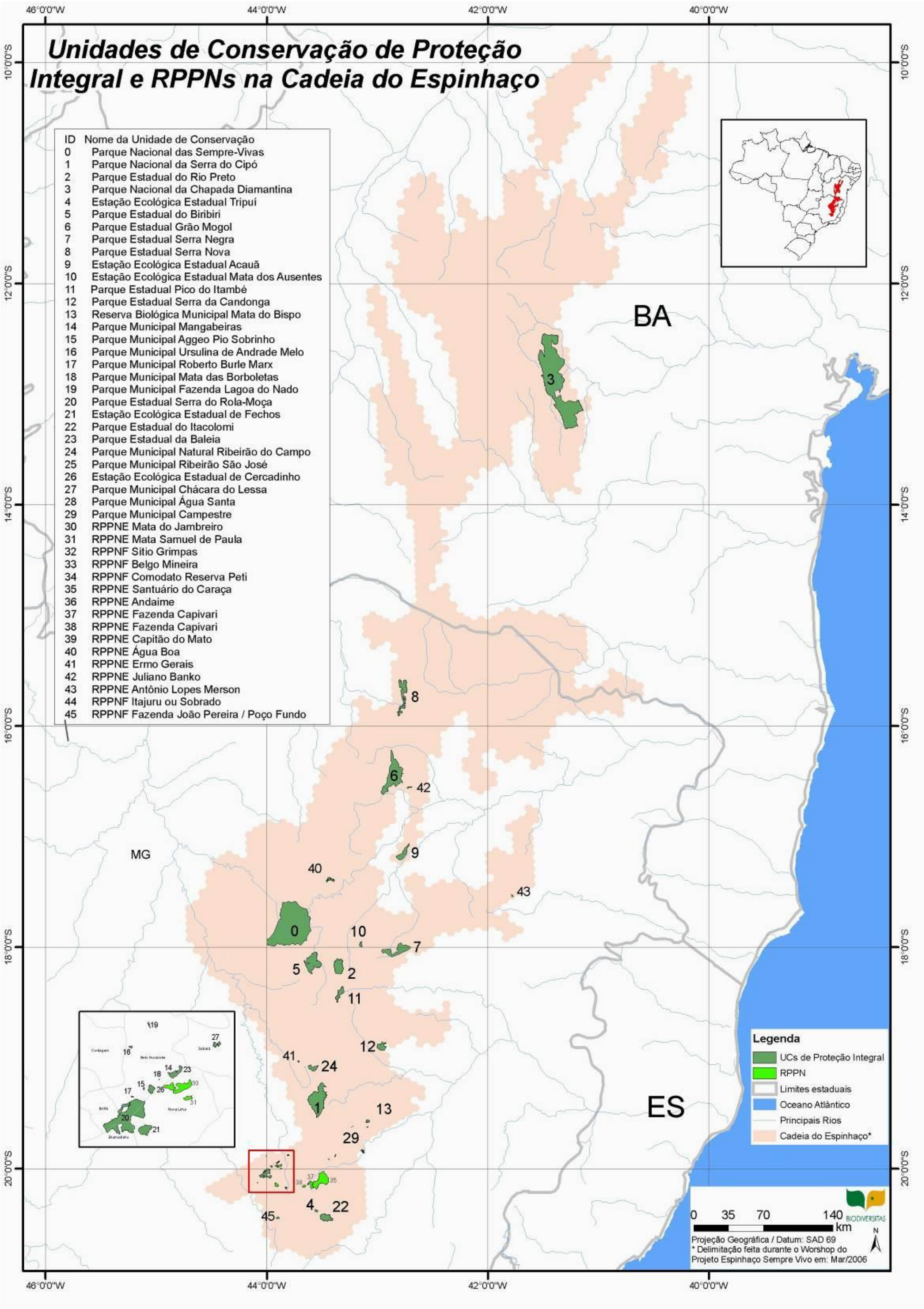

Figure 12: Map of the Espinhaço range showing the protected areas (Unidade de Concervação de Proteção integral). Number 1 is the Serra do Cipó National park where this study was realized Map from Biodiversitas fundation.

5.3.4.What about the terminology?

Considering the heterogeneity and richness of ecosystems within *campos rupestres*, it is sometimes difficult to limit them to a single name. Walter (2006) reviews the richness of the nomenclature and concepts relative to the phyto-physionomy of the Cerrado biome, reflecting the difficulty in clearly defining the different vegetation formations of the Cerrado domain (see the section 5.2.Cerrado for more details).

Magalhães (1966) considers all vegetation formations in the state of *Minas Gerais* as related to the Cerrado and was the first to use the term "*campo rupestre"* (from Latin "rupestris" meaning ''rocky'', *campos rupestres* means rupestrian grasslands) to define the main vegetation formation occurring on the mountaintops along the Espinhaço range. Without defining the *campos rupestres*, he highlights characteristic plant families, such as Melastomataceae, Eriocaulaceae, Velloziaceae and Xyridaceae and the occurrence of some endemic species. Various definitions and terminology have been successively proposed (Vasconcelos 2011), first by Eiten (1978) who notes that *campos rupestres* constitute a complex. Rizzini, in 1979, improves upon the definition and proposes subdividing the category into quartzite grasslands (*campos quartzicos*) occurring on quartzite rocks along the Espinhaço range, and altitude grasslands (*campos de altitude*) occurring on diverse crystalline rocks located in the Serra do Mar and Serra da Mantiqueira. This distinction is maintained by Semir (1991) who re-introduced the term "complex" and proposes the name quartzic rupestrian complexes (*complexos rupestres de quartzito*) to refer to the vegetation of Espinhaço range and granitic rupestrian complexes (*complexos rupestres de granito*) to refer to the vegetation of Mantiqueira range. Harley & Simmons (1986) restrict the use of "*campo rupestre*" to the vegetation that grows on quartzite-sandstone substrates. Benites et al. (2003) prefer the terms quartzite altitude rupestrian complexes and granitic altitude rupestrian complexes. While vegetation formations of *campos de altitude* and *campos rupestres* are structurally similar, their respective floristic compositions differ, and this has led to the apparent nomenclature dichotomy (Vasconcelos 2011). *Campos rupestres* is also used to designate the vegetation formations of the Espinhaço range found on ferruginous substrates (i.e., locally called "canga", e.g., Viana & Lombardi 2007).

Moreover several English translations of *campo rupestre* have also been proposed, such as "rocky grassland" (Oliveira-Filho & Ratter 2002, Alves et al. 2007) or "rupestrian field," (Marques et al. 2002, Carvalho et al. 2012) and this further exacerbates the confusion, particularly because *campo* in Portuguese means both field and grassland, while pristine *campos rupestres* were never cultivated. More and more often, the term *campo rupestre* is used (Conceição & Pirani 2005, Conceição et al. 2007b, Rapini et al. 2008), even in papers written in English (Alves et al. 2007, Conceição et al. 2007a,c, Alves & Kolbek 2010), indicating the adequacy of this terminology.

5.3.5.Are *campos rupestres* included in the Cerrado?

A major source of debate is the question of whether or not the *campos rupestres* are part of the Cerrado domain. Martius (1840/1906) initially includes *campos rupestres* in his oreadic formations[4], which later serves as the inspiration for Coutinho's (1978) "forest-ecotone-grassland" concept. Several authors agree with this and many of them currently treat *campos rupestres* as a physiognomy of the Cerrado, occurring at altitude and included in grassland formations such as the *campo limpo* (Silva & Bates 2002, Walter 2006). However, *Campos rupestres*, though usually associated with the Cerrado, also occur within the Caatinga biome in the northern portion of the Espinhaço range. Eiten (1978) considers *campos rupestres* and Cerrado as "essentially different vegetations", describing *campos rupestres* as a complex of well-drained dry grasslands, in stark contrast to the Cerrado. Similarly, in their listing of the physionomic forms of the Cerrado, Ribeiro & Walter (1998) use Magalhães' earlier work (1966) and define *campos rupestres* as a vegetation formation in its own right.

Although there is a high level of endemism in *campos rupestres*, they share some similarities with the grassland formation of the Cerrado, and some species occurring on *campos rupestres* are also found in the Cerrado (Giulietti et al. 1987). Therefore, according to a part of the literature (Silva & Bates 2002, Walter 2006, Alves & Kolbek 2010), in this study, *campos rupestres* were included in the Cerrado (Figure 11).

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[4] The term oreadic refers to a floristic province recognized by Martius (1840-1906) in Flora Brasiliensis

5.4. *Current Threats on Mountains ecosystems: focus on the campos rupestres*

In 2002, the Parties of the Convention on Biological Diversity (CBD) adopted a work program on mountain biological diversity (1) in order to reduce the loss of global and regional mountain biodiversity and (2) to help foster increased knowledge of ecosystem functioning and community composition, because, as it is often the case in tropical regions, there is insufficient understanding of critical processes (Escudero 1996, Romdal & Grytnes 2007), and this presents a serious barrier to implementing effective conservation or restoration programs. Indeed, the CBD has recognized the fragility of mountain ecosystems and species, as well as their vulnerability to man-made and natural disturbances, particularly in the current context of land-use and climate changes (CBD 2012). Mountain ecosystems are hot spots of biodiversity with many endemic species (Giulietti et al. 1997, Price 1998, Chaverri-Polini 1998, Porembski & Barthlott 2000, Barthlott et al. 2005, 2007, Kier et al. 2005, Martinelli 2007), most of which play an essential role in ensuring the regional and global diversity (Burke 2003). One of the great intrinsic values of mountains lies in their being the source of many of the world's rivers (FAO 1998). Mountain degradation has thus become a worldwide concern because of the consequences it has in terms of ecosystem service losses (FAO 1998), including degradation of water-quality, increasing soil erosion, and biodiversity loss.

There is current evidence of adverse human impact on mountains worldwide (Burke 2003), and Brazil is no exception (Jacobi et al. 2007, Ribeiro & Freitas 2010). Pending changes in Brazilian environmental legislation (Law n°12.651, May 25th 2012) will further complicate the conservation of mountain ecosystems because it eliminates hilltops as environments that can be considered Permanent Preservation Areas (PPA) (Ribeiro and Freitas 2010, Codigo florestal 2012). Mountain ecosystems are also known to be poorly resilient to disturbances and therefore require restoration once they have been degraded (Urbanska & Chambers 2002). Though well-adapted to constrained environmental conditions, such as shallow and nutrient-poor soils and endogenous disturbances (*sensu* White & Jentsch 2001) such as fire, *campos rupestres* seem highly sensitive to land conversions, mainly because of their precise adaptation to their original environments (Ribeiro & Freitas 2010).

One of the most important defining characteristics of the Espinhaço Range is the presence of gold, diamonds, and iron, which are responsible for the bulk of human activity in the region since the 18th century. Over the course of many decades, the mining industry presented the main threat to *campos rupestres*, and today, abandoned mine areas remain bare without vegetation regeneration. Poorly planned road construction is also leading to soil erosion and biological invasions (Barbosa et al. 2010). *Campos rupestres* were subjected to decades-long impacts by cattle breeding, usually associated with annual burnings intended to stimulate the regrowth of the vegetation; these activities are still a major occurrence in this region. Even if vegetation is adapted to fire, frequent fires often end up favoring some species over others. On another hand, the shallow and poor nutrient soils limit crop cultivation on *campos rupestres* contrary to the other grassland formations of the Cerrado. Some activities, such as wood extraction, eucalyptus plantation, and collection of plants with ornamental value (Orchids, Bromeliads, Eriocaulaceae) also occur, and, though currently sporadic, have already led to the diminution of some species populations (Giulietti et al. 1997). Nowadays, increasing uncontrolled tourism and human settlement also threaten *campos rupestres* (Giulietti & Menezes 2000, Plano de manejo PARNA Serra do Cipó 2009). Between the 16th century and the 1960s, Magnanini (1961) estimates that natural *campos rupestres* of Minas Gerais and Bahia were reduced by 80%.

6.Study areas: Serra do Cipó *campos rupestres*

6.1. Geographic situation

Our study area is located in the southern portion of the Espinhaço Range (Brazil) (Figure 12), in the Environmental Protected Area (Area de Proteção Ambiental in Portuguese) Morro da Pedreira, in the buffer zone of the Serra do Cipó National Park (state of Minas Gerais). The creation of the Serra do Cipó National Park and the Environmental Protected Area of Morro da Pedreira (Área de Proteção Ambiental) in 1984 has helped to preserve natural areas of campos rupestres which are the main vegetation formation on shallow soils in the Serra do Cipó region (Figure 14), usually mixed with Cerrado, Atlantic rain forest, riparian forests and small groves on deeper soils, totaling more than 1600[5] plant species (Giulietti et al. 1987).

6.2. *Climate*

The regional climate is classified as Cwb with a warm temperature, a dry winter and a warm summer, according to the Köppen system (Köppen 1900). It is markedly seasonal, with two distinguishable seasons: a rainy season from November to April and a dry season from May to October. The mean annual precipitation is 1622 mm and the mean annual temperature is 21.2°C (Madeira and Fernandes 1999).

6.3. *Study sites*

Based on the topography, we designated and studied two main grassland-types of campos rupestres. We selected 10 grasslands: 5 sites with sandy substrates located on flat areas (Sa) and 5 sites with stony substrate on slopes (St) (Table 1, Figure 13, Figure 14). The sites are at altitudes between 1100m and 1300m.

Table 1: Geographic coordinates of the 10 reference sites of *campos rupestres.* Floristic and phenological survey were realized on the 10 sites (Chapter 1 & 2); Sa1, Sa2, Sa3, St1, St2 & St3 were used as the references in the Chapter 3.

Site code	Altitude	Type of soil	Longitude	Latitude	Orientation	Slope (%)	Slope category	Topographic situation
Ca1	1156	Sandy	43°35'43,2"	19°17'6,2"	North	10%	Medium slope	Downslope
Ca2	1178	Sandy	43°34'58,6"	19°17'20"	North	8%	Gentle slope	Downslope
Ca3	1188	Sandy	43°35'15,5"	19°17'9,8"	West	4%	Gentle slope	Top of slope
Ca4	1291	Sandy	43°35'24,1"	19°17'47,3"	East	8%	Gentle slope	Top of slope
Ca5	1091	Sandy	43°34'46,6"	19°16'11,4"	North	8%	Gentle slope	Downslope
Cp1	1162	Stony	43°35'38,2"	19°17'4,7"	Northeast	16%	Steep slope	Slope
Cp2	1273	Stony	43°35'7,3"	19°17'21,6"	East	13%	Medium slope	Slope
Cp3	1188	Stony	43°35'13,8"	19°16'57,9"	East	17%	Steep slope	Slope
Cp4	1310	Stony	43°35'17,5"	19°18'2,1"	East	4%	Gentle slope	Top of slope
Cp5	1091	Stony	43°34'46,6"	19°16'11,4"	East	17%	Steep slope	Slope

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[5] Probably much more species occur but no floristic survey was carried out since 1987.

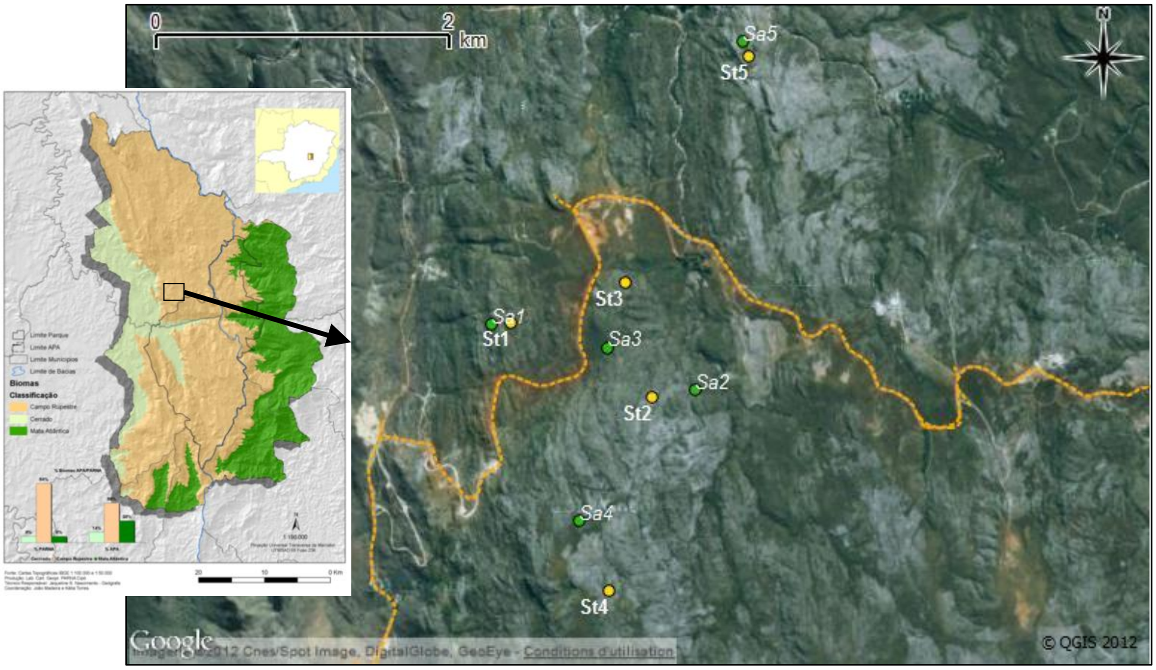


Figure 13: Map of the 10 study sites on the two main grassland-types of *campos rupestres:* sites with the sandy substrate located on flatted areas (Sa) and sites with stony substrate on slopes (St). The dashed line represents the highway MG-010. The inset shows a map of the environmental Protected Area (Area de Proteção Ambiental in Portuguese) Morro da Pedreira, which includes the Serra do Cipó National Park. *(Map realized using Plano de manejo do PARNA Serra do Cipó (2009), Google Earth image and QGIS).*

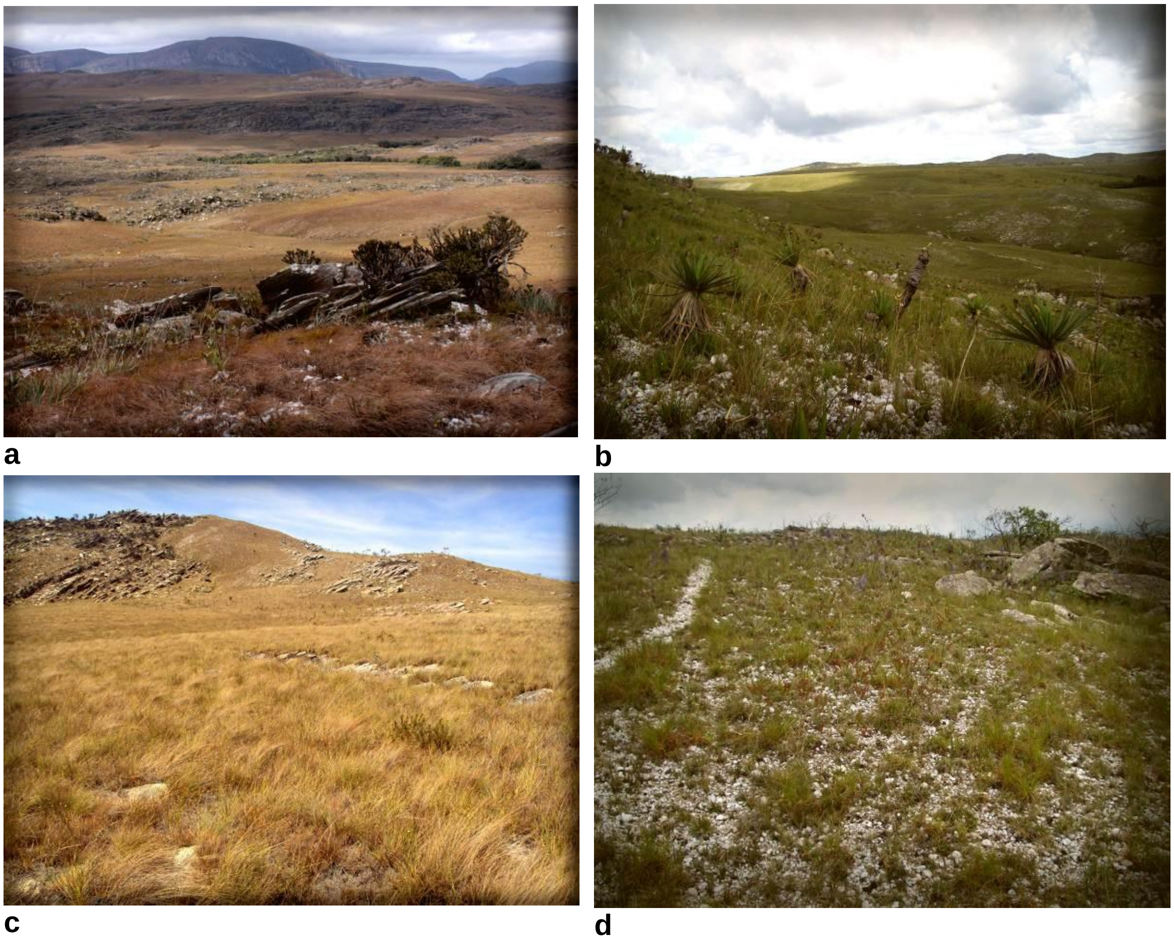


Figure 14: Photographs of the *campos rupestres* from the Serra do Cipó, the general view a) during the dry season, b) during the wet season, c) sandy grasslands and d) stony grasslands. Photo credit S. Le Stradic

A study had reported the presence of degraded areas in the region as early as 1996 (Negreiro et al. 2011), but the overall start of degradation may actually date back to 1980. In 2002, a new disturbance occurred when highway MG010 was asphalted. Degraded areas found along the road were exploited for gravel and/or were used to park machines. When the road was complete, the degraded areas left behind represented several kinds of substrate.

Small quarries are common in the region and their creation leas to vegetation being destroyed and soils being disturbed. Even when exploitation stops, soils are not entirely restituted, and they may be heavily contaminated by construction debris. These degraded areas are surrounded by pristine *campos rupestres*.

We thus also chose 9 degraded areas on 3 kinds of substrate (Figure 15): 1) degraded latossol substrate (DF), 2) degraded sandy substrate (DSa) and 3) degraded stony substrate (DSt) (Figure 16).

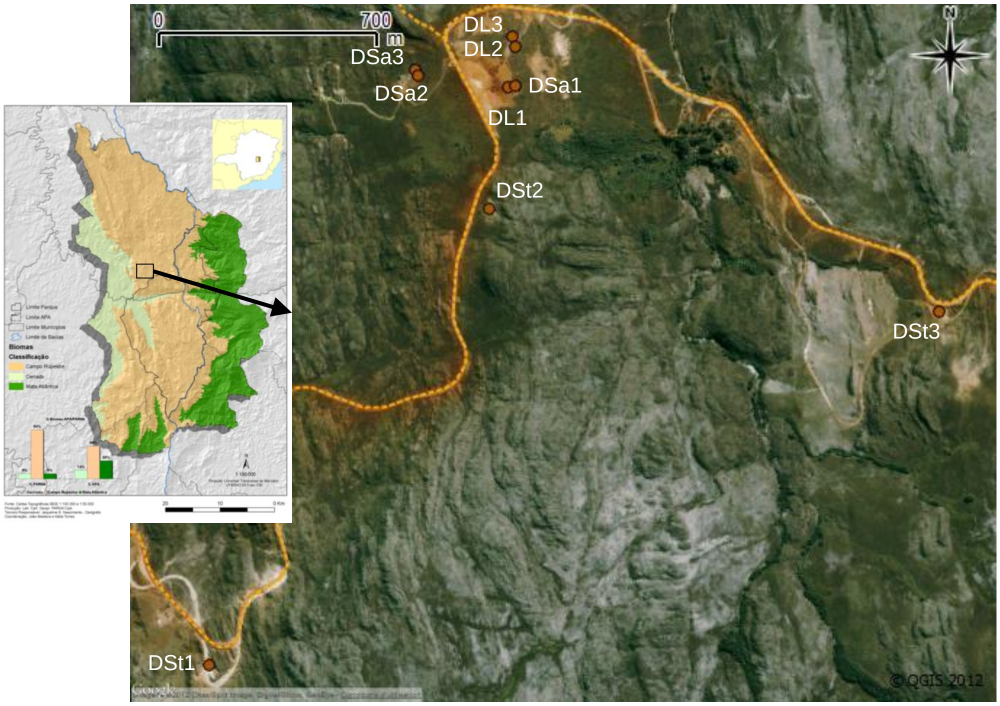


Figure 15: Map of the 9 degraded sites on three kinds of substrate: sites located on degraded latosol substrate (DL), on degraded sandy substrate (DSa) and on degraded stony substrate (DSt). The dashed line represents the highway MG-010. The inset shows a map of the environmental Protected Area (Area de Proteção Ambiental in Portuguese) Morro da Pedreira, including the Serra do Cipó National Park. *(Map realized using Plano de manejo do PARNA Serra do Cipó (2009), Google Earth image and QGIS).*

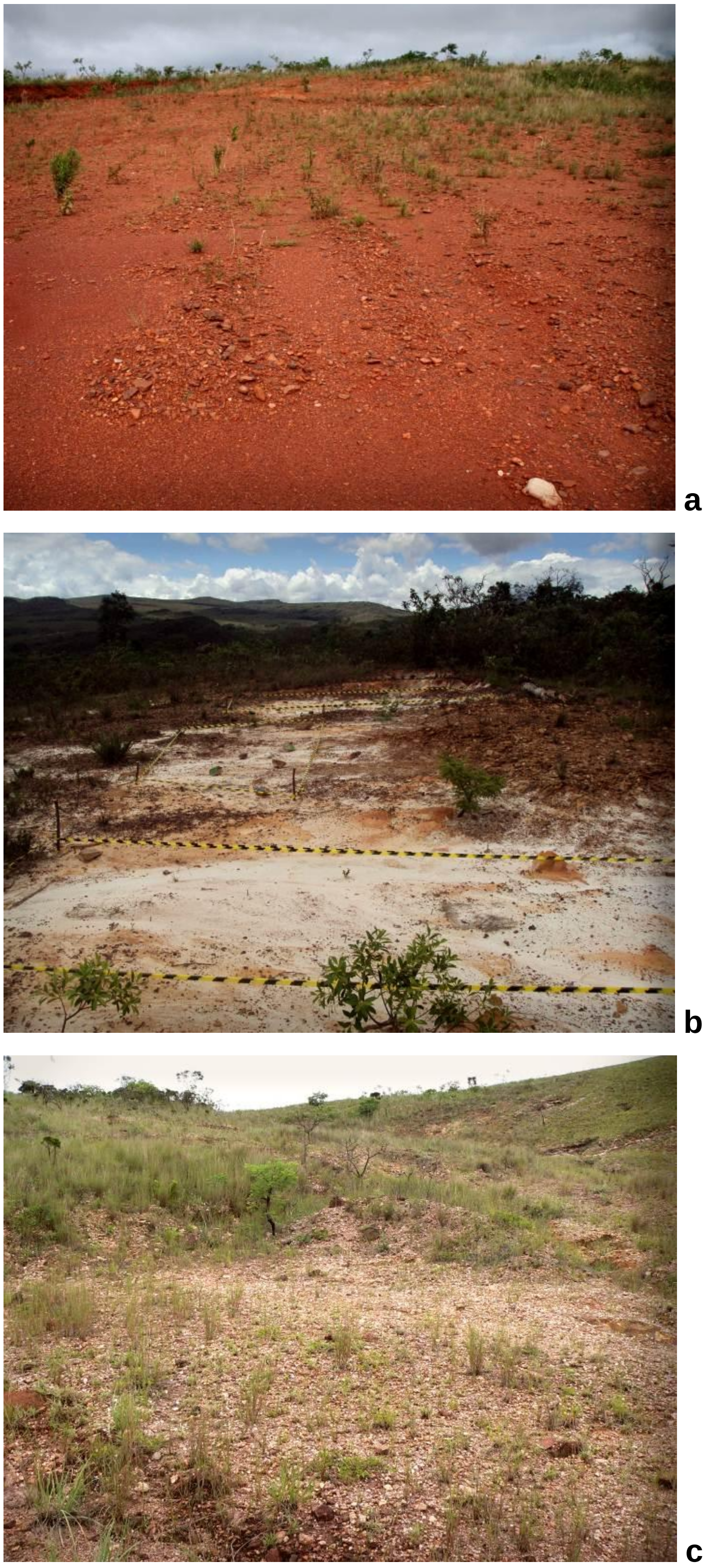


Figure 16: Degraded areas with a) degraded latosol substrate, b) degraded sandy substrate, c) degraded stony substrate. Photo credit S. Le Stradic.

Campos rupestres are peculiar species-rich tropical grasslands, but not enough is known about them at present for them to be efficiently restored. The following chapters are aimed at increasing knowledge about the functioning these grasslands and will address three restoration methods.

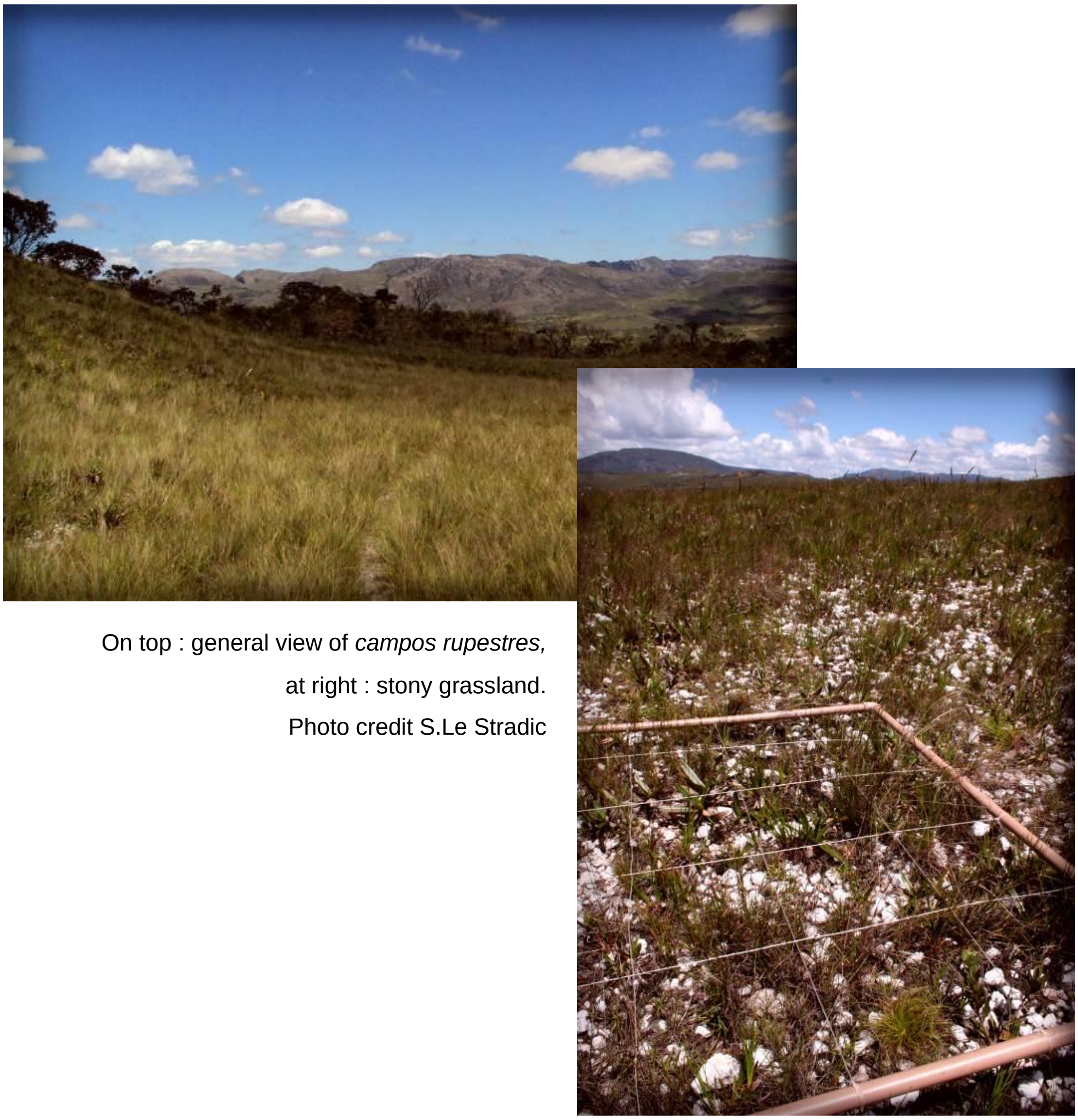
Chapter 1 will deal with the composition and structure of the two main herbaceous communities in order to define more clearly the reference ecosystem.

We will also analyze the reproductive phenological patters of both communities in **Chapter 2**. Resilience to, and the impact of, strong disturbances will be discussed in **Chapter 3**, together with some discussion of the potential for hay transfer to play a role in restoring these grasslands.

Germination behavior of some herbaceous species will be addressed in **Chapter 4**.

Finally, in **Chapter 5** species and turf transplantation will be assessed as methods of introducing native species in degraded campos rupestres. A final consideration of the main ideas and a conclusion will provide the closing material for this thesis.

Chapter 1



On top : general view of *campos rupestres,*
at right : stony grassland.
Photo credit S.Le Stradic

Chapter 1 - Baseline data for the conservation of *campos rupestres*: Vegetation heterogeneity and diversity.

Chapter 1 - Baseline data for the conservation of *campos rupestres*: Vegetation heterogeneity and diversity.

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Abstract: The recognition and the classification of plant communities are fundamental to implementing conservation programs or restoration projects. *Campos rupestres* are species-rich Neotropical mountain grasslands belonging to the Cerrado in Brazil, covering 130 000km^2 and commonly defined as a mosaic of grasslands and rocky outcrops. From a conservation standpoint we may ask: 1) Are the grasslands homogeneous or are they composed of distinct plant communities? 2) Can soil characteristics explain plant community patterns? We have selected 10 grasslands: 5 on stony substrates and 5 on sandy substrates on which we have carried out vegetation surveys and soil analyses. Species were classified according to their life-form, plant form, habitats in Brazil, distribution range, IUCN status, and life-cycle. Soil samples were collected during the rainy and dry seasons and chemical and granulometric analyses were performed. The results show that five grassland soils were richer in nutrients and have a coarser structure (stony substrate). Both soil-types are strongly acidic, present low fertility, and exhibit the following seasonal variation: phosphorus increases and pH and organic carbon decrease during the dry season. During the vegetation survey 222 species were found among which 12.6% are endemic to the Serra do Cipó region and several others are exclusively found on *campos rupestres* (38.6%). Our study brings to light the lack of information on numerous species (e.g. 21.9% of the species have an unknown distribution), underlying the need for research into their biology, distribution and ecology. There is also a clear relationship between soil and vegetation composition. The two grassland types have to be considered as two different species-rich plant communities. These differences are closely related to differences in soil granulometry and composition, which leads to significant plant community heterogeneity. Some species are confined to either one or the other grassland type, which confers a real singularity in plant composition to each community, for example *Richterago polymorpha, Lagenocarpus velutinus* and *Xyris insignis* were only found in sandy grasslands, and *Spigelia aceifolia* and *Trimezia fistulosa* in stony grasslands. No exotic species were found. Because they are seriously threatened due to land-use changes and because of their great biodiversity, *campos rupestres* must have their conservation made a priority, and this must take into account the two communities and the close relationship between their respective vegetation and soils.

Keywords: Biodiversity; herbaceous communities; mountain grassland; *Rupestrian grasslands;* Serra do Cipó.

Nomenclature: Lista de Espécies da Flora do Brasil 2010:

http://floradobrasil.jbrj.gov.br/2010/

1. Introduction

The recognition, precise description, and understanding of plant communities are fundamental to environmental management, conservation programs, biodiversity surveys, and restoration projects (Soulé and Kohm 1989, Alves and Kolbek 2010). Focusing on plant communities can help reconcile the species approach with the ecosystem approach to conservation because they are basic components of the landscape and have consequences for species survival and for ecosystem processes (Heywood and Iriondo 2003). For instance, the implementation of the conservative network NATURA 2000 in Europe is driven by bird and habitat directives, which are based on lists of habitats and species that are recognized as being of interest (European Commission 2000). These habitats are described by their environmental characteristics and their plant communities (European Commission 2007).

In 2002, the Parties of the Convention on Biological Diversity (CBD) adopted a work program on mountain biological diversity due to the lack of knowledge of ecosystem functioning and community composition (as is often the case in tropical regions) which is a common barrier to implementing conservation or restoration activities. Indeed, they recognized the fragility of mountain ecosystems and species and their vulnerability to man-made and natural disturbances, particularly in the current context of land-use and climate changes. Mountain ecosystem conservation is essential for many reasons: such ecosystems host a great biodiversity, they act as refuges for species, they are important for water resources, and their proper function insures good water quality as they participate in soil erosion control (FAO 1998). Excluding the Andean vegetation, there are three main highland vegetation formations in South America: *Tepuis* on the Guayana shield, and *campos de altitudes* (i.e. Brazilian páramos) and *campos rupestres*, both in Brazil. These formations show strong physiognomy similarities; however each is characterized by a unique flora (Maguire 1970, Giulietti et al. 1997, Safford 1999) mainly resulting from Pleistocene climatic variations (Vuilleumier 1970, Van Der Hammen 1974, Fiaschi and Pirani 2009).

Campos rupestres are included in the Cerrado domain (Brazilian savanna, covering 22% of the country), encompassing around 130 000 km^2 (6% of the Cerrado) (Barbosa 2012) and are usually found on precambrian quartzite formations above 900 meters of altitude, primarily along the Espinhaço range, the largest mountain range in Brazil. They have been stable grassland ecosystems for about 20,000 years (Barbosa 2012). *Campos rupestres* are defined as a more-or-less continuous herbaceous stratum with small sclerophyllous evergreen shrubs growing between rocky quartzic outcrops forming a rich mosaic of plant communities (Giulietti et al. 1997, Medina and Fernandes 2007, Carvalho et al. 2012). Several physiognomies have been observed, ranging from a physiognomy found on rocky outcrops with trees and shrubs to physiognomies dominated by grasses, such as grasslands or peat bogs (Alves and Kolbek 2010, Carvalho et al. 2012), occasionally separated one from another by just a few centimeters (Conceição and Pirani 2005, Alves and Kolbek 2010).

Benites et al. (2003) noted a considerable diversity of pedoenvironments associated with the vegetation mosaics of *campos rupestres*. They commonly occur on Leptosols and Arenosols [respectively Neossolos Litólicos and Neossolo Quartzarênico according to the Brazilian Soil Classification System (Embrapa 1999)] (Benites et al. 2007). Such soils are shallow, acidic and coarsely textured, with high aluminum and low nutrient content (Benites et al. 2003, 2007). Podzolization, consisting of the eluviation of aluminum and iron, associated with organic compounds from surface areas that accumulate in depth, leads to residual quartz concentration in the form of sand particles in the upper horizons (Benites et al. 2007), and is an important process that occurs in these high-altitude ecosystems. On the other hand, the local topography (e.g. quartzic rocky outcrops, stony slopes, or sandy flat areas) dictates local drainage and water availability. Although substrate and topography are commonly cited as factors contributing to the differentiation of plant physiognomies leading to high heterogeneity and rich biodiversity, few studies deal with the relationship between soil composition and vegetation.

Campos rupestres are constrained ecosystems, subjected to stressful climatic conditions with large daily temperature oscillations, intense irradiation (UV), strong winds, and a marked dry season (Giulietti et al. 1997). Despite these harsh conditions, such grasslands are important centers of biodiversity (Giulietti et al. 1987, 2005, Lara and Fernandes 1996, FAO 1998, Carvalho et al. 2012) due to adaptation processes and speciation (Giulietti et al. 2005). In the Espinhaço Range alone, more than 4,000 plant species have been reported; these comprise one of the highest levels of endemism in the Cerrado biome (Alves and Kolbek 1994, Giulietti et al. 1997, Silva and Bates 2002; Echternacht et al. 2011).

Human disturbances of *campos rupestres* began in the 18th century, and were mainly associated with mining activities (i.e. gold, precious stones, iron, manganese) in the region. Disturbances also resulted from annual anthropogenic burnings (to support cattle breeding), wood extraction, eucalyptus cultivation, harvesting of ornamental plants (orchids, bromeliads, Eriocaulaceae) (Giulietti et al. 1997), and road construction (Barbosa et al. 2010). Recent changes in Brazilian environmental legislation have weakened the already modest conservation requirements for the region, thereby increasing the threat to *campo rupestre* biodiversity and the ecosystem services that they provide. While threats increase, limited or inadequate data on conservation targets, such as plant communities (Henwood and Iriondo 2003), can prejudicially affect the conservation of the *campos rupestres*.

The huge biodiversity of the campos rupestres is commonly associated with the wide variety of habitats generated by the combination of microclimate, topography, and substrates. However, little is known about the relationship between biodiversity and habitats, and about the composition and structure of campo rupestre communities. Botanical collection in campos rupestres began in the 19th century (Saint-Hilaire 1833), but only during later decades was there a growing interest in understanding the structure and functioning of campo rupestre communities (Meguro et al. 1994, Queiroz et al. 1996, Conceição and Pirani 2005, 2007, Conceição et al. 2007a,b,c, Jacobi et al. 2007, Scarano 2007, Viana and Lombardi 2007, Borges et al. 2011). The problem is that most of these studies dealt with the shrubby physiognomy occurring on rocky outcrops while very few studies addressed physiognomies dominated by grasses, which represent the matrix and thus the quintessence of campos rupestres (Conceição and Pirani 2005, Viana and Lombardi 2007, Borges et al. 2011) and offer valuable ecosystem services such as maintaining water-quality and controlling soil erosion. Furthermore, this grassland is defined as a more-or-less continuous herbaceous layer (Figure 14) (see campos rupestres definition in Giulietti et al. 1997). However, local topography with stony slopes (Figure 14) and sandy flatter areas (Figure 14) potentially generate different environmental conditions, and probably lead to distinct plant communities, which were never studied as such.

For the first time, we address the floristic and ecological aspects of these Neotropical mountain grasslands to obtain solid information on which to base conservation strategies. Our objectives were to find out 1) whether soil properties (granulometry and chemical composition) are different between grasslands and 2) whether the grasslands have homogeneous vegetation. We hypothesized that soil composition varies at small scale, leading to plant composition heterogeneity, and that this generates distinct plant communities. We therefore presupposed that soil granulometry and composition differ with topography thus influencing plant composition. We considered the complexity of these ecosystems, which confers on them a high conservation value, and how it can have important consequences in the context of landscape fragmentation and its relevance to future conservation programs.

2. Material and Methods

2.1. Study area and sites

Our study area was located in Brazil in the southern portion of the Espinhaço Range, in the buffer zone of the Serra do Cipó National Park (state of Minas Gerais). *Campos rupestres* are the main vegetation formation on shallow soils in the Serra do Cipó region, usually mixed with savannas, riparian forests and small groves on deeper soils, totalling more than 1600 plant species (Giulietti et al. 1987). Over recent decades, the region has gone through some land conversion (e.g. pasture associated with introduction of invasive species and annual burning) and anthropological pressure due to tourism activities along a major road, the highway MG 010. On the other hand, the creation of the Serra do Cipó National Park and the Environmental Protection Area of Morro da Pedreira (Área de Proteção Ambiental) in 1984 has helped to preserve pristine areas of *campos rupestres*. The regional climate is classified as Cwb with a warm temperature, a dry winter and a warm summer, according to the Köppen's system (Köppen 1900). It is markedly seasonal, with two distinguishable seasons: a rainy season from November to April and a dry one from May to October. The mean annual precipitation and temperature are respectively 1622 mm and 21.2°C (Madeira and Fernandes 1999). Based on topography, we designated and studied two main types of *campos rupestres*. Of the 10 grasslands we selected overall, 5 sites were on a sandy substrate on flatted areas and 5 sites were on a stony substrate on slopes. Sites were located between 1100 m and 1300 m.

2.2. Soil analyses

Three soil samples were taken at each site and air dried prior to the physical (granulometry) and chemical (pH, C_{org}, total N, P, K, Mg^{2+}, Ca^{2+}, Al^{3+}) soil analyses. Each soil sample consisted of three pooled sub-samples randomly taken in each site at the 10 first cm. To assess the granulometry of the coarse fraction of the soil, each sample was sieved through 1cm and 2mm mesh sieves. The fine fraction (<2mm) was used for physical (granulometry) and chemical (pH, MO, total N, P, K, Mg^{2+}, Ca^{2+}, Al^{3+}) soil analyses: P and K in mg/dm^3, N and C in dag/kg, Mg^{2+}, Al^{3+}, Ca^{2+} in cmol$_c$/dm^3, Organic Carbon (C_{org}) in dag/kg. P, N and K were analysed with the Mehlich 1 extraction method; Ca^{2+}, Mg^{2+}, Al^{3+} with 1 mol/L KCl extraction; C_{Org} following the Walkley-Black method. Soil sampling was done once during the rainy season (February) and once during the dry season (July) (n = 3 samples × 10 sites × 2 seasons = 60 samples). Analyses were conducted at the soil laboratory of Viçosa Federal University, Viçosa, Minas Gerais, Brazil. Soil analysis followed the recommendations of EMBRAPA (1997).

2.3. Plant survey

We surveyed fifteen 1m² quadrats at each sandy site and twenty 1m² quadrats at each stony site according to the minimal area which was previously assessed in December 2008 for each grassland type (species/area curves - Mueller-Dombois and Ellenberg 1974). At each quadrat the following information was collected: (1) percent cover of bare ground, litter, moss and lichen (hereafter “cryptogams”), forbs, ligneous species, Velloziaceae, and graminoids; (2) a list of the species, (3) the abundance of each species (number of individuals or clumps per m^2), (4) the percent cover of each species visually estimated, based on the vertical projection of all aerial plant parts (Mueller-Dombois and Ellenberg 1974), (5) the frequency of each species, based on the number of subquadrats (25 20x20cm subquadrats / m^2) in which each species was found. Plants were identified by experts and by using specific literature (Giulietti et al. 1987, Forzza et al. 2010) and the Herbarium BHCB at the Universidade Federal de Minas Gerais in Belo Horizonte, Brazil.

In order to find out whether the two grassland types had different plant communities, the Importance Value Index (IVI - Mueller-Dombois and Ellenberg 1974) and Relative Dominance were calculated for each species and at each site. The IVI is the sum of the Relative Density (D_r), the Relative Dominance (Do_r) and the Relative Frequency (F_r) and allows a species with high frequency but low cover to be considered as important. IVI was used to compare the importance of each species (maximum value = 300): the higher is the IVI, the higher is the importance of the species (Muller-Dombois & Ellenberg 1974). As D_r, Do_r and F_r are proportions, they range from 0 to 100.

1) The Relative Density (D_r) is $D_r=100*D_a/D_t$, where D_a (Absolute Density) is the number of individuals / m^2 and D_t (Total Density) is the sum of the all the D_a. The

Absolute Density is D_a=Σn_i*S/A with n_i = number of individuals of species i, S= quadrat area, A= total area of sampling at the site.

2) The Relative Dominance (Do_r) is Do_r=100*Do_a/Do_t, where Do_a (Absolute Dominance) is the area in cm^2 occupied by the species / m^2 and Do_t (Total Dominance) is the sum of the all the Do_a. The Absolute Dominance (cm^2/m^2) is Do_a=100*ΣR_i*S_i/A with R_i= area covered by species i (percent cover), S_i= plot area, A= total area of sampling at the site.

3) The Relative Frequency (F_r) is F_r=100*F_a/F_t, where F_a (Absolute Frequency) is the percent of subquadrats occupied by the species at a site and F_t (Total Frequency) the sum of the all the F_a. The Absolute Frequency is F_a=100 *ΣSq_i/Sq_t with Sq_i = number of subquadrats occupied by species i and Sq_t = total number of subquadrats / site.

In order to analyse the structure and the characteristics (i.e. geographic distribution, endemism and IUCN threatening status) of the species, all species were classified according to (1) life-form according to Raunkiaer's life form modified by Mueller-Dombois and Ellenberg (1974), (2) their plant forms, (3) habitats, (4) distribution ranges, (5) IUCN status and (6) life cycle. (1) The life-forms were assessed according to Raunkiaer (1904) modified by Mueller-Dombois and Ellenberg (1974). (2) The considered plant forms were: forbs, graminoids, sub-shrub, shrub, liana, fern. (3) Habitats in Brasil were determined based on literature: *campos rupestres*, altitude grassland, cerrado (*sensu-lato* including *campos rupestres*), caatinga, Atlantic rainforest, Amazon rainforest, wet grassland (Giulietti et al. 1987, Forzza et al. 2010). (4) The distribution ranges, also based on the literature and a database, comprised: (a) endemic from the Serra do Cipó, (b) endemic from the Espinhaço Range in the state of Minas Gerais, (c) endemic from the Espinhaço Range (states of Minas Gerais and Bahia), (d) distributed in the state of Minas Gerais, (e) distributed in Brazil, (f) wide distribution (Giulietti et al. 1987, Forzza et al. 2010, database *SpeciesLink*: http://splink.cria.org.br/). (5) The IUCN status was evaluated according to Mendonça and Lins 2000: vulnerable, critical, and endangered. (6) We also included the life cycle: perennial or annual.

2.4. Statistical analyses

To compare the fine fraction granulometry between *campos rupestres* types, t-tests were performed after checking the data for normality and homogeneity of variance.

To compare the coarse fraction granulometry between grassland types, the paired t-test with estimated separate variance was performed as the variances were not homogenous. To compare chemical soil composition between grassland types and seasons we used a nested two-way ANOVA for each chemical element. Log-transformations were applied before comparing P, K, Ca^{2+}, Mg^{2+} and Organic Carbon (Sokal and Rohlf 1998).

To assess plant similarity between stony and sandy grasslands, the Steinhaus similarity index, based on species abundance, was calculated (Steinhaus = 1-Bray-Curtis index, values range between 1 and 0, the higher the Steinhaus value, the more similar plant compositions, Legendre and Legendre 1998) and an ANOSIM was performed. ANOSIM analyses were also carried out within each grassland type, to evaluate the within grassland type plant similarity. To assess the differences of the Steinhaus index when comparing sites belonging to the same or to different types of grasslands, we performed a GLM procedure using a Gaussian distribution and identity link function, with similarity index as the response variable and the modality (comparison between stony and sandy grasslands, within stony grasslands and within sandy grasslands) as explicative variables. To identify groups a ward clustering of a matrix of chord distances among sites was performed using species percent cover data. Then, to corroborate classifications and find out if the cluster overlapped or not, we plotted the cluster membership using a Correspondence Analysis (CA) on plant percent cover matrix (222 species x 175 quadrats). We therefore identified which species discriminated each groups to establish the community type.

Kruskall-Wallis tests were performed to compare plant form and life-form within sandy and stony grasslands followed by multiple comparisons with Bonferroni correction, while Wilcoxon tests were performed to test differences in plant form and life-form between sandy and stony grasslands. To test the difference between the two grassland types in the number of species per site and m^2, the number of individuals per m^2 as well as the number of each plant form per site, t-test, or Wilcoxon tests when data were not normal, were performed.

To analyse the relationship between soil and plant composition, a co-inertia analysis was run between plant and soil data. This type of analysis is used to determine if there is a co-structure between two data tables by performing simultaneous analysis of the two tables. The optimizing criterion in co-inertia analysis is that the resulting sample scores (environmental scores and floristic scores) are the most covariant

(Doledec and Chessel 1994). The co-inertia analysis was based on one CA (222 species) and one PCA (18 physico-chemical variables) at the 10 sites (10 points); a test based on permutations was performed to find out about the co-inertia significance.

All analyses were carried out in R version 2.9.1 (R Core Development Team, 2010) using ADE-4 and stats packages.

3. Results

3.1. Soil analyses

As expected, grasslands with a stony substrate (stony grasslands) presented a significantly greater proportion of gravel (gravel > 1cm represented 28%) compared to grasslands with a sandy substrate (sandy grasslands) (Table 2). On the other hand, sandy grasslands were characterized by a significantly higher proportion of fine sand (< 2mm) than stony grasslands (t= 4.65, P<0.001) (Table 2). In stony grasslands, N, P, K, Ca2+, Mg2+ concentrations and Corg content were significantly higher and the soil was more acidic than in sandy grasslands (Table 3, Figure 17). Both grasslands presented seasonal variation for P and Corg content and pH. During the dry season, P concentrations were significantly higher while Corg contents and pH were significantly lower (Table 3, Figure 17). The aluminum concentration did not vary between grasslands or between seasons (Table 3, Figure 17).

Table 2: Mean and standard error values of granulometric soil parameters, from soils collected in 5 sandy and 5 stony grasslands (3 samples / site , n=30). T-tests were run using separate variance estimates for the coarse fraction. ns: non-significant difference, *** :significant difference with *P*<0.001.

		Sandy grasslands	Stony grasslands	t value
Coarse fraction of soil	soil >1cm (%)	1.79 ± 0.71	27.63 ± 1.18	18.81***
	soil >2mm (%)	12.98 ± 2.42	60.04 ± 1.89	16.26***
Fine fraction of soil <2mm	Coarse sand (dag/kg)	19.66 ± 2.48	25.80 ± 2.42	1.63^{ns}
	Fine sand (dag/kg)	46.87 ± 2.04	37.33 ± 1.41	4.65***
	Silt (dag/kg)	29.27 ± 1.94	31.53 ± 1.49	0.85^{ns}
	Clay (dag/kg)	4.20 ± 0.43	5.33 ± 0.47	1.54^{ns}

Table 3: Results of the two-way ANOVAs performed for chemical soil parameters, from soils collected in 5 sandy and 5 stony grasslands (3 samples / site / season, n=60. ns: non-significant difference, *: significant difference with *P*<0.05, ***: significant difference with *P*<0.001.

	Two-way ANOVAs		
	Season	Grassland type	Interaction
	F	F	F
N (dag/kg)	1.09^{ns}	8.69*	1.93^{ns}
pH (H_2O)	41.99***	9.26*	0.17^{ns}
P (mg/dm^3)	188.26***	6.34*	3.49^{ns}
K (mg/dm^3)	2.63^{ns}	15.04**	1.68^{ns}
Ca^{2+} ($cmolc/dm^3$)	3.09^{ns}	18.53**	0.63^{ns}
Mg^{2+} ($cmolc/dm^3$)	0.23^{ns}	19.37**	0.79^{ns}
Al^{3+} ($cmolc/dm^3$)	0.94^{ns}	0.14^{ns}	0.82^{ns}
Organic carbon (dag/kg)	6.83*	23.18**	4.73***

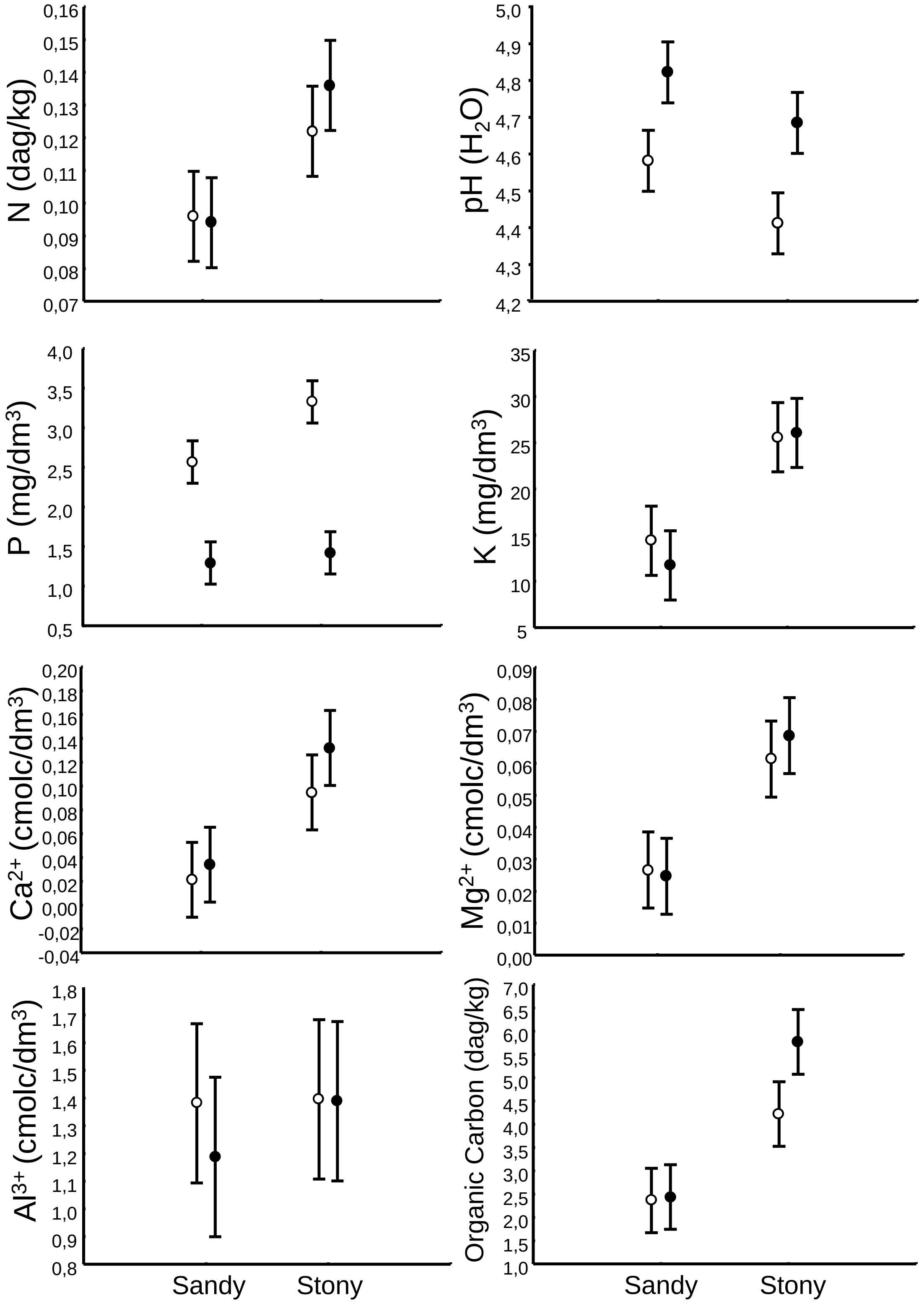

Figure 17: Mean and standard error values of chemical soil parameters, from soils collected in sandy and stony grasslands (3 samples / 5+5 sites / 2 seasons, n=60). Open circles represent dry season and full circles rainy season. See Table 2 for two-way ANOVA results.

3.2. Plant survey

The mean Steinhaus similarity index between sites belonging to different grasslands (0.25 ± 0.07) was significantly lower than the mean Steinhaus similarity index within sandy grassland sites (0.46 ± 0.04) or stony grassland sites (0.40 ± 0.06) (GLM procedure $P<0.001$). Furthermore, differences in similarity were significant between and within the grasslands ($R_{\text{between stony and sandy grasslands}}= 0.49$, $R_{\text{within stony grasslands}}= 0.45$ and $R_{\text{within sandy grasslands}}= 0.29$, $P<0.001$), highlighting also the presence of heterogeneity within the communities. A Ward clustering analysis allowed the distinction of two floristic groups based on floristic composition and structure: the sandy and the stony grasslands (Figure 18).

Axes 1 and 2 of the correspondence analysis performed on the matrix of the plant percent cover explained 47% of the total inertia. Axis 1 (29%) separated sandy from stony grasslands while axis 2 (18%) showed an inter-site variability in plant composition, particularly in the stony grasslands (Figure 19). Some species, such as *Vellozia albiflora, V. resinosa, V. caruncularis, Bulbostylis lombardii, B. paradoxa, Diplusodon orbicularis, Xyris minarum, X. melanopoda, Paepalanthus geniculatus, Sebastiana ditassoides* and *Vochysia pygmaea* were typical of the stony grasslands, while *Xyris asperula, X. insignis, X. nubigena, Syngonanthus cipoensis, Panicum cyanescens, Vellozia epidendroides* and *Rhynchospora ciliolata* were strongly associated with sandy grasslands (Figure 19). We found one species of pteridophytes and 221 species of angiosperms, distributed into 34 plant families: 120 monocotyledons and 101 dicotyledons, in the 10 investigated sandy and stony grasslands (Appendix 1). The analyses of the distribution pattern of 174 species showed that 28 species (i.e.12.6% of the total number of species) are endemic to the Serra do Cipó, while 48 species (21.6%) are restricted to the Espinhaço range whether in the state of Minas Gerais or in the states of Bahia and Minas Gerais (Figure 20, Appendix 1). Among the 160 species for which bibliographical data were available, 86 (38.6% of the total number of species) are restricted to the *campos rupestres* and 31 (13.9%) are cerrado species (Figure 20, Appendix 1). To summarize, 34.2% of the flora are endemic to the Espinhaço Range and 38.6% of the species are restricted to the *campos rupestres.* Twenty-four species (i.e. 10.7% of the total) are classified as either endangered, critical, or vulnerable according to the IUCN criteria (Appendix 1).

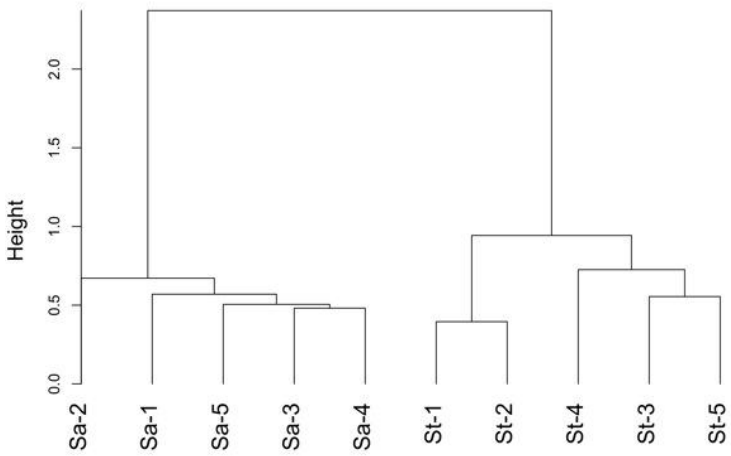

Figure 18: Ward clustering of a matrix of chord distances among sites (species data).

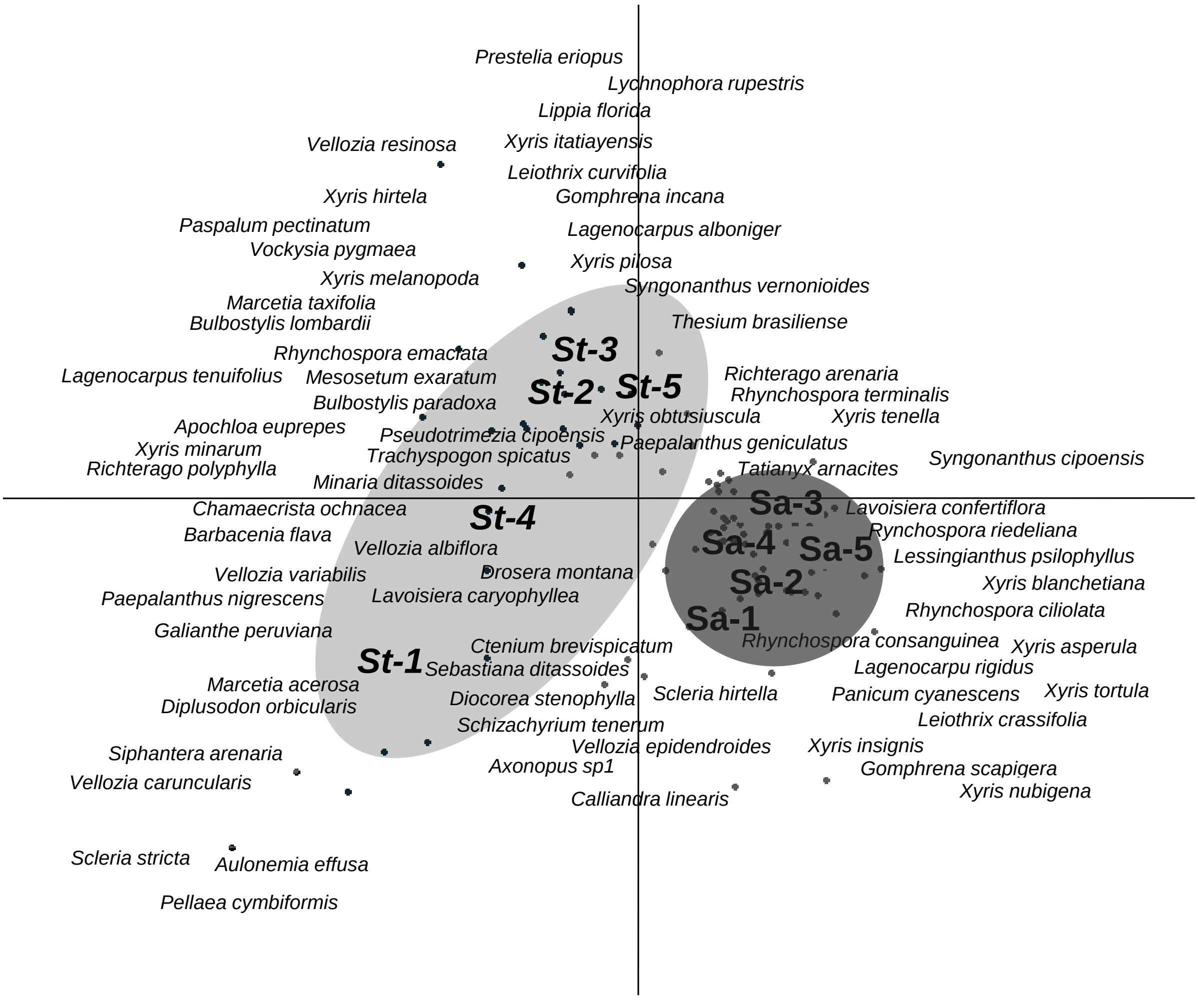

Figure 19: Correspondence Analysis run on the matrix of plant percent cover in 1m^2 quadrats in the 5 sandy (Sa) and 5 stony (St) grasslands [175 points x 222 species]. Projection of the two first axes, axis 1 (29%) and axis 2 (18%). Inertia= 0.19, *P*<0.001, Monte-Carlo permutations.

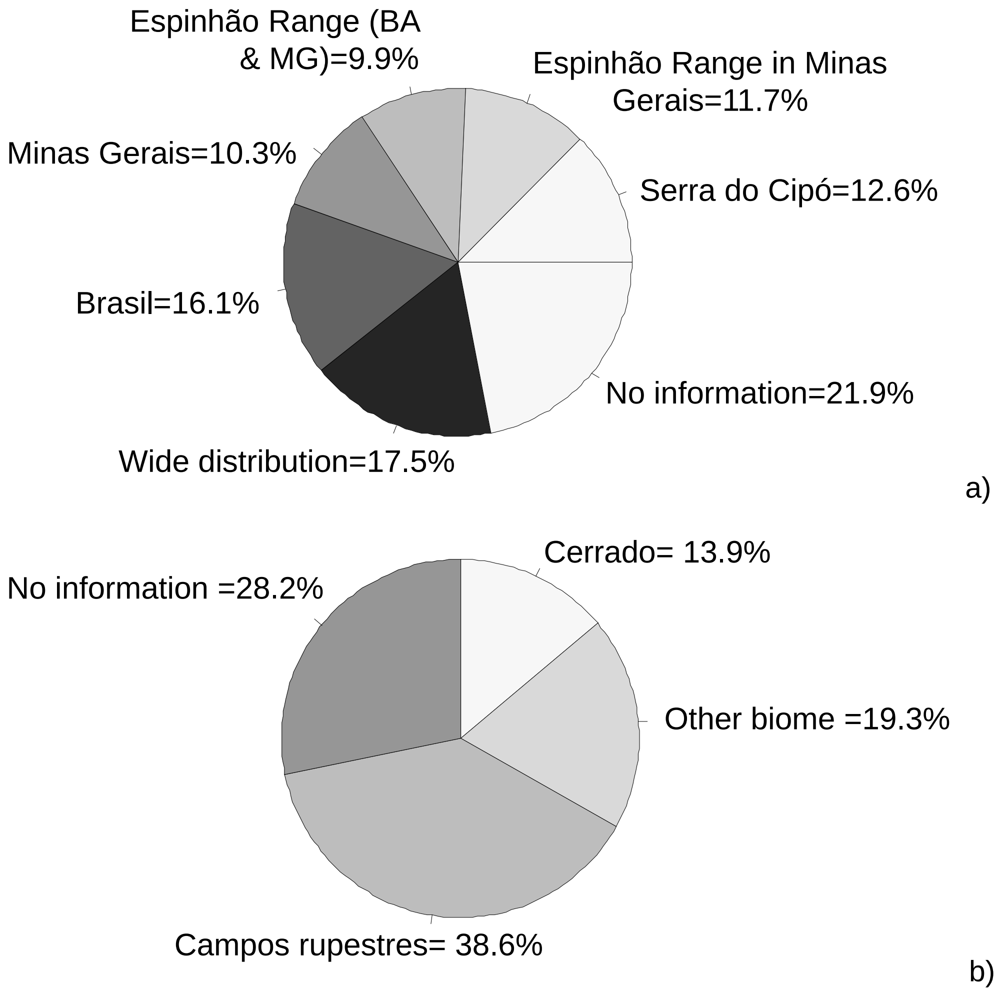

Figure 20: Pie charts representing the percentage of species according to a) their distribution range (N=174 species) and b) their habitat in Brazil (N=160 species).

One hundred and fifty-eight species were found in the sandy grasslands and 170 species were found in the stony grasslands of which 13.9% and 17.1% were endemic species, respectively (Table 4). Fifty-two species (32.9%) are exclusively found in sandy grasslands while 64 (37.6%) species are restricted to stony grasslands. A large part of the species is perennial in both communities (95.6% in sandy grasslands and 98.2% in stony grasslands), and monocotyledons represent more than 50% of the species (56.9% in sandy grasslands and 55.9% in stony grasslands) (Table 4). Only 12 species (5.3% of all species) were found in all sites, 47 species (21%) were found in 7, 8 or 9 sites while 87 species (39%) were encountered at only one site (singletons). According to the IVI and dominance values, the sandy grasslands were characterized by *Tatianyx arnacites* (with IVI and dominance values of 40.2 and 17.7, respectively)*, Homolepis longispicula* (37.3 and 12.3), *Paspalum* *erianthum* (30.0 and 7.3), *Lagenocarpus sp1* (20.7 and 12.8) and *Mesosetum exaratum* (16.2 and 6.2). These five dominant species represented 56.4% of the vegetation cover and the first 16 dominant species accounted for 80.0% of the vegetation cover (Appendix 1). In the stony grasslands, *Mesosetum exaratum* (IVI and dominance values of 43.2 and 14.7, respectively), *Tatianyx arnacites* (28.9 and 12.8), *Lagenocarpus tenuifolius* (14.9 and 8.9), *Homolepis longisticula* (14.7 and 4.8) and *Xyris minarum* (14.3 and 0.8) can be considered the main species based on their IVI values, while *Vellozia resinosa* and *V. caruncularis* can be characterized as important, having respective dominance values of 8.8 and 6.1 (Appendix 1). The top five most dominant species represented 51.3% of the vegetation cover and the top 19 dominant species accounted for 80%.

Table 4: Family and species distribution between sandy (5 sites, 15 quadrats / site, n=75) and stony grasslands (5 sites, 20 quadrats / site, n=100). ns: non significant difference, *:significant difference with $P<0.05$.

	Sandy grasslands	Stony grasslands	t-test or Wilcoxon test
Total number of families	33	34	
Total number of species	158	170	
Total number of dicotyledons	68 (43.1%)	74 (43.5%)	
Total number of monocotyledons	90 (56.9%)	95 (55.9%)	
Total number of pteridophyte	-	1(0.6%)	
Total number of annual plants	7 (4.4%)	3 (1.8%)	
Total number of perennial plants	151 (95.6%)	167 (98.2%)	
Total number of species endemic from the Serra Do Cipó	22 (13.9%)	29 (17.1%)	
Total number of species with an endangered/vulnerable/critical statue	15 (9.5%)	22 (12.9%)	
Number of species / site	81.0 ± 2.7	85.8 ± 2.5	t= 1.28 ^{ns}
Number of species / m^2	26.8 ± 0.6	29.1 ± 0.5	t= 2.93*
Number of individuals / m^2	578.8 ± 19.6	581.9 ± 17.2	W= 3711.5 ^{ns}
Abundance of forbs / site	642.0 ± 179.9	1207.6 ± 294.9	t= 1.63 ^{ns}
Abundance of graminoids / site	7853.2 ± 643.3	9955.8 ± 677.4	t=2.25 ^{ns}
Abundanceof liana / site	3 ± 1.5	7.8 ± 5.8	t= 0.79 ^{ns}
Abundance of shrub / site	10.8 ± 2.9	91 ± 46.3	W= 1*
Abundance of sub-shrub / site	188 ± 92.3	371.2 ± 112.4	W= 5 ^{ns}
Abundance of fern / site	0 ± 0	8.8 ± 8.3	-

The mean number of species/m^2 (t=2.93, $P<0.01$) as well as the mean number of shrubs (W=1, $P<0.05$) were higher in the stony grasslands (Table 4, Appendix 1). Graminoids (representing 45% and 39% of species in sandy and stony grasslands, respectively) were the dominant form of plant growth in both communities (Figure 21). Forbs (27% and 31% of species in sandy and stony grasslands, respectively) and sub-shrubs (23% and 22%) were also well represented (Figure 21). In both sandy and stony grasslands, more than 80% of the species were hemicryptophytes (Figure 22). In both types of grassland, the families with the most species were Poaceae (26 and 28 species in sandy and stony grasslands, respectively), Cyperaceae (23 and 25 species), Xyridaceae (20 and 14 species), Eriocaulaceae (9 and 14 species) and Velloziaceae (5 and 7 species) for the Monocotyledons and Asteraceae (14 and 13 species), Melastomataceae (6 and 8 species), Polygalaceae (7 and 1 species) and Apocynaceae (4 and 5 species) for the Dicotyledons (Figure 23).

We observed a strong co-structure between soil and vegetation data (RV= 0.70, $P<0.001$), revealing a significant relationship between soil and community composition and structure (Figure 24). Velloziaceae, ligneous species, and bare ground primarily characterized the stony grasslands as well as the N, P, K, Ca^{2+}, Mg^{2+} concentrations and C_{org} content while the sandy grasslands are characterized by cryptogams, graminoids, finer soil and a less acidic pH (Figure 24).

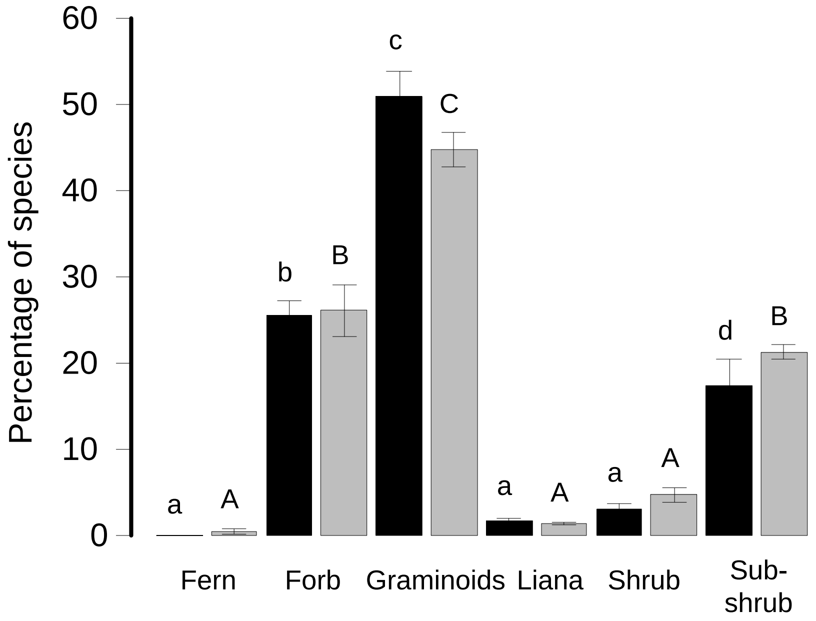

Figure 21: Percentage of species according to plant forms. Sandy grasslands (black columns) and stony grasslands (grey columns) $\chi^2=27.3$, $P<0.001$ in sandy grasslands and $\chi^2=27.0$, $P<0.001$ in stony grasslands. Lower-case letters indicate differences between forms within sandy grasslands and capital letters between forms within stony grasslands (Multiple comparisons made using the Bonferroni correction).

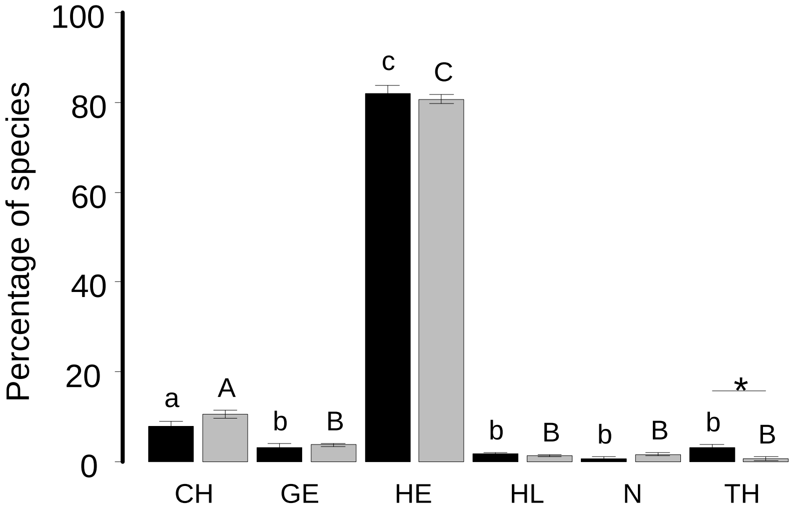

Figure 22: Percentage of species according to life forms. Life-form: CH = Chamaephytes, GE= Geophytes, HE= hemicryptophytes, HL= hemicryptophyte lianas, NA= Nano-phanerophytes, TH = therophytes. Sandy grasslands (black columns) and stony grasslands (grey columns). χ^2=24.25, *P*<0.001 in sandy grasslands and χ^2=25.96, *P* <0.001 in stony grasslands. Lower-case letters indicate differences between forms within sandy grasslands and capital letters between forms within stony grasslands (Multiple comparisons made with the Bonferroni correction), * indicates differences between groups (t-test with unequal variances).

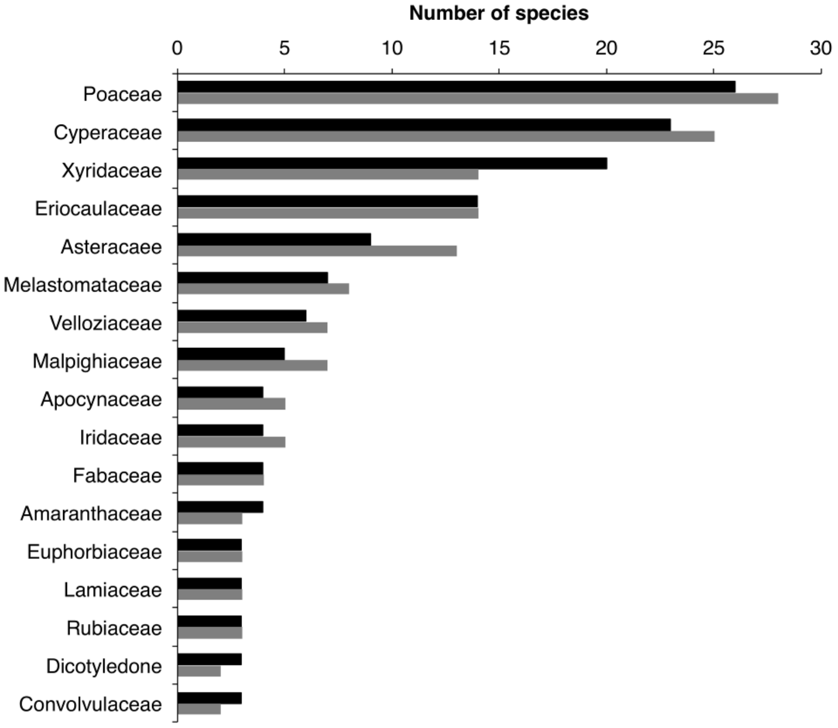

Figure 23: Number of species from the most-represented families in sandy grasslands (black columns) and stony grasslands (grey columns). (5 sites of each physiognomy, 15 1 m^2 quadrats in sandy grasslands and 20 $1m^2$ in stony grasslands).

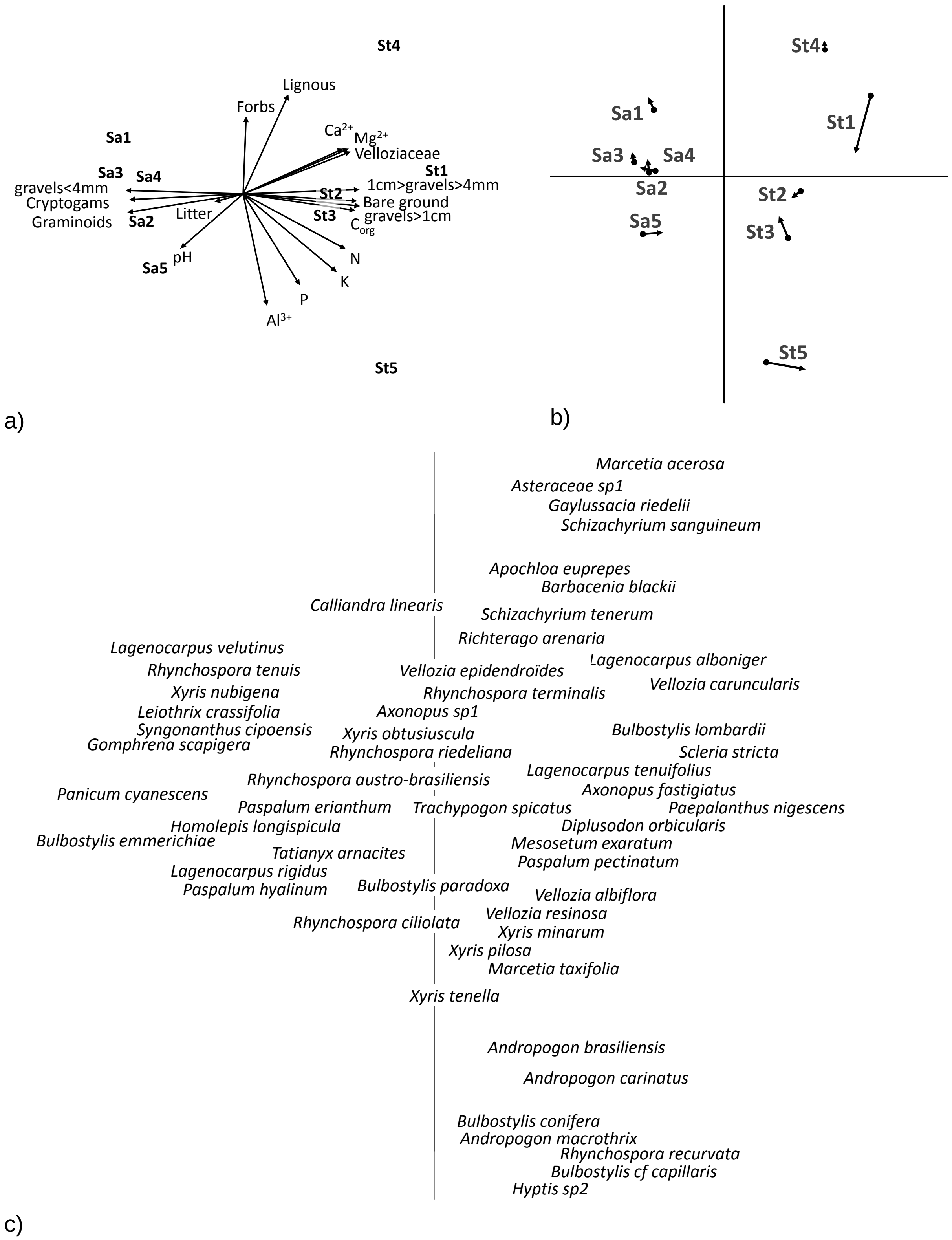

Figure 24: Co-inertia results: a) Representation of the sites, arrow heads indicating floristic data and arrow tails indicating environmental data, b) Representation of the environmental data: soil composition and granulometry [10 points x 18 variables], c) Representation of the floristic data [10 points x 222 species]. Projection of the top two axes of the co-inertia: axis 1: 79.4%, axis 2: 10.5%. RV test observations= 0.61, P<0.01 (Monte-Carlo permutations).

4. Discussion

4.1. Soils

The stony grasslands are characterized by a coarse granulometry, particularly quartzic stones, and a smaller proportion of fine sand. Indeed, as they are usually located on slopes, they are potentially more impacted by water erosion. In dry systems, water availability is a source of heterogeneity (Jobbagy et al. 1996), and local drainage further diversifies the environment by creating relatively humid or arid sites. We can expect stony grasslands to be drier than sandy grasslands since stony grasslands are never flooded while sandy grasslands can experience temporary flooding during the rainy season (Vitta 1995). *Vellozia* spp. are strongly associated with dry environments (Porembski and Barthlott 2000) and may be an indicator species for stony grassland in the *campos rupestres*.

The soils of *campos rupestres* are globally poor in nutrients: clays, which are usually associated with a higher capacity of nutrient retention, are almost entirely absent. This pattern might have been exacerbated by periods of intense leaching followed by long-term podzolization (Turenne 1970, Benites et al. 2007). In spite of this, our data indicate that the soil of stony grasslands is more acidic and richer in nutrients (N, P, K, Ca^{2+}, Mg^{2+}) and carbon content than sandy grassland soil. As sandy grasslands are found in flatter areas, they accumulate water, which slowly percolates, and this might facilitate the eluviation of the soluble organic compounds that are associated with iron and aluminum, which can leach throughout and into deeper soil. This translocation is favored by humic acid, which is common in these soils (Schaeffer and Ker 2003). Normally, at lower pH phosphorus (a critical element in the development of the vegetation (Sarmiento 1984)) precipitates, for example, with aluminum, and becomes less available to plants. However, in the stony grasslands we studied, it was found that during the dry season, soil pH was decreased while phosphorus concentrations were elevated in what may be related to a reduction in the loss of mineral nutrients due to the absence of rainfall (Sarmiento 1984).

4.2. Similarities between the two grassland types

Both sandy and stony grasslands are species-rich plant communities highlighting the relevance of *campos rupestres* for the maintenance of biodiversity. They are composed of herbaceous strata dominated primarily by Poaceae (*Paspalum, Andropogon*) and Cyperaceae (*Lagenocarpus, Rhynchospora, Bulbostylis*), and combined with Xyridaceae (*Xyris*), Eriocaulaceae (*Paepalanthus, Leiothrix, Syngonanthus*), Velloziaceae (*Vellozia, Barbacenia*) and Iridaceae (*Trimezia, Pseudotrimezia*). The predominance of monocotyledons, which has already been noted in earlier botanical surveys of *campos rupestres* (Meguro et al*.* 1994, Conceição and Pirani 2005, Viana and Lombardi 2007, Borges et al*.* 2011), indicates the presence of limiting ecological factors according to Granville (1984). The marked dominance of hemicryptophytes in both grassland types highlights a probable selective pressure by fire, which is a frequent endogenous disturbance (*sensu* White and Jentsch 2001) in savannas and tropical grasslands. As hemicrytophytes are defined by underground renewing buds, regrowth organs remain viable and allow regeneration after fire (Coutinho 1990).

Some forb and sub-shrub species are also found in these grasslands. They belong to families, such as Asteraceae (*Lychnophora, Richterago*), Melastomataceae (*Lavoisiera, Marcetia*), Fabaceae (*Chamaecrista*), Malpighiaceae (*Byrsonima*), Apocynaceae (*Minaria, Hemipigon*), Ericaceae (*Gaylussacia, Agarista*), Euphorbiaceae (*Sebastiana*), Vochysiaceae (*Vochysia*), Rubiaceae (*Declieuxia*), Lythraceae (*Diplusodon, Cuphea*). These genera have been observed previously in several *campos rupestres* in the Serra do Cipó (Giulietti et al. 1987) as well as in other areas of the Espinhaço range (Meguro et al. 1994, Queiroz et al. 1996, Pirani et al. 2003, Zappi et al*.* 2003, Conceição and Pirani 2005, Viana and Lombardi 2007, Borges et al. 2011). No exotic species were found in our study sites, even though the distance of closest approach between highway MG-010 and our study sites is just 130 m, from which we could conclude either that our sites are very well conserved or that the environmental conditions are unfavorable to the establishment of most invasives. With the recent study by Barbosa et al. (2010) indicating the presence of invasive species along the MG-010 road, we can safely rule out the latter conclusion.

4.3. Differences between the two grassland types

One of the main findings of this study was the stark heterogeneity of these grasslands: the sandy and the stony grasslands represent distinct plant communities. The main species, such as *Tatianyx arnacites, Mesosetum exaratum* and *Homolepis longispicula,* can be found in both grassland types, but with different importance indices and dominance values. On the other hand, some species are restricted to one or another grassland, conferring a real singularity and a peculiar value to each grassland type, such as *Paspalum hyalinum, Xyris asperula* and *X. insignis* in sandy grasslands and *Paepalanthus nigrescens, Prestelia eriopus, Marcetia acerosa* and

Vellozia albiflora in stony grasslands. Therefore, this study further corroborates the hypothesis that *campos rupestres* are formed by a mosaic of distinct plant communities characterized by their own floristic composition. These findings have important implications for the conservation of these plant communities that must be considered separately. Having laid the necessary ground work, the present study makes it possible, in due course, to consider issues such as remaining surface area and conservation strategy.

According to the results of the co-inertia analysis, each plant community is closely related to a specific soil composition. The nature of the substrate and its heterogeneity, even at a scale of a few centimeters, separate the grassland types from one another and determine the community composition. The extreme abiotic conditions of the *campos rupestres* have strong consequences in terms of plant adaptation to constrained environmental conditions. However, each *campo rupestre* physiognomy is characterized by its own constraints (e.g. type of substrate) which might impose different adaptations (see Carvalho et al. 2012). For instance, in stony grasslands the presence of small white stones (i.e. quartzic stones) could induce higher temperatures and higher radiations than in sandy grasslands, inducing adaptations for water-storage, transpiration control, leaf reduction, seedling adaptation to growth on sunny areas while in sandy grasslands humidity can be preserved at the ground surface (Giulietti et al. 1997).

Another part of the heterogeneity of plant composition both between and within the sandy and stony grasslands is due to endemism, which is a characteristic of the *campo rupestre* flora. Seventy percent of *Vellozia* species are restricted to the state of Minas Gerais (Mello-Silva 1995). Giulietti et al*.* (1987) noted that a large number of Eriocaulaceae species are endemic to the Espinhaço Range. For Xyridaceae, Wanderley (2011) recorded 14 endemic taxa in the Serra do Cipó and attributed the recent origin of *Xyris* species to explain their restricted distribution. Endemism in the Espinhaço Range may be explained by its tectonic history and climate fluctuations. These phenomena led to expansion following by reduction and fragmentation of populations and therefore the evolution of new species, often with very limited distribution (Alves and Kolbek 1994, Giulietti et al. 1997, Barbosa 2012). Despite the lack of geographically broader studies, many *campo rupestre* species have been said to be endangered because of their restricted distribution (Ribeiro and Freitas 2010). Numerous species (38.6%) are found exclusively on *campos rupestres*, conferring a certain uniqueness to these ecosystems, though vicariant species can contribute to a high floristic variation among them (Giulietti et al. 1997, Alves and Kolbek 2010). Alves and Kolbek (2010) have already noted that genera alone are not sufficient to separate *campos rupestres* from other vegetation formations, such as highland grasslands (*campos de altitude*), and that floristic studies at the species-level must be combined with environmental variables to help design general functioning patterns for the *campos rupestres.* Our study also brings to light the lack of information on numerous species, underscoring the need for research into their biology, distribution and ecology.

5. Conclusions

This study has shown that these neotropical mountain grasslands are species-rich communities, adapted to harsh abiotic conditions with nutrient poor soils. It has also demonstrated that there are two distinct plant communities, the sandy and the stony grasslands. The vegetation composition is strongly related to specific soil composition, and this explains why some species are confined to one or another grassland type, indicating finely tuned adaptations to environmental conditions. This complex relationship between soil and vegetation leads to a high heterogeneity and therefore generates a rich biodiversity, even at small scale and even among the herbaceous layer that was previously considered homogeneous. The large proportion of endemism along the Espinhaço Range generates variability among *campos rupestres* and confers a great conservation value, which at the moment is very threatened. It is important to consider these two grassland types as distinct plant communities, and, as consequence, ecological strategies must be targeted accordingly to improve their conservational and restorative efficacy.

Note: According to Vitta (2005), *Lagenocarpus rigidus* (Kunth) Nees subsp. *tenuifolius* (Boeck.) T. Koyama & Maguire is a synonym of *Lagenocarpus tenuifolius.* This species present two morphotypes on Serra do Cipó *campos rupestres,* while we firstly thought it was two different species. In this thesis *Lagenocarpus rigidus* subsp. *tenuifolius* designate the morphotype “glauco” and *Lagenocarpus tenuifolius* designate the morphotype “vede-amarelo.”

Transition to Chapter 2

The first chapter highlighted that *campos rupestres* host at least two kinds of tropical grasslands each characterized by its own vegetation composition and its own soil properties, but we suppose the mosaic to be even more diversified (Alves & Kolbek 2010). As for the two plant communities identified (i.e. sandy and stony grasslands), although physical factors are important to explain plant community structure, life-history traits, such as phenology, can also be of major interest to explain the different patterns that we observed.

Indeed phenology is an important aspect of population biology (Fenner 1998, Schwartz 2003, Hudson & Keatley 2010), since it affects the dynamics of interspecific interactions linked to the timing of plant reproductive and growth cycles, such as herbivory, pollination and frugivory (Van Schaik et al. 1993, Diaz et al. 1994, Apko 1997, Bosch et al 1997, Gribel et al. 1999, Conceição et al. 2007a). In addition, the study of phenological patterns is also crucial to understand plant community dynamics, biological invasion (Wilsey et al. 2011) and the co-occurrence of species, especially in species-rich tropical plant communities (Janzen 1967, Frankie et al. 1974, Gentry 1974, Grubb 1977, Fenner 1998, Batalha & Martins 2004, Pau et al. 2011). The first phenological studies were mainly realized in temperate zones where patterns are now well described. However, in tropical systems, cycles are complex and irregular as plants can display a wide variety of patterns (Sarmiento & Monasterio 1983); the major issue is therefore the recognition of some general patterns (Newstrom et al. 1994a, Morellato 2003).

The objective of the following chapter (chapter 2) is then to describe phenological patterns of both sandy and stony grasslands, to assess if flowering, fruiting and dissemination are seasonal, if phenology differs between grassland-types and to analyze which species participate in the reproductive phenology (Figure 25). This latter issue allows determining the composition of the external species pool, useful to restore degraded areas (Figure 25).

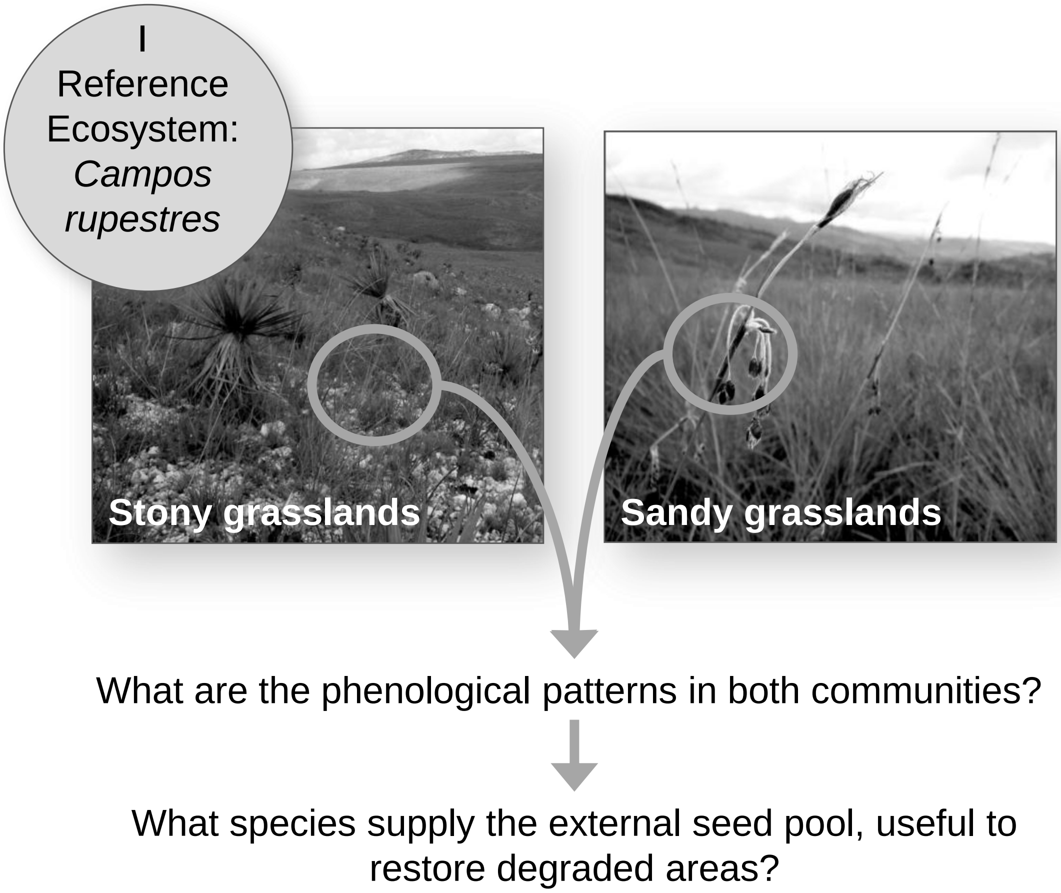

Figure 25: The theoretical objective of the second chapter is to describe the phenological patterns of two herbaceous communities; the applied objective of the second chapter is to identify the species which produce seeds and thus might potentially colonize degraded areas.

On top : *Campos rupestres*, general view ; at right : *Lavoisiera confertiflora.*
Photo credit S. Le Stradic

Chapter 2 - Reproductive phenological patterns of two Neotropical mountain grasslands.

Chapter 2 - Reproductive phenological patterns of two Neotropical mountain grasslands.

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Abstract:

In South America, just a small percentage of herbaceous vegetation has been examined from the point of view of its seasonal changes. However, the study of phenological patterns is crucial to understand plant community dynamics, especially in species-rich tropical plant communities. In a harsh and heterogeneous environment, the *campos rupestres* (Neotropical mountain grasslands located on southeastern Brazil), we monitored the phenology of the two dominant herbaceous communities, the sandy and the stony grasslands, for two consecutive years. The aim of this study was to assess if plant species reproduce seasonally; to test whether the phenological patterns as well as the fruit and flower production, are different between these two communities; to test if there are intra-specific variations in terms of fruit production between the two grassland types, considering only species co-occurring in both grasslands. Several phenological patterns occur among the herbaceous communities: likewise other physiognomies of Cerrado, herbaceous communities of *campos rupestres* have a flowering peak during the rainy season, but some species reproduce preferentially during the transition from the rainy to the dry season or during the dry season. Phenological patterns were similar in both communities, however, the amplitude of phenophases, i.e. net production by species, varied among communities according to each species' density. In both communities, Cyperaceae and Xyridaceae were families with the highest species contribution to overall phenology. Some dominant species belonging to Poaceae, among others, were not observed reproducing, which implies limited chances to disperse on degraded areas.

Keywords: dissemination, phenophase duration, flowering, fruiting, phenophase frequency, seasonality, phenophase timing.

1.Introduction

Phenology is defined as the study of the timing of recurring biological events, the causes of their timing in regard to biotic and abiotic forces, and the interrelation among phases of the same or different species (Lieth 1974). For plants, biological events or phenophases include reproduction, such as bud formation and flowering, fruiting, and seed germination, along with vegetative events like leaf flushing and shedding (Morellato et al. 2010). The cycles of plant growth and reproduction are crucial to understand ecosystem functioning (Lieth 1974) and processes of primary production (Sarmiento & Monasterio 1983) and recruitment, such as seed dispersal and seed germination (Garwood 1983, Johnson 1993, Silveira et al. 2012a). Phenological variations can be analyzed as plant adaptive strategies (Van Schaik 1993, Elzinga et al. 2007). For instance, abiotic factors, such as precipitation, temperature and photoperiod influence phenology, especially in areas with a seasonal climate; the detection of such environmental signals is fundamental since it ensures plant flowering when climatic conditions are the most suitable for reproduction (Rathcke and Lacey 1985, Fenner 1998, Shackleton 1999, Morellato et al. 2000, Ramirez 2002). Flowering time is also controlled by both genetic (Koornneef et al. 1998, Putterill et al. 2004) and biotic interactions, such as pollination, which can modulate the selection of the timing of flowering, and fruiting phenology (Fenner 1998, Elzinga et al. 2007).

In addition, phenology is an important aspect of population biology (Fenner 1998, Schwartz 2003, Hudson & Keatley 2010), since it affects the dynamics of interspecific interactions linked to the timing of plants' reproductive and growth cycles, such as herbivory, pollination and frugivory (Van Schaik et al. 1993, Diaz et al. 1994, Bosch et al 1997, Gribel et al. 1999, Conceição et al. 2007a). The study of phenological patterns is also crucial to understand plant community dynamics, biological invasion (Wilsey et al. 2011) and the co-occurrence of species, especially in species-rich tropical plant communities (Janzen 1967, Frankie et al. 1974, Gentry 1974, Fenner 1998, Batalha & Martins 2004, Pau et al. 2011).

In South America, open tropical vegetation, such as mountain grasslands, savannas, flooded savannas or grasslands, cover around 14% of land surface while areas occupied by agriculture represent 24% (Eva et al. 2004). However, on this continent, phenological studies mainly concern tropical moist forests and dry forests, while a few only describe seasonal changes of these open tropical vegetations (Morellato 2003). *Campos rupestres*, species-rich tropical grasslands, are harsh ecosystems established on quartzite-derived soils occurring in altitude between 800m and 2,000m, and covering around 130,000km^2 (Barbosa 2012*). Campos rupestres* are constituted of a very heterogeneous mosaic of stony and sandy grasslands, bogs situated along streams, and scattered rocky outcrops that harbour sclerophyllous evergreen shrubs and sub-shrubs (Giulietti et al. 1997, Alves & Kolbek 2010, Carvalho et al. 2012, Chapter 1). These grasslands are stressful ecosystems that have shallow, nutrient-poor and highly acidic soils (Benites et al. 2007, Chapter 1) that sustain a highly diverse vegetation with one of the highest levels of endemism in Brazil (Giulietti et al. 1997, Echternacht et al. 2011). Due to its coarser soil and lower water retention, the stony grasslands seem to constraint plant vegetation more than sandy grasslands (Vitta 1995, Chapter 1). *Campos rupestres* are included in the cerrado savanna domain (Silva & Bates 2002) and, like other savannas, is under a seasonal climate with a dry season from May to October and a rainy season from November to April (Madeira & Fernandes 1999).

According to some studies, the seasonal climate imposes a restrictive growing season and tends to decrease the diversity of phenological patterns within a site while aseasonal environments, such as tropical moist forests, present a higher diversity of phenological patterns (Van Schaik et al. 1993, Bawa et al. 2003, Pau et al. 2011). In the Cerrado savannas, as in other tropical vegetations characterized by seasonal climate, the leaf, flower and fruit production are strongly related to abiotic factors (VanSchaik et al. 1993, Pau et al. 2011). Regarding savannas, studies have highlighted that the majority of herbaceous species flower during the wet season (Monasterio & Sarmiento 1976, Sarmiento and Monasterio 1983, Almeida 1995, Seghieri et al. 1995, Apko 1997, Batalha & Mantovani 2000, Williams & Cook 2001, Ramirez 2002, Batalha & Martins 2004, Freitas & Sazima 2006, Tannus et al. 2006), however the occurrence of diverse strategies was already pointed out, including flowering during the dry season (Monasterio & Sarmiento 1976, Almeida 1995, Barbosa 1997, Ramirez 2002).

Due to their great diversity and heterogeneity, tropical communities may display a wide variety of phenological patterns (Sarmiento & Monasterio 1983, Newstrom et al. 1994, Morellato 2003), therefore more studies are necessary to explore the variety of possible phenological patterns in order to draw general pictures. Because of this complexity, Newstrom et al. (1994) proposed a classification to describe phenological patterns using the following variables: frequency, regularity, duration, amplitude, date or timing, and synchrony of phenological events. Here we follow this classification using frequency, duration, timing and amplitude to assess phenological patterns of the two dominant herbaceous physiognomies of *campos rupestres*: the sandy and the stony grasslands. We used quantitative amplitude of the different phenophases; although few studies incorporated quantitative data, it seems to be a good tool as it allows comparison among sites.

Our objective is to address the following questions, at the community and species level: (i) do the plant species of each grassland type flower, fruit and disseminate seasonally? ; (ii) are the phenological patterns (defined as based on frequency, timing and duration of each phenophase) similar between both physiognomies?; (iii) do the fruit and flower production differ between the grassland types, and vary among families?; (iv) are there intra-specific variations in term of fruit production between the two grassland types, considering only species co-occurring in both grasslands? We expected seasonal phenological patterns with flower peak during the rainy season. In addition, we expected that both grassland types would differ in their phenology because the constraints imposed by soil properties and topography are more severe on vegetation growing on stony than on sandy grasslands (i.e. lower water retention in stony grasslands during the rainy season (Vitta 1995, Silveira 2011).

2.Material & Methods

2.1. Study area

Our study area is located in southeastern Brazil, in the southern portion of the Espinhaço Range, the area is within the Environmental Protected Area of Morro da Pedreira, a buffer zone of the Serra do Cipó National Park (state of Minas Gerais). *Campos rupestres* are the main vegetation formation of the Espinhaço mountain range. The main herbaceous plant communities, the sandy and stony grasslands (Chapter 1), are species-rich grasslands mainly composed of Poaceae (*Paspalum, Andropogon*) and Cyperaceae (*Lagenocarpus, Rhynchospora, Bulbostylis*), with Xyridaceae (*Xyris*), Eriocaulaceae (*Paepalanthus, Leiothrix, Syngonanthus*) and Velloziaceae (*Vellozia, Barbacenia*) and of some forbs and sub-shrub species belonging to Asteraceae

(*Lychnophora, Richterago*) or Melastomataceae *(Lavoisiera, Marcetia*) among others. The climate is classified as Cwb according to the Köppen's system with warm temperatures, dry winter and rainy summer. The mean annual precipitation is 1,622mm and the mean annual temperature is 21.2°C (Madeira & Fernandes 1999). It is markedly seasonal, with two distinguishable seasons: a rainy season from November to April with higher mean temperatures and a dry one from May to October with colder temperatures (Figure 26). We defined a transition season from rainy to dry between March and June and a transition season from dry to rainy between September and December (Figure 26).

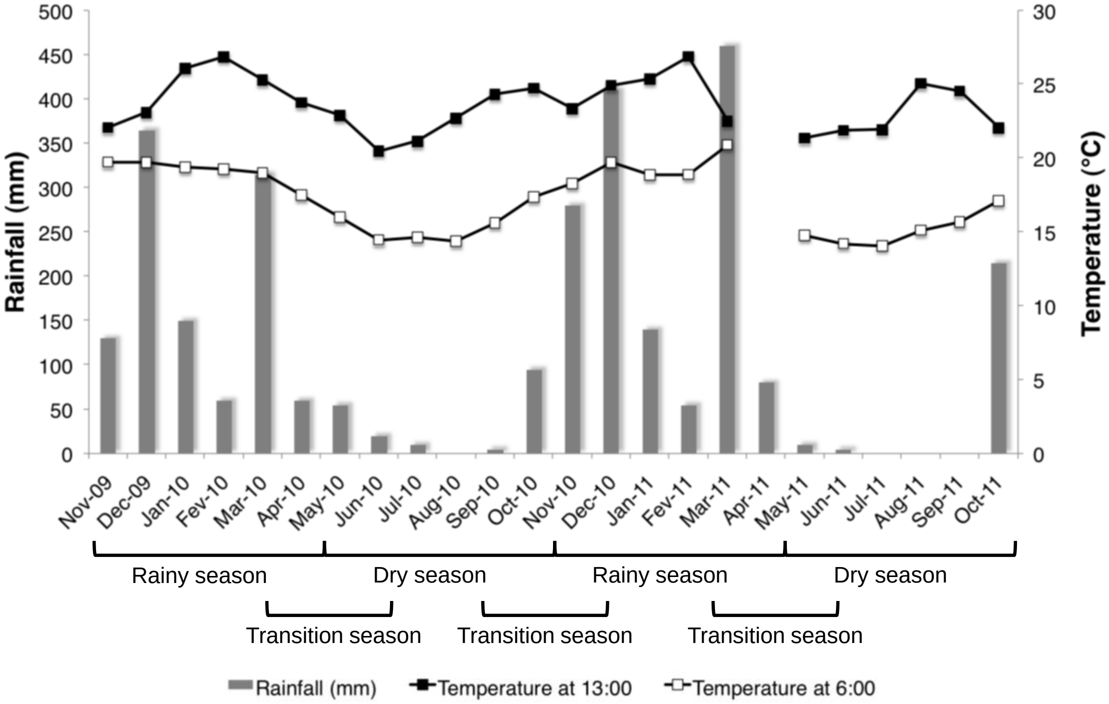

Figure 26: Distribution of mean monthly temperatures (T°C) at 6h00 (open square) and 13h00 (full square), and cumulative rainfall (mm) between November 2009 and October 2011. Temperature data provided by G.A. Sanchez-Azofeifa, Enviro-Net project, University of Alberta. Rainfall data obtained by INMET (2012).

2.2. Plant survey

To study the phenological patterns of these two main grassland-types of *campos rupestres*, we selected five sandy grasslands and five paired stony grassland sites, all located between 1,100m and 1,300m. During two consecutive years (from November 2009 to October 2011), we surveyed ten 1m² quadrats at each site monthly. For each quadrat we recorded the list of species, and for each species we recorded: (1) total number of individuals or clumps (i.e. thick group of the same species, probably clones), (2) number of individuals or clumps with inflorescence, (3) the number of inflorescences, and (4) the number of inflorescence in each phenophase: (i) flower (including flower buds and open flowers), (ii) fruit (including unripe and ripe fruits), and (iii) dissemination (dissemination signs, open fruits). Hereafter, the numbers of inflorescence in flower, in fruit and in dissemination, were designated by number of flowers, number of fruits and number of dissemination, respectively.

We then used frequency, timing and duration in order to describe and classify the main phenological strategies occurring on sandy and stony grasslands of *campos rupestres*. We classified species phenology according to four phenological frequencies: continual (**C**): phenophases always present, Sub-annual (**SB**): irregular multiple phenophases per year, Annual (**A**): one major phenophase per year, Supra-annual (**SP**): Multi-year cycles of phenophases, here designated species that flowered/fruited/disseminated only once during our two-year survey. The timing and duration of each A and SP species phenophase (flowering, fruiting and dissemination) was determined; we defined four timing strategies: occurrence of the phenophase during the (i) rainy season (from November to April) (**R**), (ii) transition between rainy to dry season (from March to June) (**RD**), (iii) dry season (from May to October) (**D**), and (iv) transition between dry to rainy season (from September to December) (**DR**). Duration was separated in two categories: short – (phenophase lasting less than two months) and long (phenophase lasting more than two months).

We also selected thirty-one species that co-occurred in both grassland types (which were present in at least two sites among the five sites sampled for each grassland-type (Appendix 2) and produced enough seeds to allow comparison between sandy and stony grasslands, in order to compare, at species level, phenological patterns between sandy and stony grasslands. For each species, for each grassland type, we assessed the fruit production by site and the fruit production per individuals.

2.3. Statistical analyses

To characterize the flowering, fruiting and disseminating seasonality of the two communities, we applied circular statistics analyses (Morellato et al. 2000, 2010). For each phenophase, the number of species on the peak date (considered as the moment where the highest number of flowers, fruits or dissemination was observed) of a given phenophase per month was treated as a circular frequency distribution with data grouped at 30° (30° = interval between 2 months) intervals, with January as the starting point (15°). The mean angle µ represents the mean date of the flowering/fruiting/disseminating period, and *r* is the measure of the concentration of the circular distribution of frequencies around the mean angle and ranges from 0 (when data are completely dispersed in all angles) to 1 (when all the data are concentrated in one angle or date) (Zar 1996). In order to describe the different phenological strategies (i.e. frequency, duration, timing) encountered on *campos rupestres,* the number of species in each category (i.e. frequency, timing, duration per grassland types) was then analyzed using Pearson χ^2 tests. Continual and sub-annual species were not included in these tests as they represented too few species.

To analyze flower and fruit production at each site according to the grassland type and plant families, GLM procedures were performed assuming a Poisson distribution and a logarithmic link function. The numbers of flowers and fruits were the dependent variables while grassland-types and families were the categorical predictors (McCullagh and Nelder 1989, Crawley 2007). For the analysis we used the seven most important families in *campos rupestres* (Chapter 1) while the other species were classified as forbs or sub-shrubs because there were too few species in the other species families. For the thirty-one species selected, GLM procedures were performed using a Poisson distribution and log link function in order to compare the species fruit production by site between both grassland types (Crawley 2007). T-tests were performed to compare the number of fruits on each individual between sandy and stony grasslands. Normality and homoscedasticity assumptions were previously checked (Sokal & Rohlf 1998).

All analyses were carried out in R version 2.14.0 (R Core Development Team, 2010) except the circular analyses that were performed using the software Oriana 3.0 (Kovach Computing Services 2012).

3.Results

One hundred and forty-six species were surveyed in sandy grasslands and 155 species in stony grasslands, of which the majority were perennial species (138 species or 94.5% and 151 species or 97.4%, for stony and sandy grasslands respectively) (Table 5). As a consequence of the high proportion of perennial species, the vegetation cover did not vary along the years. The percentage of species not showing reproductive phenophases ranged between 26.7% and 34.1% for the stony and sandy grassland species, respectively (Table 5).

Table 5: Total number of species surveyed in both grassland-types, with number and percentage of perennial and annual species in each one and number and percentage of species participating in the reproductive phenology (flower, fruit and/or dissemination).

	Sandy Grasslands		Stony grasslands	
	Number of species	Number of individuals	Number of species	Number of individuals
Total	146	29.227	155	31.354
Perennial species	138 (94.5%)	29.100	151 (97.4%)	31.327
Annual species	8 (5.5%)	127	4 (2.6%)	27
Participating in the phenology	107 (73.3%)	2,691 (9.2%)	89 (65.9%)	2,226 (7.1%)
Not participating in the phenology	39 (26.7%)	26,409 (90.8%)	46 (34.1%)	29,101 (92.9%)

3.1. *Flowering, fruiting and dissemination patterns in sandy and stony grasslands.*

The mean angle or date *μ* (measuring central tendency) and the r (measuring of concentration) were obtained for each phenophase and each grassland-type (Table 6, Figure 27). We were unable to identify a well-defined flowering, fruiting or dispersing time for the stony grassland (Figure 27 b, d and f) with marginally significant or no significant mean dates (*μ*) and a very low r; i.e. low concentration of species flowering or fruiting around the mean date. Similarly, dissemination time in the sandy grasslands did not have a significant mean date (*μ*) (Table 6, Figure 27 e), while flowering and fruiting in sandy grasslands were significant, but presented a very low r (Table 6, Figure 27 a and c).

Table 6: Flowering, fruiting and dissemination data of sandy (Sa) and stony (St) plant communities at Serra do Cipó. Circular statistics (µ: mean vector, and r: parameter of concentration, Rao's spacing test: test of unimodality and Rayleigh tests).

	Flowering		Fruiting		Dissemination	
	Sa	St	Sa	St	Sa	St
Mean vector *µ*	68.5°	26.5°	136.7°	342.0°	326.4°	355.2°
Length of mean vector r	0,26	0,19	0,24	0,12	0,08	0,19
Rao's spacing test	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Rayleigh test (Z)	5,53	3,01	4,71	1,07	0,65	3,26
Rayleigh test (*p*)	0,004	0,049	0,009	0,342	0,523	0,038

Since there were no well-defined seasonal patterns for any of the grassland types, we classified the species according to their flowering, fruiting and dissemination strategies. (i) The sub-annual reproductive phenological frequency (**SB**), is composed of six species: *Asteraceae* sp1, *Polygala appariciói, Polygala glochidiata, Polygala paniculata, Sebastiana ditassoides* and *Thesium brasiliense* (Appendix 3). (ii) The continuous reproductive phenological frequency (**C**), producing and dispersing all year long (which does not exclude the occurrence of production peaks) contained six species in both sandy and stony grasslands: *Lagenocarpus rigidus* subsp. *tenuifolius, Lagenocarpus tenuifolius, Rhynchospora ciliolata, Rhynchospora riedeliana*, *Rhynchospora pilosa* (only on sandy grasslands) and *Rhynchospora terminalis* (only on stony grasslands) (Appendix 3). In sandy grasslands (iii) 62 species (59.0%) presented an annual reproductive frequency (**A**), and (iv) 32 species (30.5%) a supra-annual frequency (**SP**). Similarly, in stony grasslands, 66 species (66.7%) had an annual frequency and 25 species (25.3%) a supra-annual frequency (Appendix 3). In both, sandy and stony grasslands, annual reproductive frequency was the most represented frequency (χ^2= 1.29, p=0.25).

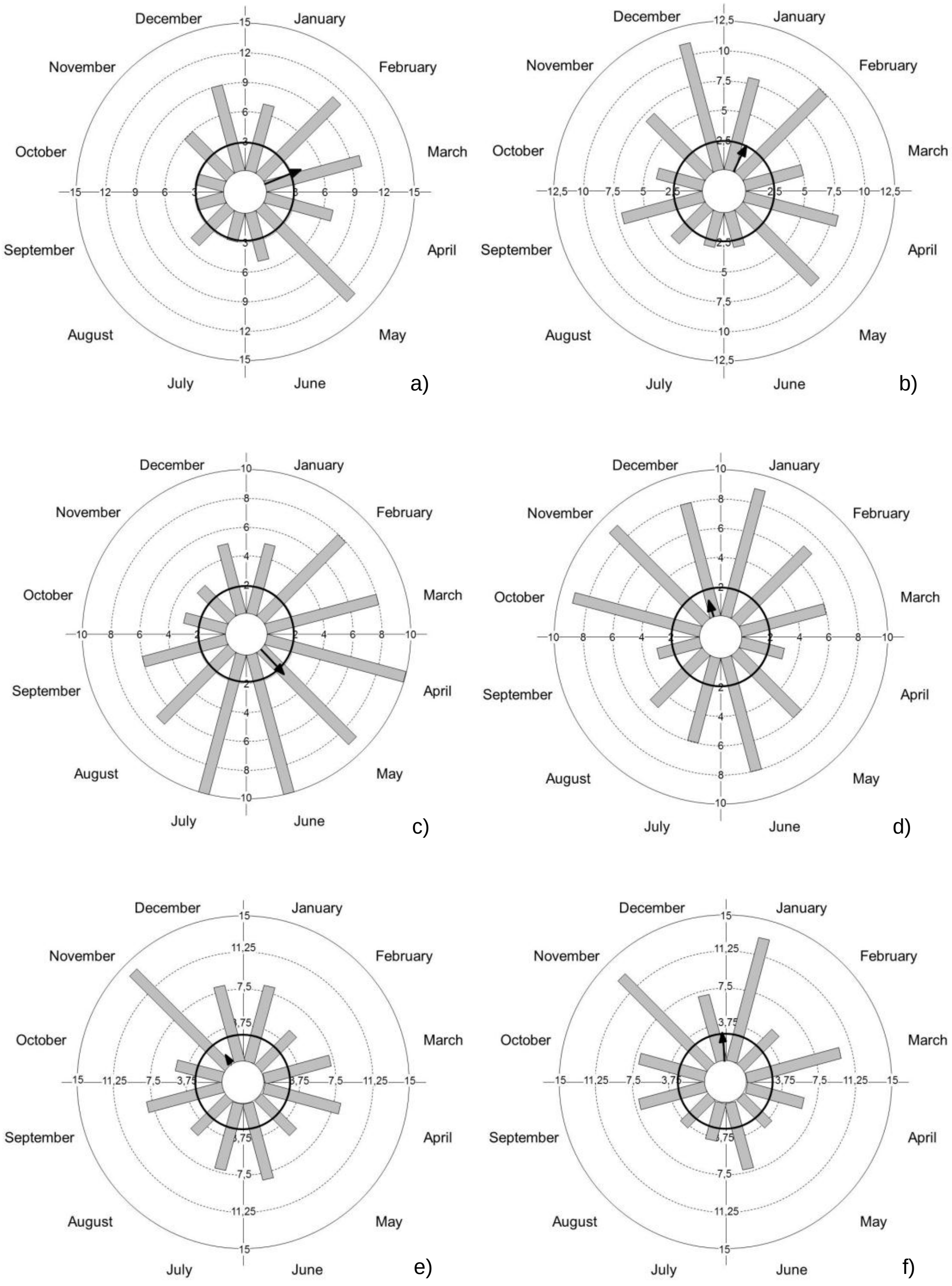

Figure 27: Flowering pattern in sandy (a) and stony (b) grasslands, fruiting pattern in sandy (c) and stony (d) grasslands and dissemination pattern in sandy (e) and stony (f) grasslands. These patterns were defined according to the number of species in each phenophase (based on the peak). Each species occurs only once. Arrows represented *μ* and the black circle the significant threshold.

Considering the timing of flowering, fruiting and dissemination, the phenological patterns did not differ between sandy and stony grasslands (Table 7). The majority of species produced flowers during the rainy season (**R**) (42.9% in sandy grasslands, and 47.5% in stony grasslands) while around 20% flowered during the transition from the rainy to the dry season (**RD**) and 14% to 20% during the dry season (**D**). Few species (less than 6%) produced flowers during the transition from dry to rainy season (**DR**). Fruits were mainly produced during the rainy (**R**) or dry (**D**) season: 30% and 33% (respectively in sandy and stony grasslands) produced fruits during the rainy season, while between 41% and 37% (respectively in sandy and stony grasslands) fruited during the dry season (Table 7). The dissemination occurred during the rainy season (**R**) (30% to 42% of species respectively in sandy and stony grasslands); other species disseminated during the dry season (**D**) (24% to 20% of species respectively in sandy and stony grasslands) or the transition from dry to rainy season (**DR**) (24% to 21%, respectively in sandy and stony grasslands) (Table 7). Among the species presenting supra-annual phenology, the majority flowered during the rainy season (representing 23.7% and 15.5% species, in sandy and stony grasslands respectively) (Table 8). Among species with an annual flowering frequency, the larger proportion produced flowers during the rainy season (24.7% and 39.5% in sandy and stony grasslands, respectively), but also during the transition from rainy to dry season (22.6% and 19.8% in sandy and stony grasslands, respectively), and during the dry season (between 17.2% and 9.3% in sandy and stony grasslands, respectively) (Table 8).

Table 7 : Number and percentage of species according to the timing of flowering, fruiting and dissemination in sandy (Sa) and stony (St) grasslands. Pearson χ^2 tests were performed, data marked with « ◊ » were not used in tests, species with continuous and sub-annual frequency patterns were not taken into account for the tests.

		Rainy season	Transition Rainy/Dry season	Dry season	Transition Dry/Rainy season	Total	Pearson χ^2 P-value
Flower	Sa	45 (42.9%)	22 (20.9%)	20 (19.1%)	6 (5.7%)	105 (100%)	χ^2= 1.05, p=0.79
	St	47 (47.5%)	19 (19.1%)	14 (14.1%)	6 (6.1%)	99 (100%)	
Fruit	Sa	32 (30.5%)	8 (7.6%)	43 (40.9%)	3 (2.9%) ◊	105 (100%)	χ^2= 0,41, p=0.81
	St	33 (33.3%)	8 (8.1%)	36 (36.4%)	4 (4.0%) ◊	99 (100%)	
Dissemination	Sa	31 (29.5%)	7 (6.7%)	25 (23.8%)	25 (23.8%)	105 (100%)	χ^2= 2,33, p=0.51
	St	41 (41.4%)	8 (8.1%)	20 (20.2%)	21 (21.2%)	99 (100%)	

Table 8: Number of species and percentage according to the timing of flowering and phenological frequency in sandy (Sa) and stony (St (grasslands). A: annual frequency and SP: supra-annual frequency. Only A and SP species participating in the flowering phenophase were taken into account.

		Rainy season	Transition Rainy/Dry season	Dry season	Transition Dry/Rainy season	Total
Sa	A	23 (24.7%)	21 (22.6%)	16 (17.2%)	2 (2.2%)	93 (100%)
	SP	22 (23.7%)	1 (1.1%)	4 (4.3%)	4 (4.3%)	
St	A	34 (39.5%)	17 (19.8%)	8 (9.3%)	5 (5.8%)	86 (100%)
	SP	13 (15.1%)	2 (2.3%)	6 (7.0%)	1 (1.2%)	

In addition, we analyzed the duration of flowering, fruiting and disseminating phenophases according to the timing of the phenophase (Table 9). There was a relationship between phenophase duration and timing in both grassland types and for the three analyzed phenophases (Table 9). In both sandy and stony grasslands, a high number of species flowering during the rainy season presented a short flowering cycle (29.5% and 34.3% of species, respectively; in sandy grasslands $\chi^2 = 12.75$, $p<0.05$ and in stony grasslands $\chi^2=7.68$, $p<0.01$), while in sandy grasslands, species flowering during the transition from rainy to dry season had a longer cycle (Table 9); there is no difference between both short and long cycles for this period in stony grasslands (Table 9). In both grasslands, many species producing fruit during the rainy season had a short cycle (between 17.1% and 20.2% in sandy and stony grasslands respectively) while species fruiting during the dry season had a longer cycle (in sandy grasslands $\chi^2 = 13.58$, $p<0.001$ and in stony grasslands $\chi^2=14.80$, $p<0.001$, Table 9). In the same way, higher proportion of species disseminating during the rainy season had a short cycle (between 24.9% and 28.3% in sandy and stony grasslands respectively. On the contrary most species had a longer cycle when disseminated during the transition season (dry to rainy) (in sandy grasslands $\chi^2 = 31.31$, $p<0.001$ and in stony grasslands $\chi^2=8.35$, $p<0.05$, Table 9). In sandy grasslands, 16% of species disseminating during the dry season had a short cycle while 7.6% had a long cycle. The proportion of species disseminating during the dry season, with a long or a short cycle in stony grasslands was the same (around 10%, Table 9). For flowering and dissemination, there was no relationship between phenophase duration and grassland-types: the number of species with short and long cycles was similar in both grasslands (for flowering, 50% of species in sandy grasslands and 58% in stony grasslands with a short cycle, χ^2=1.0, p=0.31, and for dissemination, 55% of species in sandy grasslands and 51% in stony grasslands had a short cycle χ^2= 0.29, p=0.59). There was no difference between the two grassland-types for fruiting as well: in both sandy and stony grasslands, most species had long phenological cycles (68% and 66% of species in sandy and stony grasslands, respectively, χ^2=0.11, p=0.74) (Appendix 3).

Table 9 : Number and percentage of species with long or short flowering (Fl.), fruiting (Fr.) and dissemination (Diss.) duration in sandy (Sa) and stony (St) grasslands. Long cycle is considered with a phenophase duration > 2 months and short cycle with a phenophase duration < or = 2 months. Species with continuous and sub-annual frequency patterns were not taken into account. w indicated that the χ^2 tests were realized without the data from transition season Dry/Rainy due to the low number of species. *: p-value<0.05 and **: p-value<0.01, ***:p-value <0.001.

		Duration strategies	Rainy season	Transition Rainy/Dry season	Dry season	Transition Dry/Rainy season		Pearson χ^2 P-value
Fl.	Sa	Long cycle	14 (13.3%)	16 (15.2%)	13 (12.4%)	3 (2.9%)	w	χ^2: 12.75 **
		Short cycle	31 (29.5%)	6 (5.7%)	7 (6.7%)	3 (2.9%)		
	St	Long cycle	13 (13.1%)	10 (10.1%)	9 (9.1%)	4 (4.0%)	w	χ^2: 7.68 *
		Short cycle	34 (34.3%)	9 (9.1%)	5 (5.1%)	2 (2.0%)		
Fr.	Sa	Long cycle	14 (13.3%)	6 (5.7%)	36 (34.3%)	2 (1.9%)	w	χ^2: 13.58 ***
		Short cycle	18 (17.1%)	2 (1.9%)	7 (6.7%)	-		
	St	Long cycle	13 (13.1%)	7 (7.1%)	29 (29.3%)	4 (4.0%)	w	χ^2: 14,80 ***
		Short cycle	20 (20.2%)	1 (1.0%)	7 (7.1%)	-		
Diss.	Sa	Long cycle	5 (4.7%)	4 (3.8%)	8 (7.6%)	22 (20.9%)		χ^2: 31.31 ***
		Short cycle	26 (24.9%)	3 (2.8%)	17 (16.2%)	3 (2.9%)		
	St	Long cycle	13 (13.1%)	5 (5.1%)	11 (11.1%)	14 (14.1%)		χ^2: 8.35 *
		Short cycle	28 (28.3%)	3 (3.0%)	9 (9.1%)	7 (7.1%)		

3.2. *Flower and fruit production among grassland types and among families*

The mean flower production by site was higher on sandy than on stony grasslands (respectively 227.7 ± 26.6 and 211.6 ± 12.48, z=-2.42, p=0.01). Likewise, the mean fruit production was higher in sandy than in stony grasslands (respectively 532.6 ± 45.9 and 464.8 ± 47.5, z=-6.78, p<0.001). Cyperaceae and Xyridaceae were among the families that produced a large number of flowers and fruits while Poaceae, although represented by a great number of species and covering a large area (Table 10), did not produce a significant amount of seeds. Asteraceae, Velloziaceae, Xyridaceae and several sub-shrubs produced the highest number of flowers and fruits in stony grasslands while

Cyperaceae, Poaceae and forbs had the highest flower and fruit production in sandy grasslands (Table 10). Conversely, Melastomataceae species flower production was higher in sandy grasslands, while the fruit production was greater in stony grasslands. Eriocaulaceae flower and fruit production did not differ between the two grassland-types.

3.1. Phenology and fruit production of species co-occurring in both grassland types.

Regardless of the phenophase considered (flowering, fruiting or disseminating), 26 species (83.8%) had the same phenology in sandy and stony grasslands. Only five species: *Lagenocarpus alboniger, Rhynchospora tenuis, Rhynchospora tenuis* subsp *austro-brasiliensis, Rhynchospora terminalis* and *Vellozia epidendroides,* presented different phenologies between sandy and stony grasslands, considering frequency or timing (duration was similar) of the phenophase. *Rhynchospora terminalis* had a continuous phenology in stony grasslands and an annual phenological frequency in sandy grasslands; *Rhynchospora tenuis* was supra-annual in stony grasslands and annual in sandy grasslands (Appendix 3). Individuals of *Vellozia epidendroides* flowered and fruited during the dry season in sandy grasslands while they did so during the rainy season in stony grasslands. *Rhynchospora tenuis* subsp *austro-brasiliensis* disseminated earlier and *Lagenocarpus alboniger* flowered earlier in the season in stony grasslands.

Fruit production did not vary between stony and sandy grasslands for 11 species (*Dioscorea stenophylla, Mesosetum loliiforme, Pseudotrimezia cipoana, Rhynchospora consanguinea, Rhynchospora tenuis* subsp *austro-brasiliensis, Rhynchospora terminalis, Richterago arenaria, Sisyrinchium vaginatum, Thesium brasiliense, Vochysia pygmaea* and *Xyris itatiayensis*). Ten species produced more fruits in the sandy grasslands while nine species produced more fruits in the stony grasslands (Table 11). Generally, the fruit production per individual was low and equal between both sandy and stony grasslands, except for *Lagenocarpus rigidus* subsp. *tenuifolius* which recorded a higher production per individual in sandy than in stony grasslands (Table 11).

Table 10: Flower and fruit production per site (average number and standard error) in sandy (Sa) and stony (St) grasslands for the main families based on peak production. z indicated the result of GLM procedures (family: Poisson, link: log). Letters indicate significant differences between families among grassland-types according to the result of the GLM procedures (family: Poisson, link: log).

	Mean number of reproducing species / site		Flower production			Fruit production		
	Sa	St	Sa	St	GLM procedures	Sa	St	GLM procedures
Asteraceae	3.4 ± 1.2	3.2 ± 0.4	7.6 ± 1.9 ^{a}	23.2 ± 8.4 ^{a}	8.44 ***	5.4 ± 1.5 ^{a}	8.7 ± 2.4 ^{a}	2.75 **
Cyperaceae	11.0 ± 0.4	10.6 ± 1.6	251.2 ± 25.6 ^{b}	158.1 ± 21.6 ^{b}	-14.42 ***	290.6 ± 29.6 ^{b}	170.8 ± 27.0 ^{b}	-17.43 ***
Eriocaulaceae	4.8 ± 0.5	5.6 ± 1.3	70.5 ± 14.8 ^{c}	68.9 ± 15.6 ^{c}	-0.42 ^{NS}	51.6 ± 12.5 ^{c}	49.1 ± 11.2 ^{c}	-0.78 ^{NS}
Other Forbs	9.4 ± 1.2	5.2 ± 1.4	22.5 ± 3.4 ^{d}	14 ± 3.2 ^{d}	-4.40 ***	8.5 ± 2.7 ^{d}	1.9 ± 0.5 ^{d}	-5.90 ***
Melastomataceae	2.4 ± 0.6	2.2 ± 0.5	20.2 ± 6.9 ^{d}	14 ± 5.9 ^{d}	-3.33 ***	33 ± 14.0 ^{e}	41.7 ± 15.4 ^{e}	3.17 ***
Poaceae	4.0 ± 0.6	4.4 ± 0.8	29.7 ± 6.7 ^{e}	14.8 ± 4.9 ^{d}	-6.92 ***	29.7 ± 8.8 ^{e}	9.1 ± 4.6 ^{a}	-9.87 ***
Other Sub-shrubs	4.0 ± 1.3	6.0 ± 0.5	13.1 ± 4.4 ^{f}	38.2 ± 14.8 ^{e}	10.57 ***	7.8 ± 2.1 ^{d}	37.9 ± 15.0 ^{e}	12.71 ***
Velloziaceae	0.8 ± 0.2	1.2 ± 0.4	0.5 ± 0.3 ^{g}	4.7 ± 3.7 ^{f}	4.76 ***	1.3 ± 0.6 ^{f}	11.9 ± 5.4 ^{f}	7.58 ***
Xyridaceae	11.0 ± 1.4	7.4 ± 1.8	157.2 ± 36.0 ^{h}	227.6 ± 28.1 ^{g}	11.28 ***	138.2 ± 31.3 ^{g}	177.6 ± 23.5 ^{b}	6.99 ***
GLM procedures			p>0.001	p>0.001		p>0.001	p>0.001	

Table 11: Average fruit production by site and number of fruits per individual for the 31 selected species. z indicates the result of GLM procedures with a quasibinomial error distribution and logit link function. * indicates significant differences with p<0.05. T-tests were performed using numbers of fruits per individual as dependent variables and grassland-types as categorical predictors, * indicates p<0.05.

	Fruit production / site (mean±se)				Number of fruit / individual (mean±se)			
	Sa	St	GLM procedures (z)		Sa	St	t-test	
Dioscorea stenophylla	1 ± 0	1.0 ± 0.5	0	NS	1.0 ± 0.0	0.6 ± 0.2	2,07	NS
Drosera montana	0.9 ± 0.3	9.5 ± 5.1	5,79	***	0.3 ± 0.1	0.6 ± 0.1	-1,36	NS
Lagenocarpus alboniger	2.2 ± 0.7	9.2 ± 2.0	3,9	***	1.4 ± 0.4	0.9 ± 0.1	1,25	NS
Lagenocarpus tenuifolius	8.0 ± 1.9	27.6 ± 5.8	8,92	***	2.2 ± 0.6	1.6 ± 0.5	0,73	NS
Lagenocarpus rigidus subsp. *tenuifolius*	147.5 ± 17.75	32.3 ± 20.5	-22,53	***	3.2 ± 0.2	1.5 ± 0.4	3,88	*
Mesosetum loliiforme	47.8 ± 34.7	4.3 ± 2.4	0	NS	7.9 ± 4.8	2.4 ± 0.9	1,29	NS
Paepalanthus geniculatus	26.2 ± 11.8	18.2 ± 4.5	-3,77	***	1.9 ± 0.3	1.8 ± 0.1	0,42	NS
Panicum cyanescens	22.9 ± 3.8	2.0 ± 0.6	-8,23	***	1.4 ± 0.1	1.0 ± 0.3	1,5	NS
Pseudotrimezia cipoana	5.0 ± 2.9	4.9 ± 2.2	-0,1	NS	0.7 ± 0.2	0.7 ± 0.1	0,18	NS
Rhynchospora consanguinea	6.5 ± 2.4	6.1 ± 1.4	-0,35	NS	0.7 ± 0.1	0.8 ± 0.1	-1,31	NS
Rhynchospora riedeliana	60.0 ± 20.8	44.6 ± 11.6	-4,74	***	1.6 ± 0.1	1.5 ± 0.2	0,65	NS
Rhynchospora sp1	24.7 ± 11.4	11.5 ± 7.4	-4,88	***	2.0 ± 0.8	1.6 ± 0.7	0,48	NS
Rhynchospora tenuis	34.4 ± 12.4	6.3 ± 4.5	-8,23	***	3.0 ± 0.8	1.3 ± 0.9	-1,54	NS
Rhynchospora tenuis subsp austro-brasiliensis	51.9 ± 8.9	48.5 ± 21.3	-1,01	NS	2.0 ± 0.2	2.9 ± 0.6	-1,55	NS
Rhynchospora terminalis	15.6 ± 4.7	1.3 ± 0.4	1,48	NS	0.8 ± 0.1	0.9 ± 0.2	-0,37	NS
Richterago arenaria	1.3 ± 0.4	1.6 ± 0.9	0,56	NS	0.5 ± 0.1	0.6 ± 0.2	-0,29	NS
Sebastiana ditassoides	0.8 ± 0.5	3.8 ± 1.9	2,65	**	0.5 ± 0.3	1.4 ± 0.9	-1,06	NS
Sisyrinchium vaginatum	1.5 ± 1.4	0.3 ± 0.2	-1,84	NS	0.9 ± 0.7	0.3 ± 0.2	0,86	NS
Syngonanthus cipoensis	8.6 ± 2.3	3.0 ± 0.7	-4,56	***	0.6 ± 0.1	0.6 ± 0.1	0,45	NS
Syngonanthus vernonioides	2.2 ± 0.6	17.0 ± 5.5	8,06	***	0.6 ± 0.1	0.8 ± 0.1	-1,33	NS
Thesium brasiliense	1.8 ± 0.8	2.4 ± 1.3	0,93	NS	0.5 ± 0.2	0.4 ± 0.2	0,36	NS
Vellozia epidendroides	2.4 ± 0.7	16.0 ± 7.8	7,59	***	1.1 ± 0.2	1.5 ± 0.2	-1,55	NS
Vochysia pygmaea	1.5 ± 1.0	3.1 ± 0.9	1,61	NS	0.6 ± 0.3	0.7 ± 0.2	-0,33	NS
Xyris blanchetiana	7.1 ± 1.9	2.0 ± 0.8	-3,36	***	0.7 ± 0.1	0.6 ± 0.3	0,22	NS
Xyris hilariana	17.5 ± 7.0	28.5 ± 11.6	3,43	***	0.8 ± 0.3	0.5 ± 0.2	0,87	NS
Xyris itatiayensis	1.3 ± 0.9	1.7 ± 0.9	0,52	NS	0.2 ± 0.1	0.4 ± 0.2	-0,85	NS
Xyris melanopoda	1.5 ± 1.0	9.4 ± 2.1	4,31	***	0.4 ± 0.2	0.5 ± 0.1	-0,5	NS
Xyris nubigena	13.1 ± 6.5	7.0 ± 2.7	-3,53	***	0.7 ± 0.1	0.5 ± 0.2	1,51	NS
Xyris obtusiuscula	14.7 ± 3.9	52.8 ± 14.5	13,34	***	0.9 ± 0.1	0.7 ± 0.1	1,13	NS
Xyris pilosa	41.6 ± 21.9	34.9 ± 9.3	-2,13	*	0.9 ± 0.1	0.9 ± 0.1	0,76	NS
Xyris tenella	11.2 ± 5.8	21.3 ± 7.7	4,65	***	0.8 ± 0.1	0.8 ± 0.1	0,46	NS

4. Discussion

Our study highlights that about one fourth and one third of the species have not participated in the reproductive phenology during our 2-year survey, either because they have supra-annual phenological patterns that we were not able to observe in such a short study, or because they rarely reproduce. Our results also report the high proportion of perennial species in the *campos rupestres* (see Warming 1892, Furley & Ratter 1988). Their survival does not rely only on sexual reproduction and seed production. Moreover, it has already been demonstrated that fire induces or increases reproduction in a fire-prone habitat, such as the Cerrado (Lamont & Runciman 1993, Freitas & Sazima 2006, Munhoz & Felfili 2007, Neves & Conceição 2010, Lamont & Downes 2011, Neves et al. 2011, Conceição & Orr 2012). Indeed fire-stimulated flowering species have already been observed in *campos rupestres* for some species, such as *Bulbostylis paradoxa* or some Eriocaulaceae, or Velloziaceae (Figueira 1998, Kolbek & Alves 2008, Neves et al. 2011, Ribeiro & Figueira 2011, Conceição & Orr 2012). Moreover, species such as *Tatianyx arnacites, Mesosetum exaratum, Paspalum erianthum* or *Homolepis longiscapa*, abundant Poaceae in sandy and stony grasslands (Chapter 1), recorded few reproductive individuals during these two years, hence suggesting the need for a stimulus to induce flowering and fruiting, which might be fire, among other factors.

4.1. Flowering, fruiting and dissemination patterns in sandy and stony grasslands.

In 1899 Warming wrote that, in the tropics, “different species have different flowering time, some of them even blooming in the winter, that is, in the dry season, and in consequence we may find flowers at almost all times of the year.” Even if savannas are characterized by a seasonal climate, and even if seasonal phenological patterns are expected, at the community level, *campos rupestres* produce flowers and fruits all year long and distinctive seasonal patterns are not clearly depicted even based on a circular analysis. The main issue in such tropical ecosystems, as already noticed by Newstrom et al. (1994), is then to recognize and classify those patterns. Using some classification tools based on frequency, timing and duration, we were able to underline the diversity of *campo rupestre* phenological patterns, corroborating with studies dealing with herbaceous species in savannas (Monasterio & Sarmiento 1976, Almeida 1995, Ramirez 2002).

We show that, even if flowering is distributed throughout the year, in both grassland types there is a flower peak during the rainy season, which is in agreement with results from other seasonal systems in the tropics (Monasterio & Sarmiento 1976, Seghieri et al.

1995, Ramirez 2002) as well as in the Cerrado (Barbosa 1997, Batalha et al. 1997, Batalha and Mantovani, 2000; Batalha and Martins, 2004, Munhoz & Felfili 2007). This phenological pattern is frequently related to climatic factors, especially water availability as well as the acute water shortage during the following drought (Sarmiento & Monasterio 1983, Almeida 1995, Ramirez 2002, Batalha & Martins 2004). In a seasonal system, some authors have argued that herbs must complete their vegetative growth and have to accumulate carbohydrates to flower (Batalha and Mantovani 2000, Ramirez 2002, Batalha & Martins 2004), which explains why most of the species produced flowers during late wet season or during the transition from rainy to dry season. Species with supra-annual phenological frequency flower mainly during the rainy season. This might be a strategy to avoid years of sub-optimal climate and expending high resources in optimal years (Venable 2007). We expected a shorter cycle in stony grasslands due to a potential water stress, but duration patterns are the same between both grassland types; most of the species flowering, fruiting and disseminating during the rainy season have a short phenological cycle. Thus, the strategy of these species is based on the capacity to disseminate fruits at the end of the rainy season. A relationship between seed dispersal and seedling establishment has been showed in Neotropical savannas for woody species (Salazar et al. 2011, Silveira 2011, Silveira et al. 2012a): most seeds dispersed in the wet season are non-dormant and exhibit high moisture content (Salazar et al. 2011), but we might expect that seeds produced during the rainy season and dispersing at the end of it (period of transition with the dry season) have dormancy (Silveira et al. 2012a).

On the other hand, in both grasslands, other species belonging to Xyridaceae, Asteraceae, Fabaceae, Melastomataceae or Eriocaulaceae families, flower and fruit preferentially either during the transition between rainy to dry season or during the dry season. These species are, in majority, species that have an annual flowering frequency, underlining the regularity of such pattern. On the other hand, most of these species present longer phenological cycles. One hypothesis is that these species need a longer period of vegetative growth in order to reproduce. However, another possibility is that these species, flowering and fruiting during the transition rainy to dry season or the dry season, are preferentially pollinated by animals such as wasps or dipterans which are important pollinators during the dry season while bees decrease their activities during this season (Freitas & Sazima 2006). Pollinators are commonly designated to impose selection on flowering phenology (Elzinga et al. 2007), which might explain why many species present an annual frequency. In such cases, longer cycles or massive flowering are necessary to ensure the attraction of pollinators; since the latter are attracted by a species only after a certain flower density threshold is passed (Elzinga et al. 2007). Massive flowering has already been observed for species of Velloziaceae and Xyridaceae (personal observation).

Pollination ecology is poorly studied in *campos rupestres*, but grasses and sedges are usually pollinated by the wind (Oliveira & Gibbs 2002). However, entomophily has already been demonstrated for some Eriocaulaceae and Xyridaceae species (Ramos et al. 2005, Faria Jr. & Santos 2006, Oriani et al. 2009, Oriani & Scatena 2011). Indeed, in Eriocaulaceae, pollination by small insects was pointed out to increase the reproductive success (Oriani et al. 2009). Xyridaceae, although included in the Poales, group which has usually non-attractive flowers and is therefore probably wind-pollinated (Linder & Rudall 2005), have large, colorful and attractive flowers, indicating animal pollination (Oriani & Scatena 2011). Moreover, in altitude grasslands similar to *campos rupestres,* the relationship between pollination and phenology were pointed out: grassland species with nectar- or pollen-flowers pollinated by bees flower during the rainy season with a small flowering peak observable in June because bee activity decreases during the dry season (Freitas & Sazima 2006). On the other hand, species with nectar-flowers are pollinated either by wasps and/or by dipterans reaching their flowering peak during the dry season (Freitas & Sazima 2006).

Finally, several species disseminate during the dry season or transition from dry to rainy season, including species that flower during the rainy season. These species preferentially have a long dissemination cycle, probably linked to abiotic factors, such as wind or rain. Anemochory and autochory have already been pointed out as the two main seed dispersal syndromes in *campos rupestres* (Faria Jr. & Santos 2006, Conceição et al. 2007a, Dutra et al. 2009), the end of the dry season being usually marked by more wind, this period seems then the optimal period to disseminate for this species. Zoochory has already been reported for cactaceae and woody species (Fonseca et al. 2012, Silveira et al. 2012b). No study has reported hydrochory, but the importance of water as a dispersal mechanism in *campos rupestres* cannot be underestimated: sandy grasslands are regularly flooded during the rainy season and sedges seeds are known to be buoyant (Leck & Schutz 2005).

4.2. Flower and fruit production in sandy and stony grasslands.

Our results highlight that flower production varies between sandy and stony grasslands, with a higher flower and fruit productions in sandy grasslands perhaps due to the higher plant density in this habitat (Chapter 1). Cyperaceae, Eriocaulaceae and Xyridaceae species ensure most of the flower and fruit productions in *campos rupestres*. Eriocaulaceae species are known to present a wide range of reproductive strategies, which might be affected by climate seasonality, including vegetative propagation (Figueira 1998, Coelho et al. 2006, 2007). In *campos rupestres,* Xyridaceae species have particularly been studied from the point of view of their ability to germinate since they produce many small seeds in each capitulate (Abreu & Garcia 2005), however little is known about their phenological strategies. Very few studies have been carried out on the Cyperaceae of *campos rupestres* however sedges are known to present various reproductive strategies within habitats, persistence, and ability of many species to colonize disturbed habitats (Leck & Schütz 2005). On the other hand, Poaceae and Velloziaceae, which are important families in *campos rupestres* almost did not reproduce during the study period.

4.3. Comparison between sandy and stony grasslands.

Our results show that the large majority of species co-occurring in both grasslands (83.8%) adopt the same phenological behavior, suggesting that there were no or few variations in the phenological patterns due to an important genetic control, or stony grasslands do not represent a more constrained environment. Nineteen species produced more fruits in one preferential grassland type but this only reflects that each species occurs preferentially in one grassland type (Chapter 1). Indeed, the production by individuals did not vary between grasslands except for *Lagenocarpus rigidus* subsp. *tenuifolius,* which has a significantly higher fruit production on sandy grasslands. We thus assume that these species are adapted to both habitats and their occurrence on either habitat could be linked to establishment success and/or biotic interaction.

5. Conclusion

Campos rupestres are tropical grasslands that have complex phenological patterns with diverse phenological strategies. This is the first rigorous study examining the phenology of the *campo rupestre* herbaceous flora. Like other physiognomies of the Cerrado, herbaceous communities of *campos rupestres* have a flowering peak during the rainy season; but other phenological strategies are also observed: some species flower during the transition from rainy to dry season or during the dry season. Rainy and dry seasons are both marked by fruit production. Dissemination takes place during the rainy season for species that realize their entire phenological cycle during this period (species with a short cycle); but other species disseminate during the dry season, and the transition from dry to rainy season. Most of the studied species have an annual phenological frequency; some others are supra-annual while few are continual or sub-annual. While we draw some phenological patterns for the herbaceous *campo rupestre* communities using frequency, timing and duration, we do not find differences among grassland types: both sandy and stony grasslands present similar phenological patterns. Cyperaceae, Xyridaceae and Ericaulaceae mainly ensure seed production, whereas Poaceae produce very few seeds. This underlined that Poaceae, which are an important family in *campos rupestres,* do not contribute to supply the seed pool that could disperse and establish on degraded areas. This is a strong limiting factor to the spontaneous succession of *campos rupestres*.

Transition to Chapter 3

Restoration of herbaceous plant communities, especially in altitude, is important for many reasons including their key role in maintaining habitat integrity and in the water cycle: ensuring water for drinking and irrigation, providing medicinal plants and offering cultural services, such as recreation (MEA 2005).

What about grassland restoration?

Grassland restoration projects are often hampered by abiotic constraints, such as increased soil nutrients (i.e. eutrophication and acidification) in case of degradation by intensive agriculture (Bakker & Berendse 1999) or the alteration of soil chemical and physical characteristics (i.e. limited nutrient availability, low water availability) in case of degradation by quarrying and mining activities (Yuan et al. 2006). Therefore, early studies on grassland restoration have concentrated on site limitation with a special emphasis i) on the removal of nutrients (i.e. topsoil removal, carbon addition) when extensive agriculture is the main source of degradation (Berendse et al. 1992, Bakker & Berendse 1999, Alpert & Maron 2000, Patzelt et al. 2001, Holzel & Otte 2003, Klimkowska & al. 2009, Piqueray & Mahy 2010, Török et al. 2011), or ii) on managing the soil surface (e.g. crushing, rewetting, compacting, ripping, grading, or drainage) and on adding fertilizers to improve physical conditions of mine degraded soils (Davis et al. 1985, Ash et al. 1994, Jim 2001, Wong 2003).

Unfortunately, in many cases, such measures alone are not sufficient in restoring the target species-rich grassland communities, although environmental conditions are improved (Berendse et al 1992, Donath & al 2003). Numerous studies recognized that biotic constraints often impeded the restoration of species-rich grasslands and identified as the main obstacles: 1) the lack of viable seeds in the soil seed bank and 2) the limited dispersal of target species (Wilson 2002, Shu et al. 2005, Kiehl 2010, Piqueray & Mahy 2010, Török et al. 2011).

Lack of seed bank

The potential for plant communities to regenerate after a given disturbance represents an important aspect of their resilience and thus an important point for their conservation and restoration (Leck et al. 1989, Bakker et al. 1996, Prach et al. 2001, Prach & Hobbs 2008). In general, in communities subjected to periodic disturbances, the dominant species produce large numbers of seeds that persist in the soil for a long time (i.e. persistent seed-banks); whereas the dominant species in communities without disturbance tend to produce smaller numbers of seeds, which remain viable in the soil for a short time (i.e. transient seed-banks) (Thompson et al. 1998). Although, annuals and biennials almost always have more persistent seeds than related perennials (Thompson et al 1998), Kalamees & Zobel (2002) demonstrated that the soil seed bank is important for population maintenance and regeneration in perennial grassland communities as well. On North America, Lavoie et al. (2003) noted that spontaneous regeneration from the seed bank occurred in peatlands; in mountain grasslands in South America, Funes et al. (2001) showed that the largest number of seeds, and thus the highest potential for regeneration, was found in wetter sites, but then the number decreased progressively from mesic to xeric habitats. This trend was also verified in European grasslands (Bossuyt & Honnay 2008).

In grasslands, viable seeds of the most abundant species in the established vegetation (i.e. characteristic species) are often absent in the soil seed bank either due to their low longevity or because of low seed production (Hutchings & Booth 1996, McDonald et al. 1996, Bakker et al. 1996, Bekker et al. 1997, Buisson et al. 2006); few target species build up long-term persistent soil seed banks (Von Blanckenhagen & Poschlod 2005), therefore the regeneration of natural communities from the seed-bank is low. Moreover, the seed bank of ex-arable fields present usually non desirable species (arable species), which could impede natural regeneration (e.g. competition) (Bakker & Berendse 1999, Wilson et al. 2002, Hausman et al 2007, Bossuyt & Honnay 2008) and/or lead to an undesirable restoration trajectory. Then, the potential for *in situ* spontaneous succession in several cases is slow or unpredictable (Bossuyt & Honnay 2008, Török et al. 2011).

Lack of seed dispersal:

When there is no seed bank, species have to immigrate from source populations in the surroundings of degraded sites, but dispersal is, in many cases, a limiting factor. Due to the limited dispersal properties of the species, the colonization of degraded sites by seed rain from adjacent pristine sites is often unsuccessful (Ash et al. 1994, Hutchings & Booth 1996, Bakker et al. 1996, Bradshaw 1997, Tilman 1997, Cooper & MacDonald

2000, Bischoff 2002, Wilson et al. 2002, Donath & al 2003, Shu et al. 2005, Tormo et al. 2006, Buisson et al. 2006). Cousins & Lindborg 2008 showed that grassland specialists dispersed stepwise into the fields, and the number of grassland specialists decreased with distance from the source. Then, the more a degraded area is isolated, the more complicated its natural regeneration by seed rain is, what is often observed in our currently fragmented landscape. Another issue is the immigration of non-target species (e.g. competitive exotic species), which affect/hamper the establishment of target species (Wilson 2002, Török et al. 2011).

Interventions

Spontaneous succession can be relied upon in some restoration projects and primarily concerns sites where conditions were not strongly altered by the disturbance (Prach & Pysek 2001, Prach & Hobbs 2008). For the more altered sites, the active introduction of target species appears to be essential to overcome the limited natural regeneration and the dispersal barrier. The main near-natural methods for restoring grassland communities with local target species include (based on the review from Kiehl et al. (2010) and Török et al. (2011) in Europe:

1) **Seeding of site-specific seed mixture**: Cooper and MacDonald (2000), Lindborg (2006), Martin & Wisley (2006), Jongepierova et al. (2007), Jaunatre et al. (2012)

2) **Transfer of fresh seed-containing hay / vacuum harvesting**: Coiffait-Gombault et al. (2011), Jaunatre et al. (2012) (Mediterranean grasslands), Hölzel & Otte (2003), Donath et al. (2007) (species-rich flood meadows), Edwards et al. (2007) (lowland hay meadows/ chalk grasslands), Kiehl & Pfadenhauer (2006), Kiehl & Wagner (2006) (calcareous grassland), Patzelt et al (2001), Klimkowska & al. (2009) (fen meadows)

3) **Transfer of turfs or topsoil:** Rochefort et al (2003) (peatlands), Cobbaert et al (2004) (fen plant community, after mining), Jaunatre et al. (2012) (Mediterranean grasslands).

4) **Transplants of seedlings, rhizomes, willow stem cutting**: Cooper & MacDonald (2000) (fen in mountain), Page & Bork (2005) (mountain communities)

5) **fire** (Moyes et al. 2005), **hydrography** (Dijk et al. 2007) **or grazing** (Martins & Wisley 2006, Orrock et al. 2009, Klimkowska et al. 2009) **management**.

We highlighted in the previous chapter (chapter 2) the diversity of phenological patterns occurring in *campos rupestres,* with a gradient of seed production along the year, constituting the external species pool. The next chapter (chapter 3) goal is to assess the resilience of degraded areas, i.e. are species from the external species pool able to disperse to recompose the seed bank or/and to establish in such areas? (Figure 28) Concurrently, we carried out active restoration intervention in order to overcome the dispersal filter: i.e. hay transfer (Figure 28). As the landscape becomes increasingly fragmented, regeneration of plant communities (including seed bank) mainly depends on dispersal. We thus collected hay (i.e. diaspore and plant material), potentially composed by species from the external species pool, and spread it on degraded areas. As *campos rupestres* are composed of two grassland communities, we have run the protocol on both the sandy and stony grasslands.

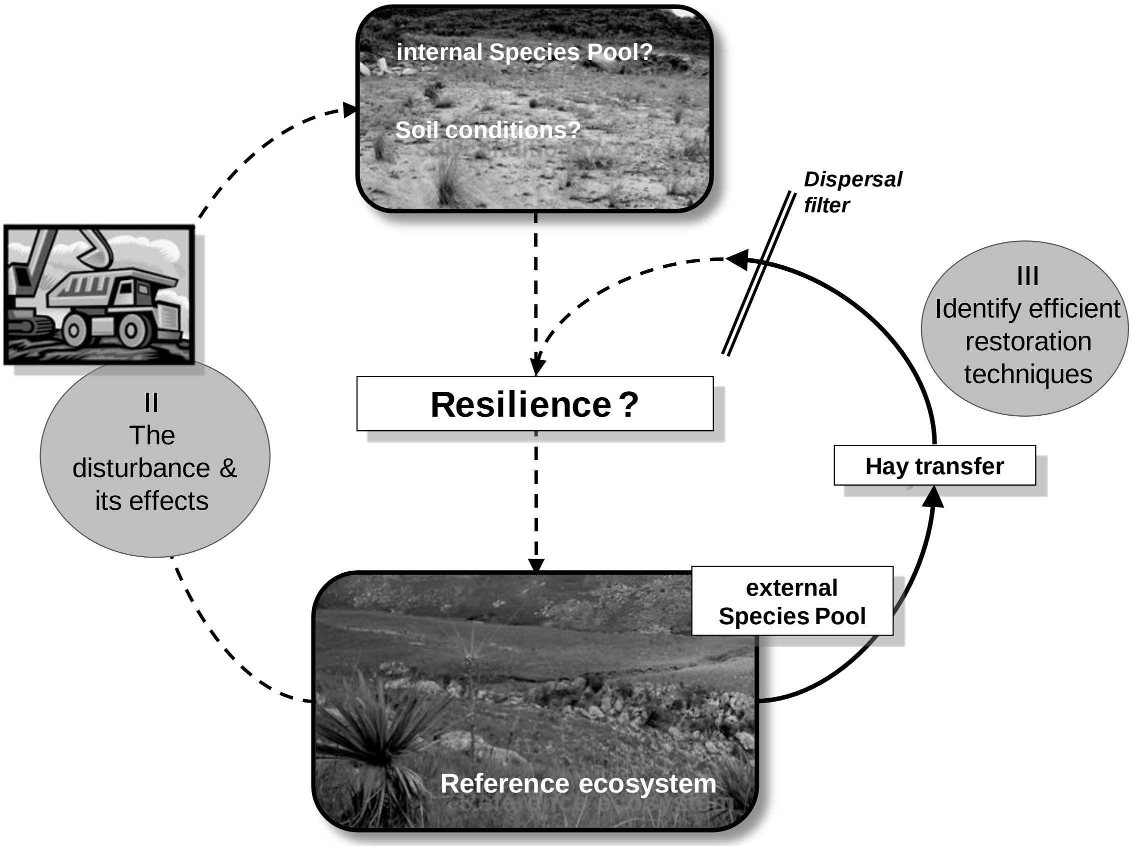

Figure 28: The first objective of the third chapter is to assess the resilience of the heavily destroyed *campos rupestres*. The second objective is to test whether hay transfer is an efficient method to overcome the dispersal filter and restore *campos rupestres*.

On top: degraded areas near the road,
at left: hay transfer on degraded areas.
Photo credit S. Le Stradic

Chapter 3 - Degradation of campos rupestres by quarrying: impact, resilience & restoration using hay transfer.

Chapter 3 - Degradation of campos rupestres by quarrying: impact, resilience & restoration using hay transfer.

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Abstract

The *campos rupestres* are species-rich tropical grasslands located in a region that is currently under assault by economic interests that are developing mining operations in the area. This study was designed firstly to evaluate the natural resilience of degraded *campo rupestre* areas by evaluating the degree of spontaneous succession eight years following the disturbance (i.e. quarrying for gravel exploitation during the asphalting of highway MG-010), by describing potential site limitations (i.e. chemical characteristics of the degraded soil) and by assessing the internal species pool, mainly represented in the seed bank. Secondly, we tested the restoration technique of hay transfer as a means of strengthening seed dispersal. Nine degraded areas representing three kinds of substrate (latosol, sandy, and stony) were selected. To evaluate the resilience, a plant survey along with seed bank and soil studies were carried out in 2010. Eight years after degradation, plant composition and soil composition differed greatly between the degraded areas and the reference ecosystem (stony and sandy grasslands). The seed banks of the reference ecosystem are extremely seed and species poor, while those of the degraded areas are mainly composed of non-target ruderal species; regeneration via the seed bank is therefore rather limited. *Campos rupestres* are poorly resilient face to a harsh degradation, which implies the necessity of restorative intervention (i.e. hay transfer). Hay transfer was carried out using hay that was collected year-round in 2010 in order to maximize the seed pool. The hay was distributed among the three kinds of degraded areas with and without geotextile at the end of 2010 according to the following protocol: hay from sandy grasslands was placed in all types of degraded areas, while hay from stony grasslands was used on stony substrates only. The seedlings that were observed on the degraded areas 14 months following hay application were mainly ruderal species. Our results highlight the inherent difficulty in restoring degraded areas of *campos rupestres* by attempting to overcome the dispersal filter using hay transfer.

Key words: grassland restoration, hay transfer, quarrying, seed bank, regeneration

1.Introduction

Humans have strongly altered the global environment especially through land-use changes (Chapin et al. 2000, Steffen et al. 2007), which has been responsible for ca. half of terrestrial ecosystem transformations (Daily 1995, Vitousek et al. 1997, Klink & Moreira 2002). These profound changes have resulted in many prejudicial effects on diversity and ecosystem services (Osborne et al. 1993, FAO 1998, Sala et al. 2000 MEA 2005). Grassland ecosystems and tropical ecosystems are expected to be the most strongly impacted by future land-use changes (Sala et al. 2000). Among the most drastic of land-use changes, quarrying and mining activities cause major soil damage, leading to uncontrolled soil erosion and water quality alteration (Pimentel et al. 1995, Valentin et al. 2005). Currently, ecological restoration has become one strategy for enhancing biodiversity, rescuing degraded areas, and reinstating ecosystem services. Ecological restoration *sensu lato* is the process of intentionally assisting the recovery of degraded ecosystems (SER 2004), including such activities as rehabilitation or reclamation (SER 2004). Many countries have already passed laws which require the reclamation, rehabilitation or restoration of quarries and mines once exploitation is over, e.g. the US Surface Mining Control and Reclamation Act of 1977; the Australian National Environment Protection Measures Act; the Canadian Law for environment quality (L.R.Q., c. Q-2, a. 20, 22, 23, 31, 46, 70 & 87); the French Décret n° 77-1133 du 21/09/77 pris pour l'application de la loi n° 76-663 relative aux ICPE; and in Brazil, Law 9605/1998, law 9985 18/07/2000 (linked to the article 225, § 1°, paragraphs I, II, III and VII of the Federal Constitution (1988)), article 19 of Law 4771/65, the technical standard ABNT 13030, SMA 08/2008 legislation (Aronson et al. 2011)). In spite of these laws and increasing restoration know-how, authorities sometimes still allow the ill-advised and widespread use of exotic species to revegetate ecologically compromised areas.

Before launching a restoration project, one must first assess the resilience of the degraded ecosystem – i.e. the efficiency with which an ecosystem returns to a reference trajectory following a disturbance or period of stress (Leps et al. 1982, Lockwood 1997, Mitchell 2000). This makes it possible to assess the impact of the disturbance (White & Jentsch 2001), and to identify whether restoration is necessary, and, if it is, to gather information useful for restoration planning (Bradshaw 2000, Prach & Hobbs 2008, Prach & Walker 2011). Two main factors hamper the resilience of a given ecosystem. The first is site limitation: oftentimes, site conditions are inappropriate due to the alteration of the chemical and physical properties of the soil (i.e. limited nutrient availability, low water availability) (Ash et al. 1994, Wong 2003, Yuan et al. 2006). The second is the lack of target species in the internal species pool, for example within the soil seed bank or among surviving individuals, or even in the external species pool from species that are capable of dispersing to the site via the seed rain (Ash et al. 1994, Bakker et al. 1996, Bradshaw 1997, Bakker and Berendse 1999, Wilson 2002, Shu et al. 2005, Kiehl 2010)). Sites degraded by quarry or mining activities often have inappropriate abiotic conditions and do not enjoy an internal species pool because the incumbent soil seed bank and vegetation have both been totally destroyed. Consequently, the seed supply in such areas is mainly dependent on seed dispersal from surrounding sites (Bradshaw 1983, 1997, Davis et al. 1985, Campbell et al. 2003, Shu et al. 2005). Spontaneous succession occurs preferentially wherever environmental conditions are not too extreme (Prach & Hobbs 2008); it is therefore often difficult to rely on spontaneous succession in case of mining degradation.

Grassland species often disperse poorly and at a low rate (Bishoff 2002, Buisson et al. 2006, Oster et al. 2009); consequently the restoration of species-rich grasslands may include direct seeding (Cooper & MacDonald 2000, Turner et al. 2006, Kirmer et al. 2012, Ballesteros et al. 2012), transposition of soil with diaspores (Rochefort et al 2003, Cobbaert et al. 2004), native species transplantation (Cooper & MacDonald 2000, Soliveres et al. 2012) and hay transfer (Hölzel & Otte 2003, Kiehl & Wagner 2006). Soil stockpiling and transposition can also be used, particularly for the rehabilitation of quarries and mines following exploitation (Ramsay 1986, Rokich et al. 2000, Koch 2007, Rivera et al. 2012). Environmental legislation usually requires that the original surface soils be conserved and replaced, and this is partly because they may contain propagules. In Brazil, despite the legal requirement to produce recovery plans, current practices are only partially effective (Neri & Sanchez 2010), and it has long been standard practice to mix topsoil with sterile soil (Griffith & Toy 2001, Toy & Griffith 2001). At the same time, it is common for topsoil stockpiles to exhibit loss of viable seed and non-negligible reduction in germination potential as a function of storage time (Rivera et al. 2012). All of these factors underscore the need for alternative restoration techniques.

In recent decades, especially in Europe, hay transfer (i.e. diaspore transfer with plant material) has been increasingly tested as a supplementary technique for overcoming the dispersal limitations of target species (Hölzel & Otte 2003, Kiehl et al. 2010, Baasch et al. 2012). Hay transfer has some advantages, such as potentially allowing the introduction of the entire species-pool of the desired community (Rasran et al. 2006), preserving genetic integrity, improving seedling recruitment by the creation of a safer site (e.g. shade), and having a relatively low implementation cost when compared to direct seeding (Hölzel & Otte 2003). This technique has already been used on various grassland types, such as calcareous grasslands (Kiehl & Wagner 2006), flood meadows (Hölzel & Otte 2003; Donath et al. 2007), chalk grasslands (Edwards et al. 2007), magnesian limestone grasslands (Riley et al. 2004), fen meadows (Patzelt et al. 2001, Klimkowska et al. 2009), peatlands (Graf & Rochefort 2008), dry grasslands (Baasch et al. 2012), and Mediterranean steppe (Coiffait-Gombault et al. 2011). However, we are not aware of its use in restoring degraded tropical grasslands. Hay transfer can be used whether the donor grasslands are dominated by perennial species (Hölzel & Otte 2003) or by annual species (Coiffait-Gombault et al. 2011), and the technique is well adapted to restoring plant communities with limited natural regeneration (i.e. from seed banks or seed rain) but only one pilot study has been carried out in tropical grasslands (Le Stradic et al. 2010).

Campos rupestres are species-rich tropical grasslands and one of the physiognomies of the Cerrado (Brazilian savanna), representing c.a. 130 000 km^2 (Barbosa 2012), and are found at altitudes ranging from 800m to 2 000m. They are composed of a mosaic of stony and sandy grasslands, bogs situated along streams, and scattered rocky outcrops that harbour small sclerophyllous evergreen shrubs and sub-shrubs (Giulietti et al. 1997, Chapter 1). *Campos rupestres* are constrained ecosystems with shallow soils that are nutrient-poor and highly acidic (Ribeiro & Fernandes 2000, Benites et al. 2007, Chapter 1). They also comprise highly diverse vegetation with one of the highest levels of endemism in Brazil (Giulietti et al. 1997, Echternacht et al. 2011, Carvalho et al. 2012). As many mountain grasslands, they play a major role in water quality control over entire large watersheds. While *campos rupestres* are encountered in a region impacted by increasing mining operations, virtually nothing is known about their resilience and restoration (Le Stradic et al. 2008, 2010). Moreover, mountain grasslands are known to be poorly resilient to disturbances and therefore usually require restoration once they have been degraded (Urbanska & Chambers 2002).

Within this context, the present study was designed to quantitatively evaluate the resilience of these tropical grasslands, to provide a description of these sites' limitations (i.e. in terms of the chemical characteristics of degraded soils compared to the reference soil), and to provide an assessment of the potential for regeneration in such sites via the seed bank. We expected these rich grasslands to be poorly resilient in the face of quarrying as it was already assumed by some authors (Negreiros et al. 2011). In addition, because Burnside et al. (2002) have noted previously that reinstallation from soil seed bank alone is often insufficient (see also Medina & Fernandes 2007, Appendix 4), we were interested in testing hay transfer as an alternative means of restoring these two peculiar grasslands.

2. Material and Methods

2.1. Study area

Our study area is located in the southern portion of the Espinhaço Range, approximately 100 km northeast of Belo Horizonte, in the state of Minas Gerais; the area is within the Environmental Protected Area (Area de Proteção Ambiental in Portuguese) of Morro da Pedreira, a buffer zone of the Serra do Cipó National Park. The climate in this area is classified as Cwb according to the Köppen's system, exhibiting warm, wet summers and dry winters. It is markedly seasonal, with two distinguishable seasons: a rainy season from November to April and a dry one from May to October. The study area mean annual precipitation is 1622 mm and its mean annual temperature is 21.2°C (Madeira & Fernandes 1999).

Reference ecosystem – The main herbaceous plant communities of campos rupestres, namely the sandy and stony grasslands (Chapter 1) (Figure 14), were taken as the reference ecosystems for this study. They are species-rich, and mainly composed of Poaceae (*Paspalum, Mesosetum, Axonopus, Andropogon*) and Cyperaceae (*Lagenocarpus, Rhynchospora, Bulbostylis*), with Xyridaceae (*Xyris*), Eriocaulaceae (*Paepalanthus, Leiothrix, Syngonanthus*) and Velloziaceae (*Vellozia, Barbacenia*), together with some forbs and sub-shrub species belonging to Asteraceae (*Lychnophora, Richterago*) or Melastomataceae *(Lavoisiera, Marcetia*) among others. The majority of the species are perennial and hemicryptophytes (Chapter 1).

Degraded areas - Three kinds of areas degraded by quarrying were selected: (i) three with stony substrates (DSt), (ii) three with sandy substrates (DSa) and (iii) three with latosol substrates (DL) (Figure 16). Studies had reported the presence of degraded areas in the region as early as 1996 (Negreiro et al. 2011), but the overall start of degradation may actually date back to 1980. In 2002, a new disturbance occurred when highway MG010 was asphalted. Degraded areas found along the road were exploited for gravel and/or were used to park machines. When the road was complete, the degraded areas left behind represented several kinds of substrate. Small quarries are common in the region and their creation leas to vegetation being destroyed and soils being disturbed. Even when exploitation stops, soils are not entirely restituted, and they may be heavily contaminated by construction debris. All of these degraded areas are surrounded by pristine *campos rupestres*, that is why we chose them as the reference ecosystem.

2.2. Resilience of the campos rupestres

2.2.1. Vegetation

In order to assess the resilience of the vegetation on the degraded areas, we compared the plant community composition in the reference ecosystem with that of the degraded areas eight years after the end of quarrying. Plant surveys were carried out in January 2010 in the following six reference grasslands: 3 stony (St) and 3 sandy grasslands (Sa). Surveys were also conducted in all degraded areas (3 kind of areas × 3 sites=9 total). For each site, 24 plots of 40cm × 40cm (0.16m^2) were investigated in order to record (1) a list of the species, (2) the percent cover of each species as visually estimated from the vertical projection of all aerial plant parts.

2.2.2. Soils

In order to assess the resilience of soil chemistry in the degraded areas, three soil samples were taken at each site (reference and degraded) and dried prior to analysis (n = 3 samples x 15 sites). Each soil sample consisted of three pooled sub-samples randomly taken from each site. To assess soil texture the coarse fraction was first separated through a 2mm mesh sieve. On the fine fraction (<2mm), physical (soil texture) and chemical (pH, C_{org}, total N, P, K, Mg^{2+}, Ca^{2+}, Al^{3+}) soil analyses were run, from which chemical concentrations were derived as follows: P and K in mg/dm^3, N and C in dag/kg, Mg^{2+}, Al^{3+}, Ca^{2+} in cmol$_c$/dm^3, Organic Carbon ($C._{org}$) in dag/kg. P, Na and K were analysed using the Mehlich 1 extraction method, Ca^{2+}, Mg^{2+}, Al^{3+} using 1 mol/L KCl extraction, and C_{org} following the Walkley-Black method. Soil sampling was carried out during the rainy season (February). Analyses were conducted at the Soil Laboratory of the Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

2.2.3.Seed banks

In order to assess potential of regeneration from the seed bank, we studied the seed banks of the reference grasslands (n=6). We also made an effort to find out what species may have colonized the degraded sites, without fully establishing themselves in the years following 2002, by studying the seed banks of the degraded areas (n=9). At each site, five 1L soil samples were taken at the end of the dry season (September), April to July being the peak period of fruit production (Chapter 2) (n = 5 samples × 15 sites). Each sample consisted of 10 pooled sub-samples, randomly taken at each site to overcome seed bank heterogeneity. Samples were washed with water on sieves with 4 mm and 200 µm mesh sizes to remove 1) plant fragments and stones and 2) the finest soil fraction (clay and silt) respectively. The remaining seed-containing soil was spread as a thin layer on trays (25cm x 35cm) on compresses placed over a 3 cm thick layer of vermiculite (a neutral substrate). Control trays (n=3) (made of compresses over vermiculite) and controls of the finest soil fraction (<200 µm) (n=3) (made of the finest fraction spread out on compresses over vermiculite) were also set in order to 1) ensure that no species could colonize the greenhouse and contaminate samples and 2) ensure that no seed <200 µm may have been lost to sieving. No seeds were found to germinate in the finest soil fraction or in any of the control trays. All trays were kept in a greenhouse, were regularly moved, and were watered. Emerging seedlings were identified on a weekly basis and removed or replanted in pots for later identification. This was done to minimize competition within the trays and to reduce susceptibility to the emission of allelopathic substances. If no germinations were observed for a period of one month, the samples were each dried and microplowed before initiating a second, fresh germination period, this procedure being a well-known technique for stimulating additional germination (Roberts 1981).

2.3. *Restoration using hay transfer*

The hay was collected monthly during 10 months to maximize seed pool (January 2010 – October 2010) on two donor sites for each kind of reference grasslands (two sandy and two stony grasslands). Once a month, hay was manually mown with a scythe and immediately collected using hand vacuum equipment of a variety normally used to suck up leaves (Coiffait-Gombault et al. 2011). Then, the hay was dried and conserved in paper bags.

The samples taken on various dates were mixed together prior to sowing. Sowing occurred in December 2010 during the rainy season. For each of the designated plots, 120g of hay was applied on 40cm × 40cm quadrats (i.e. 750 g/m2). This weight is similar to the biomass of hay that was dispersed during previous experiments in Northern Europe (Kiehl & Wagner 2006). Each treatment was replicated four times at each site in blocks (Figure 29). Prior to spreading the hay, the soil was lightly harrowed in order to improve seed adherence. This was also done on the control plots onto which no hay was transferred. All quadrats were watered (0.5 liters/quadrat), before and after sowing in order to assist the germination and facilitate the adherence of the seeds to the soil.

Two experiments were set up (Figure 29):

A) The aim of the first experiment was to assess the influence that the type of degraded area has on seedling emergence. We manipulated 2 or 3 levels of 3 treatments in a multifactorial experiment: (i) substrates of the degraded areas (Latosol (DL)/sandy (DSa)/stony (DSt)), (ii) with/without geotextile (G/wg) in order to try to improve microsite conditions for germination (i.e. potentially increased shade for germinating seeds, increased moisture and reduced the impact of rain on the soil), (iii) hay from sandy donor grasslands (HSa)/no hay (h, control) (i.e. hay provides seeds but the plant parts included in the hay also potentially increase shade, increase moisture and might slightly reduce the impact of rain on the soil).

B) The goal of the second experiment was to test the effect of the origin of the hay in order to restore both kinds of reference grasslands. On stony substrates, in addition to performing the first experiment, we spread out 120g of hay collected on stony donor grasslands (HSt) with/without geotextile (G/wg).

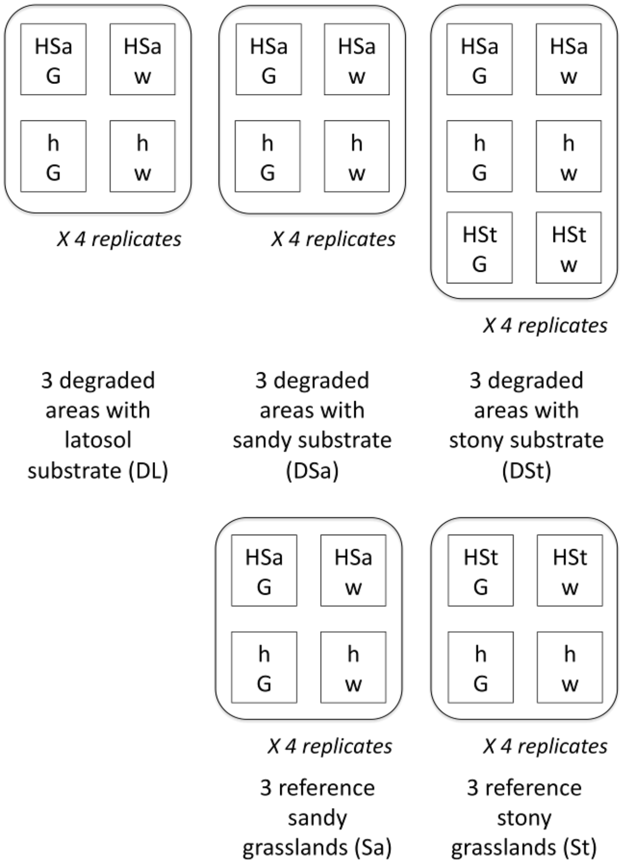

Figure 29: Experimental design of the hay transfer experiment. HSa: hay collected on the two sandy grassland donor sites, HSt: hay collected on the two stony grassland donor sites, h: control without hay, G: with geotextile, w: without geotextile. Each treatment was replicated four times at each site in blocks.

As controls, the same protocol was repeated in reference areas of sandy (3 sites) and stony (3 sites) grasslands. Hay was spread out as follows: hay from stony donor sites on stony grasslands and hay from sandy donor sites on sandy grasslands (Figure 29).

In order to assess the composition and seed abundance in the hay, six 120g samples of each kind of hay were sown in a greenhouse. Each sample was spread out in two trays of 35cm × 22cm on gauze-covered substrate composed 50% of potting soil and 50% of vermiculite. Half of the trays were covered with geotextile to test the impact of geotextile on germination. Six trays containing only substrate was installed to control seed contamination, and half of them were covered with geotextile. Trays were watered several times per week and regularly moved. Seedlings were identified, counted and removed to avoid competition. Three 120g samples of each kind of hay were also selected to perform a manual counting of seeds.

To assess the success of these restoration treatments, vegetation surveys were carried out in the field on all 40cm × 40cm quadrats in February 2012 (t_{14}=14 months). In all quadrats, (1) a list of the species, (2) the number of seedlings per species (3) the respective percent covers of bare ground, litter, and vegetation were recorded.

2.4. Statistical analysis

2.4.1. Resilience

To assess plant dissimilarity between the different types of areas (Sa, St, DL, DSa and DSt), a dissimilarity matrix using Bray-curtis indices based on species percent cover data was calculated and an ANOSIM was performed. A Correspondence Analysis (CA) on the plant percent cover recorded in January 2010 (288 quadrats × 178 species) was performed to identify groups and establish community types.

To compare soil fine fraction and soil chemical composition between types of areas, one-way nested ANOVAs were performed, followed by Tukey post-hoc tests when significant. Normality and variance homogeneity were checked and the root square transformation was applied wherever necessary (Sokal & Rohlf 1998). To analyse the soil coarse fraction between these areas, Kruskal-Wallis tests were performed, as variances were not homogenous, and this was followed by Wilcoxon tests with the Bonferroni correction when significant.

To analyse the number of species and the number of germinated seeds in the seed banks, GLM models for total germinated seeds per litre of soil as well as for total species richness found per site were built assuming a Poisson distribution of errors and a logarithmic link function (McCullagh and Nelder 1989, Crawley 2007). A dissimilarity matrix using Jaccard index, based on species presence/absence data was calculated to assess the plant composition dissimilarity between the different seed banks (i.e. from St/Sa/DL/DSa/DSt), and an ANOSIM was performed. We also performed Spearman’s correlation test to determine whether there exists a relationship between the number of seeds in the seed bank at each site and the proximity of each site either to undisturbed *campos rupestres* areas or to the road.

2.4.2.Restoration using hay transfer

To evaluate the effect of restoration treatments on vegetation cover, one-way nested ANOVAs, followed by Tukey post-hoc tests when significant, were performed on vegetation percent cover among sites. An ANOSIM was performed to estimate the similarity/dissimilarity between the different areas, using Bray-curtis indices based on species abundance. Finally, a Correspondence Analysis (CA) was performed based on the abundance of plant species recorded in February 2012 (T=14 months; 232 points × 161 species) to visualise groups and to establish community type. The effect on seedling number of (a) type of substrate, (b) geotextile and, (c) type of hay were tested using generalized linear mixed model, (LMER) assuming a Poisson error distribution and using a log link function (Crawley 2007). Fixed effects were type of substrate, geotextile and type of hay, whereas the random effects were sites and replicates (Crawley 2007). Generalized linear model (GLM) was then used to specifically compare the number of seedlings per quadrat according to the substrate, the type of hay, or the presence of geotextile.

All analyses were carried out in R version 2.9.1 (R Core Development Team, 2010) using ADE-4 and stats packages.

3.Results

3.1. *Resilience of the campos rupestres*

Eight years following their respective disturbances, the degraded sites presented large areas of bare ground, comprising 91 ± 2% in degraded areas with latosol substrate, 77 ± 2% in degraded areas with stony substrate and 97.5 ± 0.5% in degraded areas with sandy substrate. The composition of the vegetation on degraded areas was consequently very different from that in the reference *campos rupestres* (ANOSIM R=0.45, p<0.001, Table 12). Aside from the obvious large differences, the stony degraded areas actually presented a few similarities with the reference ecosystems, having common species, such as *Mesosetum loliiforme, Rhynchospora consanguinea, Echinolaena inflexa* or *Marcetia taxifolia* (Table 12, Figure 30). By contrast, the other types of degraded areas presented a plant composition completely different from that of the reference ecosystems (Bray-curtis indices = 1.00, Table 12). According to the Correspondence Analysis, the plant composition of each type of degraded area depended upon on the particular substrate, and a large heterogeneity was found within the sites of each type of degraded area (Figure 30). Numerous ruderal species are found on the degraded areas, such as *Andropogon bicornis, Chamaecrista rotundifolia* or *Zornia reticulata.*

Table 12: Dissimilarity matrix (Bray-curtis indices) of the plant composition between the degraded areas: with Latosol substrate (DL), stony substrate (DSt) and sandy substrate (DSa) and the reference grasslands: the sandy (Sa) and the stony (St) grasslands, based on species percent cover data (n=3 sites x 5 types of areas).

	DL	DSt	DSa	St
DSt	0,86			
DSa	0,913	0,829		
St	1	0,88	1	
Sa	1	0,852	1	0,366

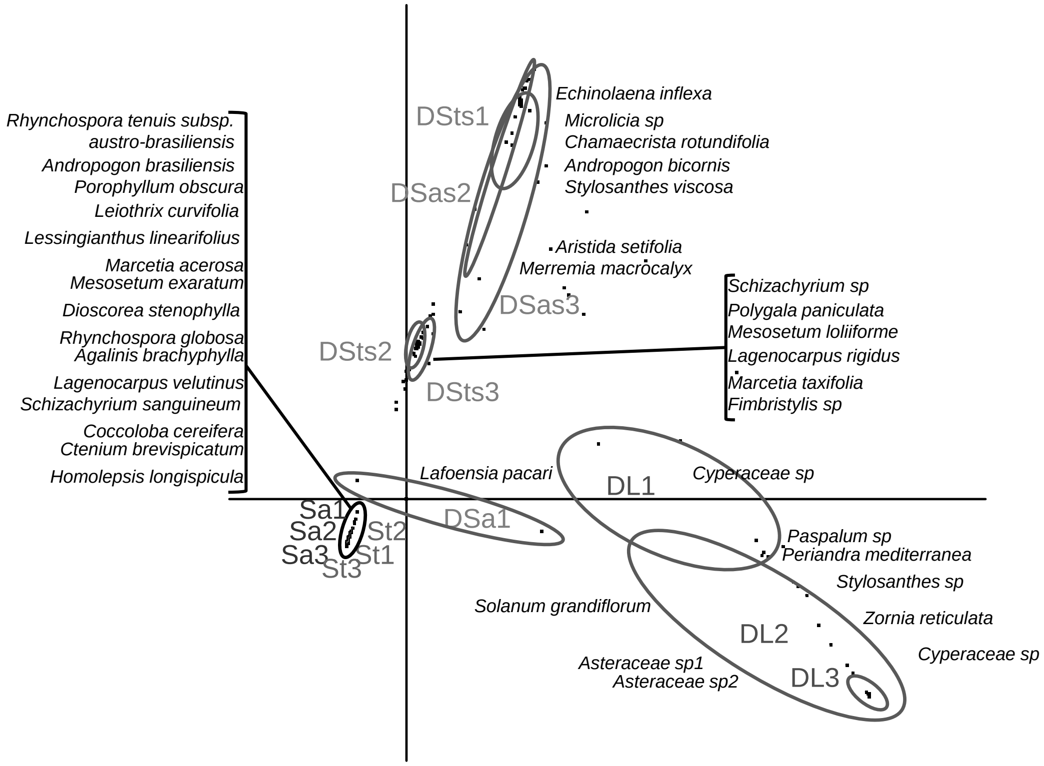

Figure 30: Correspondence analysis on the matrix of species percent cover in 40cmx40cm quadrats in January 2010, in references areas: 3 stony (St) and 3 sandy grasslands (Sa) and in degraded areas: 3 with latosol substrate (DL), 3 with sandy substrate (DSa) and 3 with stony substrate (DSt) [288 points x 178 species]. Projection of the two first axes, axis 1 (17.2%) and axis 2 (16.4%). Inertia=0.17, p<0.001, Monte-Carlo permutations.

3.2. Vegetation establishment limitation

3.2.1. Site limitation

As expected, soil texture varied among the areas: both reference stony grasslands and degraded areas with latosol and stony substrates presented a significantly larger proportion of coarse soil (soil > 2mm): more than 46% (Table 13). Sandy grasslands were characterized by a significantly higher proportion of fine sand (>46%), and degraded areas were defined by a greater portion of silt (>36%), while in the latosol degraded areas we recorded higher percentage of clay (>33%) (Table 13).

In the reference grasslands, N concentrations were significantly higher and the soil was more acidic than that of the degraded areas (Table 14, Figure 31). The reference stony grasslands were characterized by higher K and C_{org} content (Figure 31). Degraded areas having a latosol substrate presented the biggest difference in soil composition, having high Ca^{2+} and Mg^{2+} concentrations, a much higher pH than the other areas. These areas presented also a higher P concentration than the other degraded areas, with stony and sandy substrates. The aluminum concentrations did not vary between the different types of area, although a tendency for lower aluminum concentrations in degraded areas with latosol substrate was found (Table 14, Figure 31).

Table 13: Mean and standard error values of soil texture, from soils collected in reference grasslands: 3 sandy, and 3 stony grasslands, and in degraded areas: 3 latosol, 3 sandy and 3 stony (3 samples x 3 sites x 5 types of areas, n=45). Kruskal-Wallis test were run for the coarse fraction and one-way nested ANOVA for the fine fraction. NS: non-significant difference, *significant difference with *P*<0.05, *** significant difference with *P*<0.001.

		Sandy grasslands	Stony grasslands	Latosol degraded areas	Stony degraded areas	Sandy degraded areas	Kruskal-Wallis / Nested ANOVA
Coarse fraction of soil	Soil >2mm (%)	10.8 ± 3.3 ^{a}	60.5 ± 2.4 ^{b}	52.0 ± 4.1 ^{b}	46.3 ± 5.3 ^{b}	13.5 ± 2.9 ^{a}	χ^2=32.0***
Fine fraction of soil < 2mm	Coarse sand (dag/kg)	19.6 ± 2.5	25.8 ± 2.4	12.8 ± 1.8	21.7 ± 2.8	13.4 ± 1.9	F=1.6 ^{NS}
	Fine sand (dag/kg)	46.9 ± 2.0 ^{a}	37.3 ± 1.4 ^{b}	10.1 ± 0.8 ^{c}	33.7 ± 2.7 ^{b}	33.6 ± 2.0 ^{b}	F=19.2 ***
	Silt (dag/kg)	29.3 ± 1.9 ^{a}	31.5 ± 1.5 ^{a}	43.3 ± 2.1 ^{b}	36.1 ± 2.8 ^{ab}	48.7 ± 3.3 ^{b}	F=4.7 *
	Clay (dag/kg)	4.2 ± 0.4 ^{a}	5.3 ± 0.5 ^{a}	33.7 ± 1.7 ^{b}	8.4 ± 1.7 ^{a}	4.3 ± 0.7 ^{a}	F=22.6 ***

Table 14: Result of the one-way nested ANOVAs run on chemical soil parameters, from soils collected in reference grasslands: 3 sandy, and 3 stony grasslands, and in degraded areas: 3 latosol, 3 sandy and 3 stony (3 samples x 3 sites x 5 types of areas: n=45). NS: non-significant difference, * significant difference with *P*<0.05, *** significant difference with *P*<0.001. See Figure 4 for values.

	one-way nested ANOVA
N (dag/kg)	F=19.44 ***
pH (H_2O)	F=4.0.3 *
P (mg/dm3)	F=3.53 *
K (mg/dm3)	F=5.53 *
Ca^{2+} (cmolc/dm3)	F=3.71 *
Mg^{2+} (cmolc/dm3)	F=4.62 *
Al^{3+} (cmolc/dm3)	F=2.70 ^{NS}
Corg (dag/kg)	F=13.68 ***

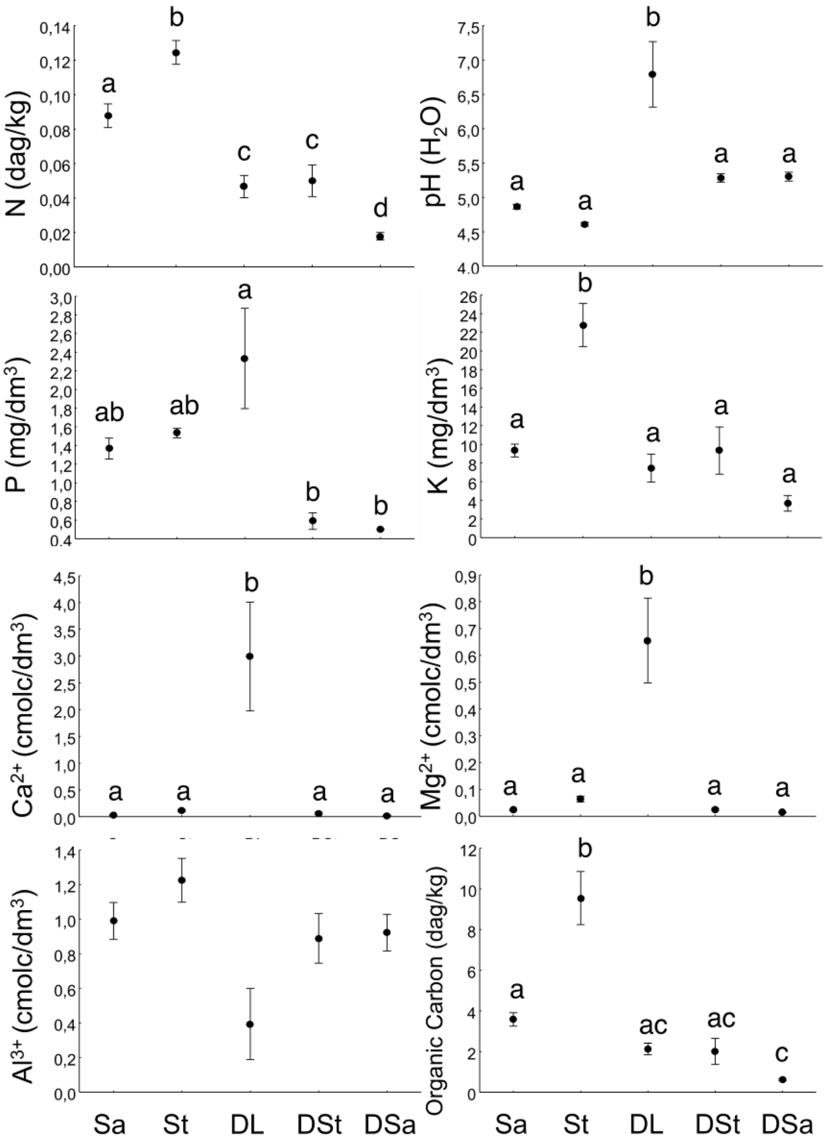

Figure 31: Mean and standard error values of chemical soil parameters, from soils collected in 3 sandy grasslands (Sa) and 3 stony grasslands (St), 3 degraded areas with latosol substrate (DL), 3 degraded areas with stony substrate (DSt), 3 degraded areas with sandy substrate (DSa) (3 samples / site / season, n=90). Full circles rainy season. See Table 3 for one-way nested ANOVA results.

3.2.2.Few viable seeds in the soils

There were many more seeds in the seed banks of the degraded areas with stony and sandy substrate than in other sites (GLM procedures p(>|Chi|)<0.001, Table 15). In the degraded areas with latosol substrates we recorded a lower number of species at each site (p(>|Chi|)<0.001, Table 15). The composition of the seed banks in the degraded areas was completely different to that in the reference grasslands (ANOSIM R=0.137, p<0.001, Table 16:). In the degraded areas seed banks were mainly composed of ruderal species such as *Aristida setifolia* or *Andropogon* sp. By contrast, in the reference grassland seed banks we recorded species such as *Tatianyx arnacites, Rhynchospora consanguinea, Rhynchospora riedeliana* or *Lagenocarpus rigidus* subsp. *tenuifolius*. Only *Mesosetum loliiforme* was found both in degraded areas with stony substrate and in reference grasslands. We found no significant relationship between the number of seeds found in the seed bank of each site and the site's proximity to natural *campos rupestres* areas (Spearman's Rho =-0.48, p=0.18) or to the road (Spearman's Rho =-0.35, p=0.34).

Table 15: Number of germinated seeds and number of species found in the seed banks of the reference grasslands (sandy (Sa) and stony (St) grasslands) and of the three types of degraded areas (with latosol substrate (DL), stony substrate (DSt) and sandy substrate (DSa)) (n= 5 samples x 3 sites x 5 types of areas). Letters indicate significant differences according to the result of the GLM procedures (family: Poisson, link: log).

	DL	DSa	DSt	Sa	St	p(>|Chi|)
Number of germinated seeds from the seed bank	10	318	361	54	50	
Mean number of germinated seeds per sample (1L)	0.67 ± 0.45 ^{a}	21.20 ± 5.71 ^{b}	24.07 ± 7.42 ^{b}	3.60 ± 0.71 ^{c}	3.33 ± 1.28 ^{c}	***
Number of species in the seed bank	3	13	20	14	15	
Mean number of species / site	1.33 ± 0.41 ^{a}	6.33 ± 3.89 ^{b}	8.33 ± 4.32 ^{b}	7.33 ± 1.63 ^{b}	7.00 ± 3.43 ^{b}	***

Table 16:: Dissimilarity matrix (Jaccard indices) of the seed bank composition between the degraded areas with latosol substrate (DL), stony substrate (DSt) and sandy substrate (DSa) and reference grasslands: the sandy (Sa) and the stony (St) grasslands based on presence-absence data (n=3 sites x 5 types of areas).

	St	Sa	DL	DSt
Sa	0,68			
DL	1	1		
DSt	1	1	0,95	
DSa	1	1	0,93	0,77

3.3. Restoration using campo rupestre hay transfer

3.3.1.Vegetation cover

More than one year after the hay was transferred, vegetation cover in degraded areas was quite low in comparison to the vegetation cover found on reference grasslands (F=106.1, p<0.001) (Figure 32). Moreover, plant community composition in degraded areas was still completely different from that of reference grasslands even with hay transfer (ANOSIM R= 0.53, p<0.001, Figure 33). Axis 1 of the correspondence analysis separated the reference grasslands from the degraded areas while axis 2 underlined a high heterogeneity among the degraded areas, each one characterized by its own plant composition (Figure 33), still mainly composed by ruderal species. No effect due to hay transfer was observed.

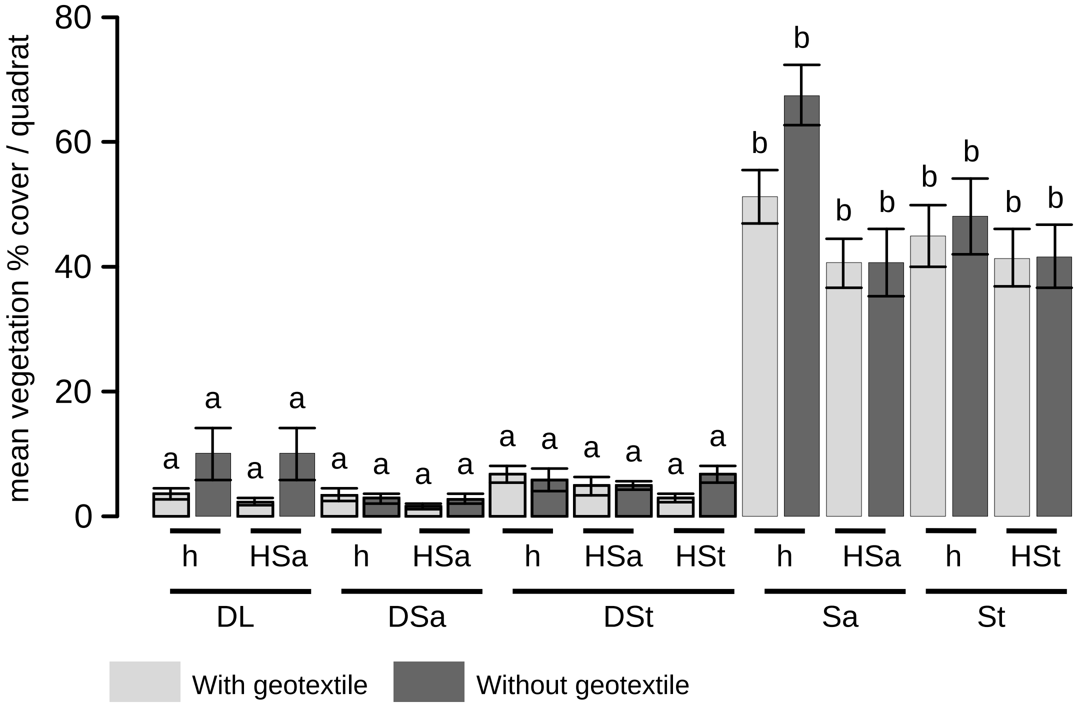

Figure 32: Mean vegetation percent cover per 40cmx40cm quadrat according 5 types of areas: degraded areas with latosol substrate (DL), with sandy substrate (DSa), with stony substrate (DSt), reference sandy grassland (Sa) and reference stony grassland (St), and 2-3 level of 2 treatments: with hay from sandy grassland (HSa) / with hay from stony grassland (HSt) / without hay (h), and with geotextile (clear grey) / without geotextile (dark grey). Letters according the result of one-way nested ANOVAs, followed by Tukey post-hoc tests.

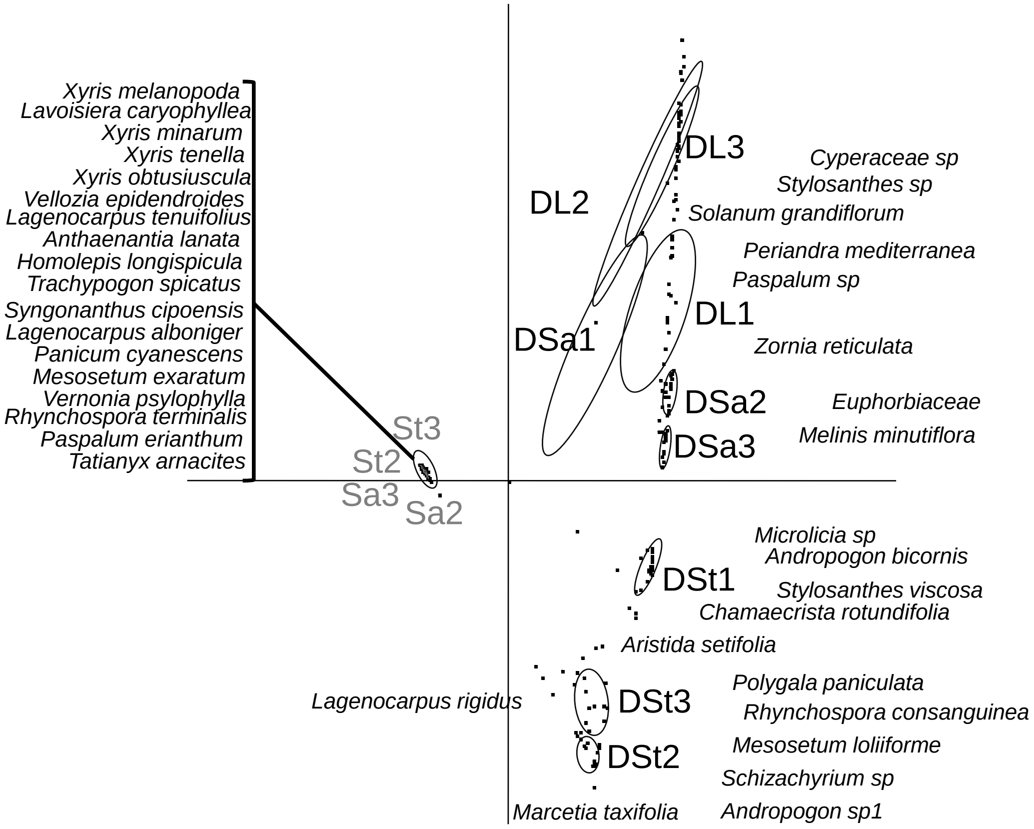

Figure 33: Correspondence analysis run on the matrix of the species abundance in February 2012 in 40cmx40cm quadrat after hay transfer in reference grasslands: 2 stony (St) and 2 sandy grasslands (Sa) and in degraded areas: 3 with latosol substrate (DL), 3 with sandy substrate (DSa) and 3 with stony substrate (DSt) [232 points x 161 species]. Some quadrats received hay and some not and some had geotextile and some not. Projection of the two first axes, axis 1 (17.2%) and axis 2 (14.2%). Inertia=0.23, p<0.001, Monte-Carlo permutations.

3.3.2.Effect of substrate on the number of seedlings

Substrate type in the degraded areas had a major effect on the total number of seedlings. Fourteen months after the beginning of the experiment, quadrats on latosol substrate (DL) recorded many fewer seedlings (4.0 ± 0.6) than quadrats on sandy substrates (DSa) (25.1 ± 4.4) and stony substrates (DSt) (27.7 ± 3.7) which had the highest number of seedlings (LMER procedures with z=2.1, p=0.03). Like quadrats in the latosol substrate, those in reference sandy grasslands (Sa) recorded few seedlings (Figure 34). There was a significant interaction between substrate and hay (z=3.64, p<0.001): quadrats with hay (HSa) recorded lower seedlings on degraded sandy grasslands (DSa). Geotextile alone generally did not influence the number of seedlings per quadrat (18.6 ± 3.3 on quadrat with geotextile and 19.3 ± 2.7 on quadrat without geotextile, LMER procedures z= 0.64, p=0.52). However there was a significant interaction between substrate and geotextile (z=-1.91, p=0.05): on the reference sandy grasslands (Sa), quadrats with geotextile recorded more seedlings (Figure 34). Hay did not seem to influence the number of seedlings per quadrat (z=0.33, p=0.74). Finally, we found a significant interaction between the substrate, the type of hay and the geotextile: on degraded stony (DSt) and sandy substrates (DSa), quadrats without hay and with geotextile recorded more seedlings (36.6 ± 13.9 on sandy substrates and 31.5 ± 9.9 on stony substrates, z=-3.17 for degraded sandy substrates and z=-2.45 on degraded stony substrates, p<0.001) (Figure 34).

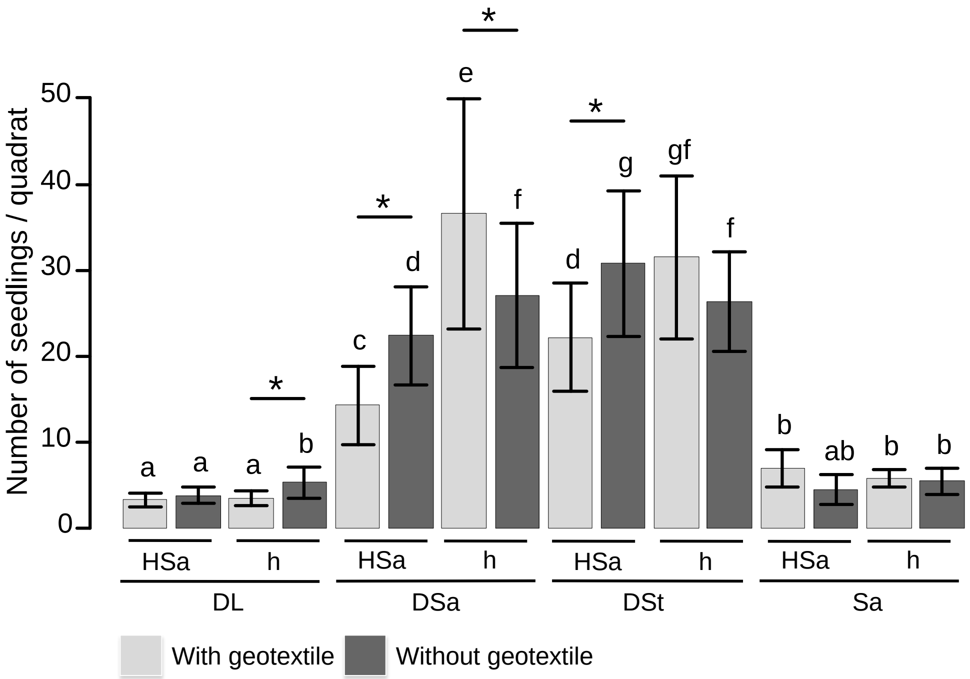

Figure 34: Mean number of seedlings occurring per 40cm×40cm quadrat on reference sandy grasslands (Sa) and on the 3 types of degraded areas: with latosol substrate (DL), with sandy substrate (DSa) and with stony sustrate (DSt) and 2 levels of 2 treatments: with hay (HSa) / without hay (h) and with geotextile (in clear grey) / without geotextile (dark grey). Letters indicate significant differences according to the result of the LMER procedures (family: Poisson, link: log), *: indicate difference between with and without geotextile.

3.3.3.Effect of the type of hay on the number of seedlings

As previously shown, the kind of substrate had a great influence on the number of seedlings: many more seedlings became established in the stony degraded areas (DSt) (26.7 ± 3.1) than in the reference grasslands (5.7 ± 0.8 in reference sandy grasslands

(Sa) and 7.6 ± 1.00 in reference stony grasslands (St), LMER procedure p(>|Chi|)<0.01, Figure 35). Considering only the stony degraded substrate (DSt), where two kinds of hay were spread, there were more seedlings on quadrats without hay (z=4.39 p<0.001) while lower numbers of seedlings were counted on quadrats where hay from stony grasslands was spread (z=-2.27, p<0.05). Geotextile had a negative overall effect on seedling recruitment (z=4.10 p<0.001). However, there was a significant interaction between the type of hay and geotextile: with no hay (i.e. control quadrats), more seedlings per quadrat were found with geotextile (31.5 ± 9.8). On the contrary, on quadrats with hay, the highest number of seedlings per quadrat was found without geotextile (30.8 ± 8.8 and 31.5 ± 8.9 respectively with hay from sandy and stony grasslands, LMER procedure z=7.12, p<0.001) (Figure 35).

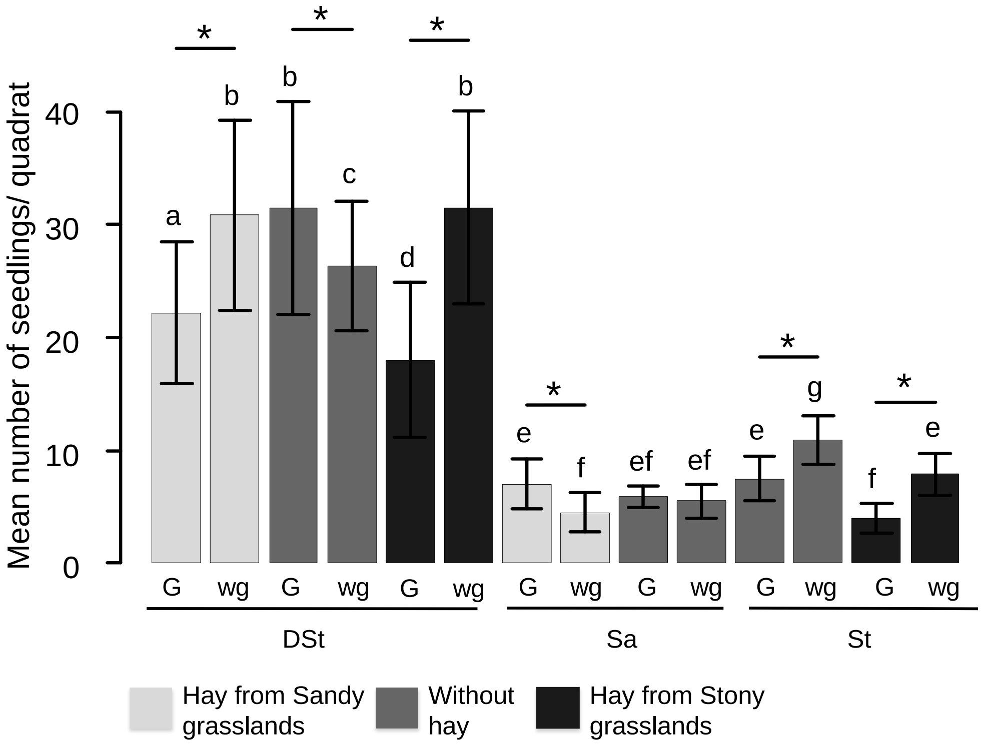

Figure 35: Mean number of seedlings occurring per 40cmx40cm quadrat on reference areas: sandy grasslands (Sa) and stony grasslands (St) and on degraded areas with stony substrates (DSt) according and 2 or 3 levels of 2 treatments: with hay from sandy grassland (clear grey) / with hay from stony grassland (grey) / without hay (dark grey), and with geotextile (G) / without geotextile (wg). Letters indicate significant differences according to the result of the LMER procedures (family: poisson, link: log), *: indicates difference between with and without geotextile.

On the reference stony grasslands, hay had a negative impact on the number of seedlings (LMER procedure z=-2.87 p=0.004), as did geotextile, which decreased the number of seedlings (z=2.21 p=0.02) (Figure 35). On the reference sandy grasslands, hay did not influence on the number of seedlings (z=-0.88 p=0.37), while geotextile had a positive impact on seedling establishment (z=-2.06 p=0.03) (Figure 35).

3.3.4.Limitation

The hay collected in stony donor grasslands had fewer seeds than the hay collected in sandy donor grasslands (157 ± 26 seeds vs. 361 ± 102 seeds in 120g of hay, GLM procedures z=-15.12, p<0.001). Both hays were mainly composed of Cyperaceae (*Rhynchospora sp.* and *Lagenocarpus sp.*), Poaceaea and Xyridaceae. Hay spread in control trays in the greenhouse recorded only a single, unique germination (*Diplusodon orbicularis)* from hay collected on stony grasslands.

4.Discussion

4.1. Resilience of campos rupestres

According to the stability-diversity hypothesis, biodiversity should promote resistance and resilience to disturbance (McNaughton 1977, Pimm 1984, Tilman & Downing 1994). While some studies have demonstrated that the *campos rupestres* are particularly resilient to endogenous disturbance (*sensu* White & Jentsch 2001), such as fire (Neves & Conceição 2010, Hernandez 2012), we have shown that species-rich *campos rupestres* present very low resilience to severe anthropogenic degradation (i.e. exogenous disturbance). Indeed, eight years after quarrying, bare ground still dominated the degraded areas and species composition remained very different from reference *campos rupestres*. Some characteristic *campo rupestre* species, such as *Tatianyx arnacites, Mesosetum exaratum, Homolepis longispicula, Lagenocarpus rigidus* subsp*. tenuifolius,* or *Vellozia caruncularis* (Chapter 1)*,* did not recolonize the degraded areas although large populations of them occurred in adjacent *campos rupestres*. Various hypotheses could explain the lack of regeneration in such degraded areas (Bradshaw 2000, Campbell et al. 2003): i) species in the surroundings do not produce seeds, but we already showed that seeds are produced on the surrounding (Chapter 2); ii) these seeds do not disperse far enough to reach degraded sites; iii) dispersed seeds arrive to degraded areas but do not germinate or are not viable; iv) dispersed seeds are able to germinate but the development of seedlings are hampered by constrained abiotic environmental conditions or lack the of symbiotic interaction with facilitating arbuscular mycorrhizal fungi (AMF) (Carvalho et al. 2012).

Site conditions are regularly pointed out as a factor which hampers the resilience of a given ecosystem. Quarrying has strongly impacted soil composition of degraded areas, which is poorer in nitrogen and organic carbon, both of which are essential elements to plant growth. The reference grasslands are oligotrophic with low phosphorus and potassium (Ribeiro & Fernandes 2000, Benites et al. 2007, Chapter 1); similarly degraded areas are also characterized by extremely low potassium and phosphorus, except latosol degraded areas, which tend to have higher phosphorus content together with higher magnesium and calcium and pH less acidic. Whereas there is little fine sand in the degraded areas having a latosol substrate, we noted a higher proportion of clay and silt in these areas. These elements may be related not only to a higher capacity of nutrient retention, but also to a higher compaction of the soil, which is somewhat unfavorable to plant establishment. By contrast, the two other degraded areas (i.e. with stony and sandy substrates) presented a soil composition that as more similar to that of the reference grasslands. The higher proportion of silt was not linked to a general increase in nutritional content; on the contrary, lower nitrogen and organic carbon content were found to better characterize these soils.

The fact that vegetation composition of *campos rupestres* is highly related to soil composition (Ribeiro & Fernandes 2000, Chapter 1) might explain why the plant composition of the degraded areas appeared to be quite different from those of the reference grasslands. Depletion in N content may be a strong limiting factor. Negreiros et al. (2009) demonstrated that *campos rupestres* seedlings may grow in high fertility substrate conditions, even though such vegetation is adapted to low nutritional quality soils. However, modification of soil composition in the interest of re-establishing species-rich grasslands (Gough and Marrs 1990, Römermann et al. 2005) may be dangerous. Indeed, if soil nutrient content is improved, it could facilitate the establishment of non-native and/or ruderal species (Hobbs and Huenneke 1992, Shea & Chesson 2002, Hansen & Clevenger 2005, Barbosa et al. 2010).

Secondly, regeneration of reference *campo rupestre* grasslands from the seed bank is limited because their seed banks are poor in species and in seeds relative to other habitats, such as some nearby gallery forests (Medina and Fernandes 2007). In European grasslands, Bekker et al. (1997) noted that usually species associated with poor nutrient conditions were relatively scarce in the seed bank. Moreover, the severe five-month dry season can lead to unfavorable environmental conditions for seed bank formation; indeed, wetter sites typically record the largest number of seeds in mountain communities (Funes et al. 2001). The ability to form a seed bank seems to vary in *campos rupestres*: while some species appear not to form seed banks (Velten & Garcia 2007), others may form only a small persistent seed bank (Velten & Garcia 2007, Giorni 2009, Silveira 2011). The diminished seed banks might be associated with the low quantity of annuals, which are obligate seeder species, in *campos rupestres* where perennial species are dominant (Chapter 1). However, in German grasslands, Hölzel & Otte (2004) found large proportion of perennial species with a strong tendency for seed accumulation in the soil. In addition, the lower density of emergences could also reflect the large quantity of dormant seeds reported before for some *campo rupestre* species (Gomes et al. 2001, Silveira & Fernandes 2006, Garcia et al. 2011, Silveira et al. 2012a).

Eight years after the end of the disturbance, the seed banks of degraded areas are rich in species and seeds but mainly composed by non-target species (i.e. ruderal species), while target species, such as *Tatianyx arnacites, Lagenocarpus rigidus* subsp. *tenuifolius* or *Rhynchospora riedeliana* are absent although forming seed bank on reference grasslands. As previously discussed, *campos rupestres* species are not likely to form seed banks, and the type of the disturbance studied here (i.e. quarrying) does not leave much hope for the conservation of a seed bank. The absence of seeds from adjacent *campos rupestres s*uggests that the dispersion of these species to the degraded sites is limited. Both anemochory and autochory are the main dispersal modes in *campo rupestres* (Conceição et al. 2007a, Dutra et al. 2009). Sedges, common on *campos rupestres*, are known to have buoyant seeds (Leck & Schütz 2005) that are probably dispersed by rain and water runoff. Zoochory was also reported in Melastomataceae (Lima et al. 2013), but more studies are needed to assess the dispersion pattern in these tropical grasslands. Considering the poverty of *campos rupestres* species in the seed bank, it is clear that the use of bulk topsoil transposition (Ramsay 1986, Rokich, et al. 2000, Reis et al. 2003, Koch 2007, Rivera et al. 2012) would be limited to reestablish *campo rupestre* vegetation in degraded areas, however this could be useful to improve edaphic conditions.

4.2. Restoration using campo rupestre hay transfer

Our results have shown that hay transfer is not a successful means of restoring degraded areas of *campos rupestres*. The method, which proved effective in Europe (Hölzel and Otte 2003, Kiehl et al. 2010, Coiffait-Gombault et al. 2011), appears inapplicable to the present tropical context. More than one year after the beginning of the experiment, established vegetation on degraded sites was mainly composed by ruderal species, which had either germinated from the seed bank or had been dispersed from the ruderal species that were already established in these degraded areas. Though both hays contained large numbers of seeds, the hay from the stony grasslands contained relatively fewer seeds than the hay from the sandy grasslands. Because the vegetation in the degraded areas is very sparse, we believe that competition with ruderal species is not the reason why the grassland species that were contained in the hay were unable to establish themselves. There are several hypotheses that could be explain why vegetation composition in the degraded areas remained quite different from that in the reference ecosystems, among them: i) failure in seed germination (i.e. seed dormancy, unviable seeds, unfavorable germination conditions) and/or ii) unfavorable site conditions leading to poor seedling establishment.

Among the factors that may have hampered the success of the hay transfer, poor target site condition (such as soil nutrient status and moisture regime) is one that has already been pointed out (Hölzel & Otte 2003). The nature of the substrate also appears to be important in the present study. Low nitrogen and organic carbon content or higher pH, calcium and magnesium might explain why the seedlings did not establish. Soil structure can also limit seedling establishment since higher soil compaction, especially in degraded latosol substrates (i.e. high silt and clay content), can hamper root development (Dexter 2004). However, we noted that degraded stony substrate seems to offer better conditions to seedling establishment than other substrates. Stones have been shown to positively influence the surroundings of seedlings (Carlucci et al. 2011) in dry environments i) by increasing shade, thus reducing evaporation (Fowler 1988); ii) by allowing water condensation (especially on large stones), thus increasing soil moisture and microbial activity under stones (Lahav & Steinberger, 2001); iii) by enhancing soil moisture (Noy-Meir 2001).

The second hypothesis is that germination issues (i.e. unviable seeds, dormant seeds or unvaforable condition to germinate) might be responsible to the restoration failure (i.e. species composition and seed densities). Despite the fact that the hay contained a large number of seeds, we recorded few germination events in the reference grasslands where germination conditions were supposed to be optimal. This result could not have been due to competition with the native established vegetation because we recorded only one seedling under the controlled conditions of the greenhouse. Perennial resprouter species, common in Neotropical grasslands (Hoffman 1998, Neves et Conceição 2010, Fidelis et al. 2010), are expected to have fewer viable seed sets than nonsprouter species due to a likely higher genetic load among resprouters (Lamont & Wiens 2003). The limited soil resources and genetic predisposition of some species to use resources for structural components rather than for seed production have also been argued already argued to explain the poor seed quality (Meney 1997 cited in Leck & Schutz 2005). Besides the presence of unviable seeds in the hay, the presence of dormant seeds could also limit germination (Gomes et al. 2001, Silveira & Fernandes 2006, Garcia et al. 2011, Silveira et al. 2012a) to a degree similar to what could be expected from having unfavorable germination conditions to begin with. On reference sandy grasslands, the geotextile had a positive effect on seedling recruitment, while on reference stony grasslands germination occurrence was impacted negatively by both hay and geotextile. In these latter grasslands the vegetation is more open, so species may not be well adapted to the shade provided by the geotextile and the plant parts of the hay (Franco 2002). Indeed, the small-sized seeds of the herbaceous species of *campos rupestres*, such as Xyridaceae, are light demanding (Abreu & Garcia 2005, Oliveira & Garcia 2005). In degraded areas, it is mainly ruderal species that germinate, and the combination of hay and geotextile was found to have a generally negative effect on seedling recruitments. However, in these areas, quadrats with geotextile alone (i.e. without hay) recorded the highest number of seedlings.

5.Conclusion

We have shown that *campos rupestres*, species-rich mountain grasslands, are poorly resilient to anthropogenic disturbances, such as quarrying. The poor seed banks of the reference grasslands limit the use of only bulk topsoil transposition to re-establish *campo rupestre* vegetation; even if this could be suitable to improve edaphic conditions of the degraded areas. We have argued that soil alteration has prejudiced the establishment of native species while favoring ruderal and/or exotic species. In addition, the restricted dispersal of target species from *campos rupestres* serves to limit the recomposition of a seed bank and the establishment of *campo rupestre* communities in degraded areas. This implies that human intervention is absolutely necessary for rapidly re-establishing the main species. Although site conditions present a barrier (i.e. soil structure and composition) to vegetation establishment, the failure of seed to germinate seems to be the primary challenge to reintroducing target species by hay transfer or seeding. Indeed shade generated by hay and geotextiles may have hampered ruderal seed germination, but other factors related to germination (i.e. seed dormancy, unviable seeds, minimum temperature to germinate, etc.) could have frustrated our target species as well. This is why germination studies of the dominant species (Poaceae, Cyperaceae) are needed in order to understand germination behavior and limitation and to improve seeding success. In the meantime, other restoration techniques (such as seedling transplantation, turf transplantation) must be tested on these ecosystems. In conclusion, the protection of these grasslands must be made a high conservation priority.

Transition to Chapter 4

Chapter 3 shows that hay transfer is not a successful way to restore degraded *campos rupestres,* despite the large seed input. Several hypotheses are possible to explain this failure among which a possible germination issue. Successful restoration is often limited by the lack of information on how to reintroduce propagules, as well as the biology and ecology of these propagules; the establishment of target species requires knowledge of their germination behavior (Budelsky & Galatowitsch 1999, Leck & Schutz 2005). The restoration of some communities depends on the availability of viable seeds and non-dormant seeds; it also depends on suitable condition to germinate: some species germinating only under particular conditions (Leck & Schutz 2005).

We then assessed the germination behavior of some common species in *campos rupestres* (germinability and viability) as well as their response to fire-related cues. *Campos rupestres* are a fire prone environment which burns from time to time. In several fire-prone environments, fire was already pointed out as a factor enhancing germination (Keeley & Fotheringham 2000, Bond & Keeley 2005, Keeley et al. 2011). This has never been tested in *campos rupestres.*

Chapter 4

Vellozia variabilis. Photo credit S. Le Stradic

Chapter 4 - Diversity of germination strategies and dormancy of graminoid and forb species of *campos rupestres.*

Chapter 4 - Diversity of germination strategies and dormancy of graminoid and forb species of campos rupestres.

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Abstract:

In ecological restoration, the lack of information regarding the ecology and the biology of the target species hinders restoration actions. *Campos rupestres*, one physiognomy of the Cerrado, is a fire-prone environment, and the relationship between fire and germination is poorly understood for Cerrado species and is unknown for *campo rupestre* species. The aim of this work is to explore the diversity of germination strategies in the herbaceous communities of the *campos rupestres*. We also assess the germination of seeds produced immediately following a fire. Finally, we test whether seed dormancy evolved in species that shed seeds during unfavorable conditions for seedling establishment. Fifteen abundant species were selected, belonging to the Cyperaceae, Poaceae, Velloziaceae, Xyridaceae, and Asteraceae families. Seeds were subjected to various treatments (constant 25°C as control, temperature variations, heat, water, smoke, charred wood, and germination in *campo rupestre* soil), their germination behavior was studied, and viability tests were performed on ungerminated seeds. Additionally, seeds from four Cyperaceae and Poaceae species that produced seeds after an August 2011 wildfire were collected and germinated at 25°C. Our results showed that herbaceous species of *campos rupestres* have a wide range of germination strategies; some species belonging to the *Velloziaceae* and *Xyridaceae* families produce non-dormant, fast-germinating seeds, while species of Cyperaceae and Poaceae show an extremely low, or null, germination, due to a high proportion of unviable or embryo-lacking seeds. Moreover, our study found virtually no evidence that fire has a direct effect on seed germination in *campo rupestre* species; heat and charred wood did not promote germination while smoke enhanced the germination of only one grass species, *A. torta*, and improved the germination (MGT and synchrony) of Xyridaceae and Velloziaceae species. On the other hand, fire seems to have a positive effect on seed production: Cyperaceae and Poaceae both produce seeds rapidly following a fire and recorded high germination in this study. Finally, we have shown that some seeds are physiologically dormant and that seed dormancy has evolved at least five times in the studied herbaceous flora of *campos rupestres.* Our results suggest that herbaceous seed dormancy evolved independently of phylogeny. Seed dormancy and seed bank formation are essential to understanding herbaceous germination behavior as it applies to restoration projects aimed at improving vegetation establishment in disturbed areas.

Key-words: Fire-related cues, mountain grasslands, physiological dormancy, temperature, viability

1.Introduction

Two main factors can hamper natural succession in species-rich grasslands: (1) limitations in overall site condition and (2) the lack of target species from the seed bank or the seed rain (Bakker and Berendse 1999, Wilson 2002, Myers et al. 2009). To restore grasslands, several methods can be used to overcome the lack of seed sources on-site and the lack of seed dispersal, such as targeted sowing or hay transfer (i.e. the transfer of plant material containing diaspores) (Kiehl et al. 2010). Seed biology is among the key elements necessary for understanding community processes (such as plant establishment, succession, and natural regeneration strategies [Vásquez-Yanes & Orozco-Segovia 1993]), and for providing a theoretical framework for restoration. Seeds are essential to ensuring reproduction success and are under a strong selective pressure; without successful germination, establishment is not possible (Jurado & Moles 2002). On the other hand, a poor seed set in source communities and/or low seed viability are other factors that can impede community regeneration. Thus, the lack of information on the ecology and biology (e.g. the details of germination) of the main or target species hinders ecological restoration efforts.

The Cerrado, the Brazilian Neotropical savanna, originally covering c.a. 2.2 million km^2 or 23% of the country (Oliveira & Marquis 2002), is a species-rich and heterogeneous savanna composed by a mosaic of tropical grasslands, savannas and seasonal forests (Batalha et al. 2011). *Campos rupestres*, one of the Cerrado physiognomies, are species-rich grasslands established on quartzite-derived soils, found at altitudes of between 800m and 2000m, covering around 130 000km^2 (Barbosa 2012). They are a mosaic of stony and sandy grasslands, bogs along streams, and scattered rocky outcrops with sclerophyllous evergreen shrubs and sub-shrubs (Alves & Kolbek 2010, Carvalho et al. 2012, Chapter 1). They are constraint ecosystems occurring on shallow, highly acidic, and nutrient-poor soil (Benites et al. 2007, Chapter 1), and at the same time harboring a highly diverse flora with one of the highest levels of endemism in Brazil (Alves & Kolbek 1994, 2010, Giulietti et al. 1997, Echternacht et al. 2011). Like all savannas, *campos rupestres* are ecosystems subjected to recurrent fires (Simon et al. 2009), an essential factor controlling vegetation dynamic in savannas (Sarmiento 1984, Bond et al. 2005, Cochrane 2009). Miranda et al. (2002) and Simon et al. (2009) have argued that fire serves as an ecological determinant of the Cerrado by maintaining open vegetation physiognomies such as grasslands.

Fire can enhance plant populations or drastically damage them. In fire-prone environments plant community assemblages comprise species that are able to persist and/or to thrive in the face of repeated defoliation (Bond & Keeley 2005). These species can be classified as (1) fire-resistant, conserving part of their aboveground biomass; (2) sprouters, recovering after fire via vegetative regeneration; and (3) seeders, germinating from the seed bank or from newly dispersed seeds (Hoffmann 1998, Keeley & Fotheringham 2000, Pausas et al. 2004, Bond & Keeley 2005). Resprouting and fire-triggered seedling recruitment are among the most functionally important traits in fire-controlled environments (Bond & Keeley 2005). In the case of obligate seeders (species which are not able to resprout after fire), regeneration from seeds is the only way to subsequently recover from disturbances. The persistence of seeder species on a site depends on: (1) the ability to produce seeds during the inter-fire period, (2) seed survival during fires, and (3) the degree to which recruitment of new individuals is enhanced by fire (Pausas et al. 2004). Many species in fire-prone environments have some of their recruitment processes restricted to the first post-fire year (Bond & VanWilgen 1996) because they are stimulated by some fire factors. In such cases, germination is usually triggered by either heat or smoke (or charred wood), and an increase in above-ground temperatures and smoke production are the direct consequences of fire (Keeley and Fotheringham 2000, Bond & Keeley 2005).

The relationships between germination patterns and fire are well-documented in fire-prone environments in Spain (Gonzalez-Rabanal & Casal 1995, Pérez-Fernández & Rodríguez-Echeverría 2003, Crosti et al. 2006), in Australian (William & al. 2003, 2005) and African savannas (Gashaw & Michelsen 2002, Danthu et al. 2003, Dayamba et al 2008), in African *fynbos* (Keeley & Bond 1997), and particularly in California Chaparral (Keeley et al. 1985, Keeley 1987, Keeley & Fotheringham 1997, 1998, Keeley & Bond 1997). To the best of our knowledge, there is one known multi-species study (Ribeiro et al. 2012) dealing with heat shock effects on the seed germination of woody Cerrado species, but the effects of fire on the germination of herbaceous species, together with the effects of fire-related cues, remain quite elusive. In *campos rupestres*, germination has been studied for some of the species typical of these grasslands, such as Xyridaceae (Abreu & Garcia 2005, Giorni 2009, Carvalho 2012), Velloziaceae (Garcia & Diniz 2003, Garcia et al. 2007), Eriocaulaceae (Oliveira & Garcia 2005, 2011, Nunes et al. 2008, Schmidt et al. 2008), Fabaceae (Gomes et al. 2001, Silveira et al. 2005, Silveira & Fernandes 2006), Melastomataceae (Ranieri et al. 2003, Silveira et al. 2004, 2012, Garcia et al. 2006) and Asteraceae (Velten & Garcia 2005, Garcia et al. 2006). These studies mainly deal with the effect of light and temperature on germination, singling them out as the most important abiotic factors that control germination (Heschel et al. 2007), though no study has been carried out to verify the impact of fire on germination.

Seed dormancy is among the most important regeneration traits of a given ecosystem. Dormancy evolved in species/populations as a mechanism for preventing seeds from germinating under unfavorable conditions for seedling establishment (Linkies et al. 2010, Silveira et al. 2012a). Although there has been recent progress in understanding the germination of *campos rupestres* species, more study of dormancy and its geographic and phylogenetic distribution is needed in order to understand the dynamics of adaptive strategies in *campos rupestres* flora (Baskin & Baskin 2005). Seed dormancy in many woody flora taxa from the *campos rupestres* appears to be determined by phylogeny (Gomes et al. 2001, Silveira & Fernandes 2006), but the determinants of dormancy in *campos rupestres* herbaceous flora and the historical forces driving its evolution are essentially unknown (Garcia et al. 2011).

The aim of this work is to explore the diversity of germination strategies in the herbaceous and dominant communities of the *campo rupestre* flora. To accomplish this task we i) describe the baseline germination behavior at 25°C that would exist in nature, in the presence of temperature fluctuations and soil; ii) test the hypothesis that seeds respond positively to fire-related cues; iii) test the hypothesis that species producing seeds immediately after a fire experience more significant, faster, and more synchronic germination compared to regular pre-fire seeders; and finally iv) test the hypothesis that seed dormancy evolved in species shedding seeds during unfavorable conditions for seedling establishment.

2.Material and methods

2.1. Seed collection

Fifteen abundant species from *campos rupestres* were selected according to their importance value index (IVI), from a phytosociological study (Chapter 1), and seed availability. Our sample included five sedges, two grasses, four Velloziaceae, two Xyridaceae and two Asteraceae (Table 17). All species are perennial hemicryptophytes (except for *Vellozia variabilis* which is nanophanerophyte), have an abiotic dispersal mode, and occur in both sandy and stony grasslands (Figure 14). All species were to observed re-sprout after a fire (Chapter 1). Seeds were collected manually in 2010 from different populations and from randomly selected individuals in unburnt (for at least the past 5 years) areas in the Private Reserve Vellozia, Serra do Cipó (19°17 S; 43°33 W), in the southern part of the Espinhaço Range, Minas Gerais, Brazil. There, the climate is classified as Cwb, having a warm temperate, a cool dry season (from May to October) and a warm rainy season (from November to April), according to the Köppen system. The mean annual precipitation is 1622 mm and the annual temperature is 21.2°C (Madeira & Fernandes 1999).

To compare seed germination between pre-fire and post-fire conditions, seeds of four herbaceous plants were collected from recently burned (experienced fire in August 2011) *campos rupestres* (Appendix 5). Seeds from two sedges (*Bulbostylis emmerichiae* and *Bulbostylis paradoxa*) were collected on December 2011 and seeds from two grasses (*Homolepis longispicula* and *Paspalum pectinatum*) were collected in January 2012. Nearly 2 weeks after the fire, these plant species had already re-sprouted and produced flowers (Le Stradic, personal observation).

Table 17: Plant list with family, plant form, distribution range, period of dissemination, mean IVI in both sandy and stony grasslands and mean relative dominance in both sandy and stony grasslands (Chapter 1). Family: P: Poaceae, C: Cyperaceae, A: Asteraceae, V: Velloziaceae and X: Xyridaceae. Plant forms: F: Forbs, G: Graminoids, Ss: Sub-shrub. Distribution range (Giulietti et al. 1987, Forzza et al. 2010, database *SpeciesLink*: http://splink.cria.org.br/): (a) Serra do Cipó, (b) Espinhaço range in the state of Minas Gerais, (c) Espinhaço Range, (d) State of Minas Gerais, (e) Brasil, (f) Wide distribution. Dissemination period (Chapter 2): R: rainy season, RD: transition rainy to dry season, D: dry season, DR: transition dry to rainy season. Mean IVI and Mean relative Dominance (Chapter1).

					Mean IVI		Mean	
	Family	Plant form	Distribution range	Dissemination period	Sandy grasslands	Stony grasslands	Sandy grasslands	Stony grasslands
Aristida torta (Nees) Kunth	P	G	f	D	0,312	0,292	0,087	0,05
Echinolaena inflexa (Poir.) Chase	P	G	f	RD	1,174	0,25	0,407	0,06
Lagenocarpus alboniger (A.St.-Hil.) C.B.Clarke	C	G	c	DR	0,905	3,69	0,579	2,26
Lagenocarpus rigidus (Kunth) Nees subsp. *tenuifolius* (Boeck.) T.Koyama & Maguire	C	G	c	D & DR	20,72	5,029	12,83	2,69
Rhynchospora ciliolata Boeck	C	G	c	RD	2	0,143	1,226	0,06
Rhynchospora consanguinea (Kunth) Boeck	C	G	e	R	8,072	4,295	0,481	0,15
Rhynchospora riedeliana C.B. Clarke	C	G	c	RD	9,443	4,315	3,806	1,45
Lessingianthus linearifolius (Less.) H.Rob.	A	Ss	c	D	0,035	0,127	0,005	0,02
Richterago arenaria (Baker) Roque	A	F	b	RD	1,517	1,909	0,38	0,58
Vellozia caruncularis Mart. ex Seub.	V	F	b	R	0,544	9,369	0,384	6,13
Vellozia epidendroïdes Mart. ex Schult. & Schult.f.	V	F	b	DR or RD	7,721	5,761	4,435	2,71
Vellozia resinosa Mart.	V	F	d	DR	0,115	12,4	0,09	8,78
Vellozia variabilis Mart. ex Schult. & Schult.f.	V	F	f	D	0,343	0,794	0,284	0,57
Xyris obtusiuscula L.A.Nilsson	X	G	e	DR	5,453	11,26	1,25	1,21
Xyris pilosa Kunth	X	G	a	DR	1,736	7,267	0,39	1,07

2.2. Germination e*xperiments*

Seeds were set up to germinate under laboratory conditions. All seeds were monitored for 30 continuous days (Baskin et al. 2006) and they were checked for germination every 24 hours and were considered germinated upon radicule emergence. For the Poaceae, we used the entire diaspore without removing accessory structures such as lemma and palea (Baskin et al. 2006). We will henceforth refer to the achenes of the Asteraceae as seeds. Seed viability was assessed on all species through seed dissection procedures followed by a tetrazolium test on fresh seeds. Five replicates of 20 seeds were cut and placed in a 1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (TTC) for 48h under dark conditions in chamber at 25°C (Peters 2000).

Seeds were set to germinate in Petri dishes (five replicates of 20 seeds/treatment), covered with filter paper, and moistened with Nistatina® suspension to prevent the development of fungus. We assessed the effect of fluctuating temperatures, heat, smoke, charred wood and soil on seed germination. Seeds were placed in germination chambers kept at the constant temperature of 25°C (for the control group and the heat, smoke, charred wood, and soil treatment groups) or fluctuating temperatures of 15°C/25°C and 20°C/30°C based on a 12-hr photoperiod (with highest temperature corresponding to the daytime portion of the cycle). For the soil treatment, seeds were sown in a 1cm deep layer of soil that had been collected in the natural grasslands from randomly selected locations. We expected the soil, by retaining more water, to modify imbibition which is an essential prerequisite for germination. Seeds were exposed to 27 µmol m^{-2} s^{-1} light conditions because the small-sized seeds of the herbaceous species of *campos rupestres* are light-demanding (Abreu & Garcia 2005, Munné-Bosch et al. 2011, Oliveira & Garcia 2011).

For the heat treatment, heat shocks were used to air-dry seeds in an oven at 100°C for 5 minutes, prior to sowing (Keeley et al. 1985, Gonzãlez-Rabanal & Casal 1995, Keeley & Bond 1997). For the cold smoke treatment, smoke was obtained by burning leaves and stems of wood material and funneled by a hose into an otherwise pure water sample. Seeds were watered using a 1:10 diluted solution of this smoked water. For the charred wood treatment, seeds were watered with 10 ml of an aqueous suspension of charred wood (Gonzãlez-Rabanal & Casal 1995, Perez Fernandez & Rodriguez 2003). This suspension was obtained from the combustion of dried plant material collected in the grasslands in order to contain representative species of the *campos rupestres*. A starting biomass of 408 g was burned, resulting in 50g of charred wood, and sieved (2mm). The charred wood was diluted with distilled water to a concentration of 10 g of charred wood per liter of water.

2.3. Pre-fire vs. post-fire germination

Seeds of the four post-fire germinating species were set to germinate in Petri dishes (5 replicates of 20 seeds/species), covered withfilter paper, and moistened with Nistatina® suspension. Seeds were placed in germination chambers kept only at the constant temperature of 25°C based on a 12-hr photoperiod, and this can be considered the optimum conditions for germination in the *campos rupestres* (Abreu & Garci 2005, Garcia et al. 2007, Silveira et al. 2012a).

2.4. Evolutionary ecology of seed dormancy

In this study, seed dormancy is defined as the absence of germination in viable seeds that are subject to conditions that are favourable to germination (Hilhorst 2011). We used Baskin & Baskin's (2004) dormancy classification system and Baskin & Baskin's (2005) dichotomous key to determine seed dormancy classes. Physical dormancy implies that the seed/fruit coat is impermeable to water. To determine if diaspores were water impermeable, four replicates of 25 seeds (100 seeds for *Xyris*) were weighed on a digital balance before being soaked in tap water for 72h at room temperature and reweighed. Seed permeability was determined by the increase in seed mass between dried and soaked seeds (Silveira et al. 2012a).

To better understand the evolution of seed dormancy in the herbaceous flora of *campos rupestres*, we built a phylogenetic tree showing relationships among the studied taxa (Appendix 6). By having a phylogenetic hypothesis for the 15 species and the reconstruction of ancestral characters, we were able to make inferences on the evolution of seed dormancy (Forbis et al 2002, Silveira et al. 2012a). To determine whether seed dormancy evolved in species shedding seeds under conditions unfavourable to seedling establishment, we grouped species according to the seasonal peaks in seed dispersal: the rainy season (R - December to February), the rainy to dry transition season (RD - March-May), the dry season (D - June-August), and the dry to rainy transition season (DR - September-November), following chapter 2. The rainy-to-dry season and the beginning of the dry season were considered as unfavorable seasons for seedling establishment due to the relative scarcity of water.

2.5. Statistical analyses

For each replicate, we calculated final germination percentage, mean germination time (MGT) according to Labouriau (1983) and germination synchrony (*$\bar{E}$)* (Ranal & Santana 2006):

$$MGT = \sum_{i=1}^{k} n_i t_i / \sum_{i=1}^{k} n_i$$

where t_i is the time between the start of the experiment and the i^{th} observation, n_i is the number of germinated seeds at time *i* (not the accumulated number) and *k* is the last time of germination.

$$\overline{E} = -\sum_{i=1}^{k} f_i \log_2 f_i \text{ with } f_i = n_i / \sum_{i=1}^{k} n_i$$

where f_i is the relative frequency of germination, n_i is the number of germinated seeds on day *i* and *k* is final day of observation. Low $\overline{E}$ values indicate more synchronized germination and high $\overline{E}$ values indicate asynchronous germination.

For *A. torta, L. linearifolius, V. caruncularis, V. epidendroides, V. resinosa, V. variabilis, X. obtusiuscula*, and *X. pilosa* (other species showed low or no germination), the effect of the various treatments (25°C, 15°C/25°C, 20°C/30°C, soil, heat, smoke water and charred wood) on germination percentage were tested using GLM procedures employing a quasibinomial distribution and a logit link function. The same type of GLM was also used to study the effect of species on the percentage of viable and empty seeds. The effects of the treatments on MGT were tested using GLM procedures employing a gamma distribution and an inverse link function. To analyze $\overline{E}$, for each species, simple ANOVAs, followed by post-hoc tests (Tukey tests) were performed in which $\overline{E}$ was treated as the dependent variable with and treatment as the categorical predictor. Normality and homoscedasticity assumptions were checked and a square root transformation was applied wherever necessary (Sokal & Rohlf 1998).

To assess the differences in germination percentage between pre-fire vs. post-fire species as well as the differences between pre-fire vs. post-fire Poaceae and Cyperaceae species, GLM procedures were performed, again based on the quasibinomial distribution and logit link function, and germination percentage was treated as the dependent variable. The same sort of GLM analysis was also used to test the effect of species on germination percentage. For the effect of species on MGT, we turned to a gamma distribution and inverse link function based GLM analysis similar to what was used to analyse the relationship between MGT and treatment type. This time, for $\overline{E}$, simple ANOVAs, followed by post-hoc Tukey tests were performed with $\overline{E}$ treated as the dependent variable and species as categorical predictors. As before, normality and homoscedasticity assumptions were checked and a square root transformation was applied wherever necessary. The seed permeability study was analysed using paired t-tests to quantify the differences in biomass between dried and soaked seeds . All analyses were carried out in R version 2.9.1 (R Core Development Team, 2010).

3.Results

3.1. Intraspecific patterns of seed germination requirements

Seeds of *Echinolaena inflexa, Lagenocarpus alboniger, Lagenocarpus rigidus* subsp. *tenuifolius, Rhynchospora ciliolata, Rhynchospora consanguinea, Rhynchospora riedeliana* , and *Richterago arenaria* recorded low or null germination percentage irrespective of the treatment (Table 18). *Vellozia epidendroides, Vellozia resinosa* and *Xyris pilosa* experienced a germination percentage higher than 79% at 25°C, but the 15°C/25°C fluctuating temperature treatment had a negative effect on their germination (Table 18). *Xyris obtusiuscula*, which germinated around 30% at 25°C, recorded a lower germination percentage when subjected to the 20°C/30°C fluctuating temperatures (10%) (Table 18). Generally speaking, fluctuating temperatures had a negative overall effect on the MGT of all species (Table 19). The 20°C/30°C fluctuating temperatures increased the germination synchrony ($\overline{E}$) only for *X. pilosa* (Table 20). Soil had a negative effect on seeds of *Lessingianthus linearifolius, V. epidendroides,* and *V. resinosa*, decreasing the germination percentage (Table 18), but improved the MGT of *Vellozia variabilis* (Table 19). *Vellozia caruncularis* and *V. variabilis* had high germination percentage (always >75% and >88% respectively) no matter the treatment (respectively F=0.87, p=0.52 and F=1.75, p=0.14) (Table 18). Germination percentage of *Aristia torta* which was lower at 25°C, was not negatively or positively affected by any treatment (Table 18).

Table 18: Germination percentage (mean and standard error) for each species, according to each treatment. GLM procedures (with quasibinomial distribution) were performed for *Aristida torta, Lessingianthus linearifolius, Vellozia caruncularis, Vellozia epidendroides, Vellozia resinosa, Vellozia variabilis, Xyris obtusiuscula* and *Xyris pilosa*.

Species	25°C	15°C/25°C	20°C/30°C	Charred wood 25°C	Water smoke 25°C	Heat 25°C	Soil 25°C	GLM
Aristida torta	9.00 ± 2.10 ^{a}	5.00 ± 3.06 ^{a}	10.00 ± 3.95 ^{a}	7.00 ± 2.24 ^{a}	21.00 ± 6.94 ^{b}	1.00 ± 1.12 ^{c}	9.00 ± 4.81 ^{a}	F=3.45 **
Echinolaena inflexa	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	-
Lagenocarpus alboniger	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	-
Lagenocarpus rigidus subsp *tenuifolius*	0.00 ± 0.00	4.00 ± 2.10	1.00 ± 1.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	-
Rhynchospora ciliolata	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.12	0.00 ± 0.00	1.00 ± 1.12	0.00 ± 0.00	0.00 ± 0.00	-
Rhynchospora consanguinea	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.12	-
Rhynchospora riedeliana	0.00 ± 0.00	3.00 ± 2.24	1.00 ± 1.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	-
Lessingianthus linearifolius	41.00 ± 1.12^{a}	52.00 ± 5.18^{a}	33.00 ± 10.69^{a}	24.00 ± 4.11 ^{a}	25.00 ± 6.12^{a}	37.00 ± 10.69^{a}	7.00 ± 3.79^{b}	F=5.71 ***
Richterago arenaria	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.12	0.00 ± 0.00	0.00 ± 0.00	-
Vellozia caruncularis	84.00 ± 4.11	86.00 ± 6.22	80.00 ± 6.85	90.00 ± 3.95	82.00 ± 3.79	75.00 ± 6.37	86.00 ± 7.37	F=0.87 ^{NS}
Vellozia epidendroides	83.00 ± 3.79 ^{a}	32.00 ± 1.37 ^{b}	78.00 ± 7.20 ^{a}	9.00 ± 2.44 ^{c}	85.00 ± 3.06 ^{a}	85.5 ± 1.63 ^{a}	27.5 ± 6.79 ^{b}	F=48.80 ***
Vellozia resinosa	91.00 ± 3.01 ^{a}	37.00 ± 4.63 ^{b}	93.50 ± 1.12 ^{a}	90.00 ± 3.95 ^{a}	94.00 ± 4.47 ^{a}	86.00 ± 3.14 ^{a}	30.00 ± 5.86 ^{b}	F=43.28 ***
Vellozia variabilis	88.00 ± 3.35	90.00 ± 1.77	92.00 ± 2.85	97.00 ± 3.35	97.00 ± 2.24	96.00 ± 2.09	95.00 ± 2.50	F=1.75 ^{NS}
Xyris obtusiuscula	29.00 ± 8.95 ^{a}	28.5 ± 6.94 ^{a}	10.00 ± 2.34 ^{b}	2.00 ± 1.37 ^{c}	41.00 ± 8.91 ^{a}	27.00 ± 6.02 ^{a}	-	F=9.79 ***
Xyris pilosa	79.50 ± 5.03 ^{a}	28.5 ± 4.29 ^{b}	74.50 ± 5.55 ^{a}	15.00 ± 3.54 ^{c}	72.00 ± 7.20 ^{a}	71.00 ± 6.03 ^{a}	-	F=38.72 ***

Table 19: Mean germination time MGT in days (mean with standard error) for each species according to each treatment. GLM procedures (with Gamma distribution) were performed for *Aristida torta, Lessingianthus linearifolius, Vellozia caruncularis, Vellozia epidendroides, Vellozia resinosa, Vellozia variabilis, Xyris obtusiuscula* and *Xyris pilosa*.

	25°C	15°C/25°C	20°C/30°C	Charred wood 25°C	Water smoke 25°C	Heat 25°C	Soil25°C	GLM
Aristida torta	12.16 ± 1.34^{a}	22.66 ± 5.06^{b}	19.62 ± 3.25^{a}	16.12 ± 3.45^{a}	9.44 ± 1.09^{a}	6.00 ± 0.00^{c}	15.12 ± 3.84^{a}	F=3.45 ***
Echinolaena inflexa	-	-	25.00 ± 0.00	-	-	-	-	
Lagenocarpus alboniger	-	-	26.00 ± 0.00	-	-	-	-	
Lagenocarpus rigidus subsp *tenuifolius*	-	29.66 ± 0.28	30.00 ± 0.00	-	-	-	-	
Rhynchospora ciliolata	-	-	29.00 ± 0.00	-	20.00 ± 0.00	-	-	
Rhynchospora consanguinea	-	-	-	-	-	-	23.00 ± 0.00	
Rhynchospora riedeliana	-	23.75 ± 0.17	26.00 ± 0.00	-	-	-	-	
Lessingianthus linearifolius	5.99 ± 0.31^{a}	8.90 ± 0.64^{b}	8.15 ± 0.43^{c}	6.05 ± 0.16^{a}	6.59 ± 0.14^{a}	6.38 ± 0.43^{a}	5.20 ± 1.52^{a}	F=9.84 ***
Richterago arenaria	-	-	-	-	7.00 ± 0.00	-	-	
Vellozia caruncularis	5.28 ± 0.38^{a}	9.75 ± 1.26^{b}	7.24 ± 0.43^{c}	5.11 ± 0.59^{a}	5.02 ± 0.69^{a}	5.45 ± 0.52^{a}	4.05 ± 0.20^{d}	F=11.21 ***
Vellozia epidendroides	13.93 ± 0.68^{a}	23.87 ± 1.18^{b}	10.29 ± 0.71^{c}	13.26 ± 1.90^{a}	13.65 ± 0.38^{a}	10.33 ± 0.58^{c}	12.32 ± 0.79^{a}	F=20.30 ***
Vellozia resinosa	7.04 ± 0.40^{a}	21.02 ± 0.31^{b}	8.53 ± 0.55^{c}	7.96 ± 0.46^{c}	7.21 ± 0.30^{a}	7.91 ± 0.58^{b}	6.46 ± 0.12^{a}	F=93.86 ***
Vellozia variabilis	5.86 ± 0.38^{a}	7.94 ± 0.29^{b}	6.86 ± 0.54^{a}	6.04 ± 0.59^{a}	5.27 ± 0.39^{a}	5.77 ± 0.29^{a}	3.75 ± 0.26^{c}	F=13.30 ***
Xyris obtusiuscula	15.51 ± 0.29^{a}	15.17 ± 0.68^{a}	23.80 ± 1.45^{b}	13.00 ± 0.00^{a}	16.51 ± 1.91^{a}	15.10 ± 1.50^{a}	-	F=8.40 ***
Xyris pilosa	10.24 ± 0.44^{a}	17.77 ± 1.06^{b}	14.89 ± 0.87^{c}	10.76 ± 0.69^{a}	8.10 ± 0.80^{d}	10.55 ± 0.77^{a}	-	F=22.24 ***

Table 20: Germination synchrony (mean and standard error). Low values indicate more synchronized germination and high values indicate asynchronous germination.

	25°C	15°C/25°C	20°C/30°C	Charred wood 25°C	Water smoke 25°C	Heat 25°C	Soil 25°C	ANOVA
Aristida torta	0.40 ± 0.18	0.21 ± 0.18	0.31 ± 0.18	0.34 ± 0.20	0.75 ± 0.28	0.00 ± 0.00	0.50 ± 0.32	F=0.71 ^{NS}
Lessingianthus linearifolius	0.87 ± 0.16^{ab}	1.53 ± 0.14^{a}	1.23 ± 0.37^{a}	0.96 ± 0.17^{ab}	0.82 ± 0.13^{ab}	1.11 ± 0.21^{ab}	0.26 ± 0.26^{b}	F=3.54 *
Vellozia caruncularis	1.56 ± 0.08	1.87 ± 0.07	1.90 ± 0.21	1.53 ± 0.07	1.50 ± 0.20	1.60 ± 0.11	1.58 ± 0.06	F=1.96 ^{NS}
Vellozia epidendroides	2.57 ± 0.03^{a}	1.64 ± 0.06^{b}	2.16 ± 0.06^{ab}	1.10 ± 0.15^{d}	1.63 ± 0.06^{b}	2.24 ± 0.08^{ac}	1.90 ± 0.26^{bc}	F=18.50 ***
Vellozia resinosa	1.92 ± 0.07^{a}	1.98 ± 0.10^{a}	1.78 ± 0.10^{a}	0.96 ± 0.12^{b}	0.79 ± 0.10^{b}	2.21 ± 0.12^{a}	1.45 ± 0.09^{b}	F=32.50 ***
Vellozia variabilis	1.55 ± 0.04	1.69 ± 0.07	1.88 ± 0.09	1.52 ± 0.17	1.42 ± 0.16	1.57 ± 0.07	1.54 ± 0.08	F=2.29 ^{NS}
Xyris obtusiuscula	1.53 ± 0.14^{a}	1.62 ± 0.22^{a}	0.82 ± 0.29^{a}	0.00 ± 0.00^{b}	1.37 ± 0.17^{a}	0.99 ± 0.33^{a}	-	F=4.82 **
Xyris pilosa	2.22 ± 0.13^{a}	1.88 ± 0.19^{a}	1.14 ± 0.16^{b}	0.72 ± 0.10^{b}	1.13 ± 0.23^{b}	2.46 ± 0.06^{a}	-	F=24.60 ***

3.2. Effects of fire-related cues

A. torta presented higher germination percentage (21%) with smoke water while heat decreased its germination (1%) (Table 18). The heat treatment also decreased the MGT of *V. resinosa* but did not affect the other species (Table 18, Table 19, Table 20). No fire-related cues affected germination percentage of *L. linearifolius* (Table 18). Charred wood negatively affected the germination percentage of *V. epidendroides, X. obtusiuscula* and *X. pilosa*, but increased the MGT of *V. resinosa* (Table 18, Table 19). In addition, smoked water improved the MGT of *X. pilosa* (Table 19) and increased the synchrony ($\overline{E}$) for *V. epidendroides, V. resinosa* and *X. pilosa* (Table 20).

3.3. Viability

Species, such as *E. inflexa, L. alboniger, R. ciliolata,* and *R. arenaria* exhibited a seed viability rate of less than 10%. Seed viability of *A. torta, R. riedeliana, L. rigidus* subsp. *tenuifolius, R. consanguinea*, and *L. linearifolius* ranged from more than 10% to less than 42%, while seeds of Xyridaceae and Velloziaceae often had viability higher than 85% (GLM procedure F=75.81, p<0.001) (Table 21). Among the species with low seed viability, *E. inflexa, R. ciliolata, L. linearifolius, L. alboniger*, and *A. torta* also had many empty seeds (more than 50%; GLM procedure F=88.76, p<0.001) (Table 21). For the Xyridaceae and Velloziacaea, the percentage of empty seeds was close to 10%.

3.4. Pre-fire vs. post-fire germination

Species fruiting under pre-fire conditions (i.e. annual seeders) had germination parameters that contrasted significantly with those of species fruiting after fire occurrence. We found significant differences in all germination parameters between the two species pools. Overall, post-fire germination was characterized by higher germination percentage, low germination time, and higher synchrony (for germination percentage, GLM procedure with poisson distribution F=4.64, p<0.05, for MTG, GLM procedure with gamma distribution f=39.70, p<0.001 and for the synchrony, t-test t=-2.3, p<0.05, Appendix 7). Poaceae species flowering immediately after fire registered a higher germination percentage than Poaceae species flowering in the absence of fire (respectively 51.00% ± 9.58% and 4.50% ± 1.83%, GLM procedure, F=30.37, p<0.001). The same pattern could be observed for Cyperaceae species for which germination percentages were improved for species flowering immediately after the fire than for species flowering without fire (respectively 76.50% ± 5.61% and 0.00% ± 0.00%, GLM procedure, F=600.85, p<0.001). Among species fruiting after fire, *Homolepis longispicula, Bulbostylis emmerichiae*, and *Bulbostylis paradoxa* germination percentage were higher than 75%, while *Paspalum pectinatum* registered lower germination (Figure 36). The two grasses *H. longispicula* and *P. pectinatum* had the shortest MGT in comparison with the other species (Figure 36). The two sedges, *B. emmerichiae* and *B. paradoxa*, also presented a low MGT equivalent to those of *L. linearifolius*, *V. caruncularis*, *V. variabilis*, and *V. resinosa* (Figure 36).

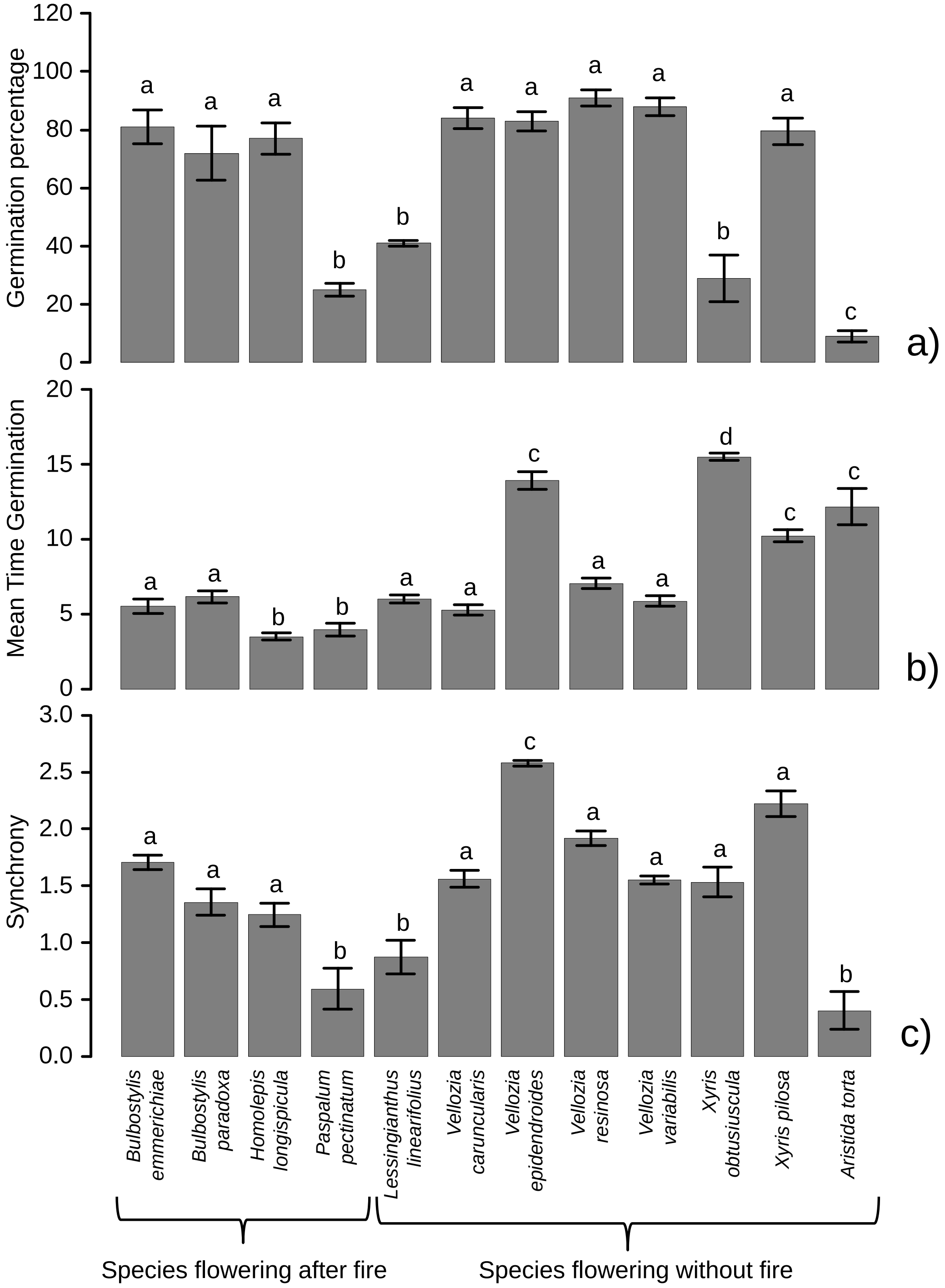

Figure 36: Germination percentage (%) (a), Mean germination time (b) and synchrony (c) at 25°C, for species which flower immediately after fire and species which flower without fire. Letters indicate significant difference according (a) GLM procedure (quasibinomial error distribution and logit link function) with F=25.43, p<0.001, (b) GLM procedure (Gamma error distribution and inverse link function) with F=52.78, p<0.001, (c) simple ANOVAs, followed by post-hoc tests (Tukey's "Honest Significant Difference") F=31.70, p<0.001).

3.5. Evolutionary ecology of seed dormancy

The seeds from eight of the 15 species showed germination percentages lower than 10% under conditions that are suitable for germination. However, *E. inflexa*, *L. alboniger*, *R. ciliolata*, and *R. arenaria* produced high percentages of unviable seeds and embryoless seeds (Table 21). Thus, for these four species, lack of germination is attributed to low seed quality, as opposed to seed dormancy. Dormant seeds of *A. torta*, *L. rigiddus*, *R. consanguinea*, and *R. riedeliana* in percentages ranged from 68 to 100% (Table 21). Although 29% of *X. obtusiuscula* seeds germinated, nearly 57% of viable seeds did not germinate (Table 21). The seeds of all five species were therefore considered dormant.

Table 21: Viable, empty and dormant seeds (mean percentage and standard error) for each species. Dormant seeds were calculated as the final germination percentage over the total number of viable seeds. ND: non-dormant seeds.

Species	Viable seeds (%) (mean ± se)	Empty seeds (%) (mean ± se)	Dormant seeds (%)
Aristida torta	28.00 ± 3.79	55.00 ± 5.00	67,9
Echinolaena inflexa	0.00 ± 0.00	13.52 ± 2.45	ND
Lagenocarpus alboniger	7.00 ± 1.37	54.00 ± 4.11	ND
Lagenocarpus rigidus subsp. *tenuifolius*	38.00 ± 3.47	14.50 ± 3.11	100
Rhynchospora ciliolata	5.00 ± 1.77	80.00 ± 2.50	ND
Rhynchospora consanguinea	39.50 ± 5.75	0.50 ± 0.56	100
Rhynchospora riedeliana	30.00 ± 4.68	37.00 ± 2.24	100
Lessingianthus linearifolius	41.00 ± 1.12	57.00 ± 1.37	ND
Richterago arenaria	1.00 ± 1.11	84.00 ± 4.47	ND
Vellozia caruncularis	86.00 ± 4.47	11.00 ± 5.70	ND
Vellozia epidendroides	89.50 ± 2.98	6.50 ± 2.27	ND
Vellozia resinosa	93.50 ± 2.44	3.00 ± 1.37	ND
Vellozia variabilis	89.00 ± 3.26	2.00 ± 2.23	ND
Xyris obtusiuscula	67.00 ± 2.85	3.00 ± 1.37	56,7
Xyris pilosa	89.50 ± 4.79	1.50 ± 0.68	ND

The increase in seed weight after soaking in tap water ranged from 6.2 to 217%. This increase in seed weight was significant for all studied species, except *X. pilosa* (Appendix 8), meaning that all species produce water-permeable seed coats. Mature seeds of the five dormant species produced differentiated embryos; these seeds are therefore considered physiologically dormant (PD).

Based on the reconstructed phylogenetic tree of the studied species, non-dormant seeds were assumed to be the ancestral condition and PD seems to be a derived character that was selected for several times throughout the evolution of the herbaceous flora of *campos rupestres* (Figure 37). We did not to find significant relationship between seed dormancy and the peak of seed dispersal (X^2=0.3, p= 0.6) or between seed dormancy and the amplitude of seed dispersal (X^2=0, p= 1). We thus conclude that seed dormancy is unrelated to dispersal phenology.

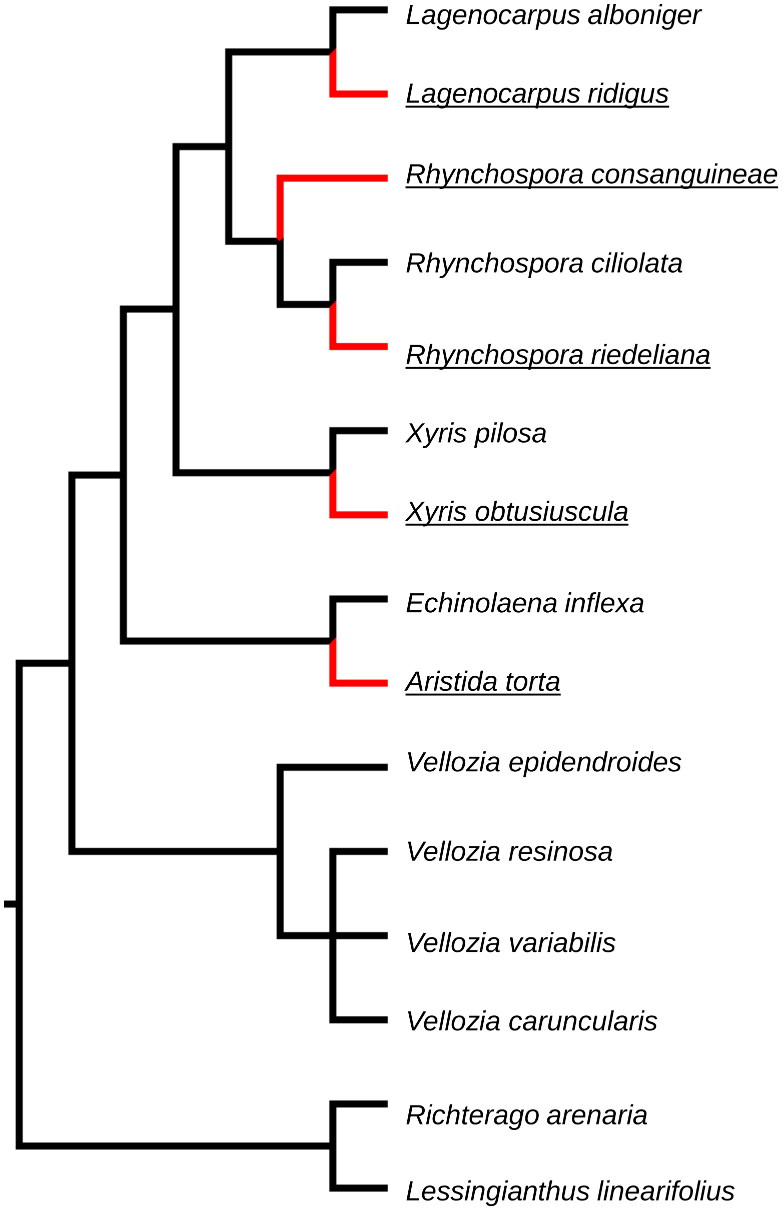

Figure 37: Reconstructed phylogenetic tree of the fifteen species studied, species with dormant seeds are underlined.

4.Discussion

The results of our study show that graminoid and forb species of *campos rupestres* have evolved into a great diversity of life histories represented by a variety of seed germination behaviors. There is clear difference in germination strategies among species: *Vellozia* and *Xyris* species produce non-dormant, fast-germinating seeds, other species produce dormant seeds, while species of Cyperaceae and Poaceae showed extremely low or null germination.

Fluctuating temperatures had an overall negative effect on germination percentage and tended to increase the mean germination time of most species. It has already been demonstrated that cold temperatures (<20°C) have an unfavorable effect on the germination of Xyridaceae and Velloziaceae species (Abreu & Garcia 2005, Garcia et al. 2007). On the other hand, studies of species from Cerrado or *campos rupestres*, show that alternating temperatures enhance the germination of some species, such as *Syngonanthus elegantulus* Ruhland, *S. elegans* (Bong.) Ruhland, and *S. venustus* Silveira (Oliveira and Garcia, 2005), but either decreased or had no effect on the germination of species such as *Eremanthus elaeagnus* (Mart. ex DC.) Schultz-Bip, *E. glomerulatus* Less, *E. Incanus* (Less.), Less. (Velten and Garcia, 2005), and Melastomataceae sp. (Carreira and Zaidan, 2007). In addition, Souza (2010) observed that fluctuating temperatures of 20-35ºC and 20-40ºC increased the germination of *Lagenocarpus rigidus.* The closed species in our study, *L. rigidus subsp. tenuifolius,* and the other Cyperaceae, such as *L. alboniger, R. ciliolata,* and *R. riedeliana,* also experienced some germination under fluctuating temperatures (<5%), but had no germination under any of the other treatments. Indeed, among the 15 species tested, 7 had only sporadic germination. Pearson et al. (2002) showed that alternating temperatures favor germination in tropical large-seeded pioneers, whereas we have small-seeded non-pioneer species whose grassland habitats have only been stable for c.a. 20 000 year (Barbosa 2012). For these small-sized seeds, light is probably a more reliable cue of favorable conditions for establishment than alternating temperatures. Since most small-sized seeds lack the reserves needed to germinate under burial conditions (Milberg et al. 2000), it is very likely that photoblastism evolved independently in the lineages of small-sized species from *campos rupestres* (Abreu & Garcia 2005, Garcia et al. 2007, Oliveira & Garcia 2011, Silveira et al 2012). The seeds of *A. torta, L. linearifoilus*, all *Vellozia sp*., and all *Xyris sp*. that we have studied are non-dormant, do not exhibit integument inhibition, and germinated without treatment or scarification. We propose that low temperature, rather than fluctuating temperature, is what is most responsible for decreasing germination percentage, indicating that these species probably do not germinate during the dry season when temperatures are cooler.

The rigors of the environment will be of great significance to seeds germinating under natural conditions (Harper & Benton 1966). When a dry seed enters the soil, imbibition occurs prior to germination: a seed must absorb a certain amount of water to germinate, the critical hydration level being species-specific (Hadas & Russo 1974). Water imbibition is crucial to the germination of species, especially *L. linearifolius, V. epidendroides* and *V. resinosa* suggesting consequently that these species need an important water supply to germinate, and this is provided only during the rainy season. Unlike filter paper, soil modifies moisture and water potential, delaying or inhibiting water imbibition and therefore germination. Harper & Benton (1966) demonstrate that a seed sown on a substrate germinates only if it absorbs water from that substrate more rapidly than it loses it to the atmosphere; for this to occur, the seed must make good contact with the available water, the tension on the water must be relatively low, or the surrounding atmosphere must be moist. These conditions may not have all existed simultaneously in our germination chambers. Water supply is thus an important factor in *campo rupestre* species germination.

Among the fire-related cues tested, heat, which is a direct effect of fire (Keeley and Fotheringham 2000), had a negative effect on the germination of *A. torta,* but did not have any significant impact on the other species. Heat-shock-stimulated germination is common in Fabaceae, Malvaceae, or Convolvulaceae, which have hard water-impermeable seed coats. Heat-stimulated seeds exhibit physical dormancy imposed by a dense palisade tissue (Keeley and Fotheringham 2000, Ribeiro et al. 2012); heat disrupts this tissue, resulting in increased water permeability, but this may not be the case for *A. torta*. All of the species we studied have water-permeable seed coats to begin with, and they do not evolve towards physical dormancy. In the *campos rupestres,* heat-shock stimulated germination may be restricted only to those clades/species where physical dormancy has occurred (Gomes et al. 2001, Silveira & Fernandes 2006). In addition, although the seed coats of these species are permeable, heat does not prejudice germination, indicating that our species are fire-tolerant, like those from other fire-prone grasslands in southern Brazil (Overbeck et al. 2005, Overbeck & Pfadenhauer

2007).

On the other hand, germination might be stimulated chemically by smoke or charred wood in fire-prone habitats. Charred wood effects are probably chemically-mediated, however the particulary chemical compounds in charred wood that enhance germination remain unknown (Keeley 1987, Pérez-Fernández & Rodríguez-Echeverría 2003). Unlike the species from Mediterranean-like ecosystems, our results show that charred wood inhibits or decreases the germination of seeds of *X. pilosa, X. obtusiuscula, V. epidendroides,* and *V. resinosa* while smoked water had a positive effect on the mean germination time and/or the germination synchrony of these species, and increased the germination of *A. torta*. Smoke does not change imbibition ability (Keeley & Fotheringham 1997, 2000), however the seed-coats of smoke-stimulated species are intrinsically structurally quite different from those of heat-stimulated species: (1) the outer seed coats are highly textured, (2) the outer cuticle is poorly developed, (3) the dense palisade tissue in the seed coat is lacking, and (4) the subdermal membrane is semi-permeable, allowing water passage but blocking the entry of larger solutes (Keeley and Fotheringham, 1998). Smoke must therefore change the characteristics of this semi-permeable subdermal cuticle and allows the diffusion of solutes that would otherwise be blocked (Keeley and Fotheringham 1997). Keeley & Fotheringham (1997, 2000) hypothesized that the strongest and the most consistent compounds responsible for triggering germination through smoke were nitrogen oxides. Recently, a butanolide compound (karrikinolide) was designated as the chemical compound present in the smoke responsible for either triggering germination or for breaking seed dormancy (Flematti et al. 2004, Bradshaw et al. 2011a, Long et al. 2011a, Keeley et al. 2011).

In this study, smoke-induced germination was observed only in *A. torta*. Smoke also decreased the mean germination time and increased germination synchrony in most studied species. It was has been independently demonstrated that a vast array of species responds to butanolide, including species occurring in non-fire-prone environments (Long et al. 2011a,b). Bradshaw et al. (2011a) therefore suggest that organic matter decay, rather than fire, was the primary force in the development of smoke-mediated germination and that this trait probably developed early in the evolution of angiosperms. However this point is controversial (Keeley et al. 2011, Bradshaw et al. 2011b), since 1) the evolution of angiosperms are suspected to be related to novel fire regimes during the Cretaceous (Bond & Scott 2010); and 2) the spread of grasslands and savannas was promoted in part by fire later (Bond et al. 2003). We therefore suppose that fire was a strong selective pressure in *campos rupestres*.

In the Mediterranean region, smoke and charred wood effects are similar, both increasing germination (Keeley & Fotheringham 1998, Pérez-Fernández & Rodríguez-Echeverría 2003). In our case, effects of charred wood and smoke are antagonistic. A first hypothesis might be that the chemical compounds produced by smoke and charred wood are different and so behave differently. A second hypothesis is that some seed responses require the combination of heat and smoke application, so that only the interaction of both stimuli can affect germination (Thomas et al. 2003, 2007). A third hypothesis is that our seeds need time to become sensitive to fire-related cues (Long et al. 2011a,b). The fourth, according to Bradshaw et al. (2011a), is that seed germination triggered by smoke is not a fire-adapted plant trait and our species do not present fire-related cues for germination; it is rather quite the opposite, since charred wood significantly inhibits or decreases the germination of some of our seeds.

Therefore, our study has highlighted the point that species from *campos rupestres* exhibit different behaviors, when faced with fire, from those of species in other fire-prone environments, such as the Mediterranean ecosystems, where some species are very sensitive to fire-related cues (Keeley et al. 1985, Keeley & Fotheringham 1997). Mediterranean vegetation seems to have expanded in the late Tertiary under tropical conditions, while its origin is usually attributed to the onset of Mediterranean-type climates during the Quaternary (Verdú et al. 2003). Pausas & Verdú (2005) noted that in the Mediterranean basin, resprouter species correspond to older lineages (Tertiary), and non-resprouters (i.e. seeders) to younger lineages occurring during the Quaternary under Mediterranean conditions. Thus, Mediterranean species present variable behavior in response to fire-related cues (Crosti et al. 2006) and consequently, in such areas, resprouting is not the only way to recover after a disturbance, much unlike *campos rupestres*. Indeed our results did not show many direct effects of fire on germination, despite the fact that all these species occur in a fire-prone environment, suggesting then that sprouting is the predominant mechanism for recovering after fire.

In Brazil, the large presence of resprouters has already been noted in open vegetation (Hoffman 1998, Overbeck & Pfadenhauer 2007); after fire, resprouting provides persistence in the environment as an alternative to seedling establishment (Hoffmann

1998, Fidelis et al. 2010). Sexual regeneration of species occurring in fire-prone environment is disadvantaged by recurrent burnings because seed supply is reduced; this is why vegetative reproduction may increase under frequent fire regimes (Setterfield 2002, Hoffmann 1998). Resprouting improves fitness in fire-prone environments only if self-replacement is unlikely when the parent dies (i.e. production of few seeds), or if post-fire conditions for seedling recruitment are unfavorable or unpredictable (Enright et al. 1998). However, due to the variety of germination behaviors (Crosti et al. 2006), the lack of knowledge is a significant limitation to drawing overall conclusions since some species, which were not tested, may actually have their germination enhanced by fire. Moreover, the differential effect of charred wood and smoked water suggest that smoke may stimulate germination of the seed bank from surrounding populations. Smoke may also favor the flowering of the surrounding population (Lamont & Downes 2011).

Our results also indicate that some species, such as *R. ciliolata* or *R. arenaria*, produce many well-developed embryoless seeds or unviable seeds, such as in *L. rigidus subsp. tenuifolius, R. consanguinea*, or *R. riedeliana*. This pattern seems to be common in Cyperaceae, Asteraceae, and Poaceae from other vegetation-types (Overbeck & Pfadenhauer 2007). All the studied species are resprouters (personnal observation). Low fecundity among resprouters in comparison to nonsprouters has already been noted (Lamont & Wiens 2003, Lamont et al. 2011). Three mechanisms have been suggested to explain these trends: resource limitation, breeding system limitation, and the genetic load (Lamont & Wiens 2003). According to these authors, resource limitation could explain the low seed set but does not explain the lower viability of intact seeds. Lamont & Wiens (2003) point out that there is no evidence that resprouters are always outbreeders with self-incompatibility. Finally, it has been suggested that this trend could better be explained by a high genetic load of resprouters in association with strong self-incompatibility. Deleterious somatic mutations accumulate over successive disturbance events and they could be shared when outcrossing occurs between parents; since most mutations are harmful, this gradually leads to poor fruit and seed set as the plant ages (Lamont & Wiens 2003, Lamont et al. 2011).

Sometimes, resprouters can be pollen-limited (Anderson & Hill 2002). In our case we showed that the pre-fire flowering Cyperaceae and Poaceae, which are wind-pollinated, have large numbers of unviable seeds while Velloziaceae and Xyridaceae, which are animal-pollinated, had high seed viability. However, Asteraceae species, although animal-pollinated, registered low germination,and had many empty seeds. More studies are needed to understand the low viability observed in common species of *campos rupestres*.

In fire-prone grasslands, plant species could be classified into two groups according to survival after fire: (1) the sprouters/resprouters which are able to regrow after fire from belowground organs and (2) the seeders which germinate after fire from the seed bank or from newly dispersed seeds (Hoffman 1998, Lamont & Wiens 2003, Pausas et al. 2004, Pausas & Verdú 2005). The 15 studied species (representing the Xyridaceae, Velloziaceae, Asteraceae, Poaceae, and Cyperaceae families), collected in areas unburnt for at least the past 5 years, belong to the first group: all resprouted after fire and there was little evidence that their seed germination is enhanced by fire. On the contrary, the non-sprouters are commonly called obligate seeders, because their establishment from seed germination is the only way they can recover. *H. longispicula, P. pectinatum, B. paradoxa* and *B. emmerichiae*, whose seeds we collected after a fire, also belong to the first group (resprouters) since they are able to re-establish rapidly by resprouting after fire. Interestingly, they also produced viable seeds after the fire, resembling the seeders, but this may indicate that the ultimate role of seeds for these resprouters might be dispersal rather than recovery. Indeed, we found Poaceae and Cyperaceae, which were collected in unburnt areas and which had a lower or null germination rate, Poaceae and Cyperaceae species collected just after fire recorded a high germination percentage with lower mean germination time. To produce, lot of flowers just after fire favors outcrossed breeding that ensures vigorous seedlings with a wide habitat tolerance (Lamont & Wiens 2003). Moreover fire decreases competition and increases resource availability (i.e. water, nutrients, light, and space); the strategy of producing seeds only after fire improves the chance of establishment of these seeds. Thus, Lamont et al. (2011) noted that a superior fitness lies with those resprouters that have high levels of vegetative recovery, and retain the ability to produce seeds since this gives greater adaptive flexibility.

Finally some species, such as *A. torta, X.obtusiuscula, L. rigidus* subsp*. tenuifolius, R. consanguinea* or *R. riedeliana*, had some viable seeds which did not germinate, therefore leading to the conclusion that they are dormant. Seeds of these species presented water-permeable seed coats and well-developed, differentiated embryos. Therefore, seeds of the five dormant species (one third of total species) are physiologically dormant (Baskin & Baskin 2005). Physiological dormancy occurs in the vast majority of species of sedges (Leck & Schutz 2005) and grasses (Baskin & Baskin 2000), but there were no reports on primary dormancy in the Xyridaceae (despite secondary dormancy has been recently reported in *Xyris*; Garcia et al. 2011). Seed dormancy in temperate grasses is widely recognized (Baskin & Baskin 2000) as a consequence of a chemical inhibition or mechanical resistance of glumes, lemmas and palea (Gasque & García-Fayos 2003, Baskin et al 2006, Ma et al. 2010). Since different classes of dormancy require different methods of dormancy breaking (Hilhorst 2011), the determination of the dormancy class is important in providing the grounds for dormancy overcome and use of native species in the restoration of the *campos rupestres*.

By assuming that nondormant seeds comprise the ancestral state, we have been able to show that seed dormancy evolved at least five times in the herbaceous flora of *campos rupestres*. Physiologically dormant and nondormant seeds are distributed over the entire phylogenetic tree of gymnosperms, basal angiosperms, and eudicots. Linkies et al. (2010), therefore, have proposed that the gain and loss of physiological dormancy likely occurred several times during the evolution of flowering plants. To the best of our knowledge this is the first record of primary dormancy in sedges, grasses, and xyrids in tropical mountain grasslands (Leck & Schutz 2005, Garcia et al 2011).

The evolution of seed dormancy was independent of phylogeny, indicating several and independent origins, thus lending support to the hypothesis of convergent evolution of physiological dormancy. Seasonality seems to drive seed dormancy in temperate sedges (Leck & Schutz 2005), though we did not find a correlation between seed dormancy with dispersal phenology, species geographic distribution, or any life-history trait. Our nondetection of a correlation between dormancy and life-history traits may actually be due to the small sample size (15 species). Hence, it is difficult to infer the selective pressures that drive the evolution of dormancy. Further studies on the evolution of seed dormancy, particularly if they include a large number of additional species, will be needed in order to obtain a practical framework in which the relationship between seed dormancy and species life-history can be broadly tested (see Silveira et al. 2012a).

5.Conclusion

Our results have demonstrated that herbaceous species of *campos rupestres* exhibit a wide range of germination strategies; some species, belonging to the *Velloziaceae* and

Xyridaceae families, produce non-dormant, fast-germinating seeds, while species of Cyperaceae and Poaceae show extremely low, or null, germination. Moreover, while heat and charred wood do not promote germination, smoke enhances the germination of one grass, *A. torta*, and improves the germination (MGT and synchrony) of Xyridaceae and Velloziaceae species. Smoke as a fire-related cue remains a controversial topic. Our study shows almost no evidence that fire has a direct effect on seed germination of *campo rupestre* species. Regeneration after fire occurs preferentially by re-sprouting. Poaceae, Cyperaceae (with a pre-fire flowering) and Asteraceae species, although they represent the most abundant family of *campos rupestres*, were characterized by low germinability and high amount of unviable or embryoless seeds contrary to Xyridaceae and Velloziaceae. Low seed set could be explained by genetic load. On another hand fire could have a positive effect on seed production: some Cyperaceae and Poaceae resprouted and produced seeds rapidly after the fire. Such seeds had fast and high germination suggesting that these resprouters species are able to produce viable seeds in order to establish rapidly in newly available microsites. Moreover we showed that some seeds are physiologically dormant and that seed dormancy evolved at least five times in the studied herbaceous flora of *campos rupestres.* Our results suggested that evolution of these herbaceous seed dormancy was independent of phylogeny while seed dormancy in many woody flora taxa from the *campos rupestres* appears to be determined by phylogeny (Gomes et al. 2001, Silveira & Fernandes 2006). This suggests that the ecological and historical forces driving the evolution of seed dormancy differ in the woody *vs.* herbaceous flora. Understand herbaceous germination behavior, seed dormancy and seed bank formation is now essential in order to extent restoration project and improve vegetation establishment in disturbed areas.

Transition to Chapter 5

In chapter 4, we reported that some species had high germinability, such as Velloziaceae or Xyridaceae, while others, such as Cyperaceae or Poaceae, representing an important family in these grasslands, have embryoless, non viable or dormant seeds. This hampers considerably the potential to use them to restore degraded areas, since both low germinability and low viability limit the value of direct seeding. Germination therefore seems to be a key issue to restore *campo rupestre* grasslands. However without knowledge on the germination behavior of most of the herbaceous species and faced with the difficulty to obtain seedlings from the main species from seeds, it is necessary to find other ways to reintroduce target species (Figure 38). In the next chapter (chapter 5) we tested the translocation of eight species (accessory technique to increase target species according to Török et al. 2010) as well as the translocation of vegetation turfs on degraded areas in order to restore the sandy and stony grasslands (Figure 38).

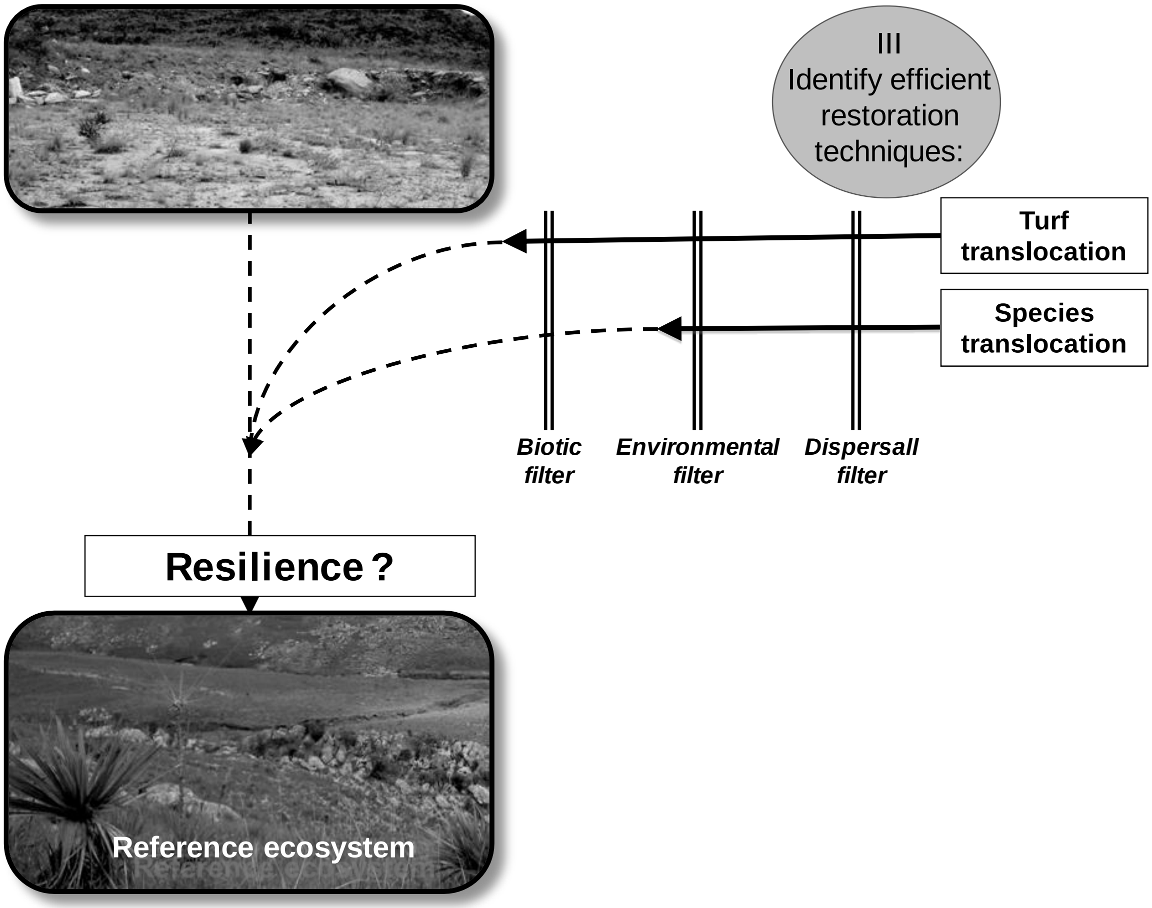

Figure 38: The objective of the fifth chapter is to test whether species and turf translocation are efficient techniques to restore *campos rupestres.* Both techniques aimed to overcome the dispersal filter. Using species translocation we expected to overcome the critical phase of the establishment in the degraded areas and to improve environmental conditions bringing together soil and translocated plant. Using turf translocation, we aimed to bring to the degraded areas i) a pool of target species, ii) soil of the reference ecosystem and iii) possible associated microorganisms (Carvalho et al. 2012); overcoming therefore the environmental filter and a part of the biotic filter.

On top : turf translocation,
at right : *Paspalum erianthum* translocation
Photo credit S. Le Stradic

Chapter 5 - Restoration of *campos rupestres:* species and turf translocation as techniques for restoring highly degraded areas.

Chapter 5 - Restoration of campos rupestres: Species and turf translocation as techniques to restore highly degraded areas.

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Abstract:

The restoration of highly degraded sites usually cannot rely on natural succession. Because site conditions and dispersal are common limiting factors, ecological restoration requires active re-introduction of native species. Species and turf translocation can be a suitable method for ensuring that the desired range of species is introduced and that the issues affecting seedling establishment are overcome. In order to test these two techniques, i.e. species and turf translocation, as possible methods for the restoration of Neotropical grasslands, two experiments have been carried out. Firstly, eight herb and forb species dominant in the reference grassland ecosystems were translocated from a donor site to a degraded area with sandy substrate and to a reference sandy grassland (as a control). Two translocation periods were tested: the end of the rainy season (in March 2011) and beginning of the rainy season (in November 2011). In one of the treatments we varied the nutrient levels between the following 2 alternatives: NPK 10.10.10 and no added fertilization. Survival and growth of translocated plants were recorded every three months over a 1 year period. Among the eight transplanted species only one, the grass *Paspalum erianthum,* survived, grew and produced flowers. Mortality of the other species was high, probably due to the trauma of transplantation, and it was also shown that nutrient supply had a negative impact. In a second experiment, turf translocation was tested in degraded areas with sandy and stony substrates. Translocation was carried out according to the following two schemes: 1) turfs from reference sandy grasslands were transferred onto a degraded area with sandy substrate having two different 10-cm-deep turf sizes: 40x40cm and 20x20cm (n=8); 2) 10-cm-deep turfs of 20x20cm from reference sandy and stony grasslands were transferred to the stony degraded soil (n= 8). This restoration method allows the introduction of native species on the degraded areas: although the number of translocated individuals decreased during the first 3 months, it stabilized afterwards. Transplantation of large turfs makes it possible to introduce a greater number of species, and this means that a potentially bigger species source becomes available to colonize degraded areas. Turf translocation should only be used with the understanding that the extant plant communities from which donor material is drawn will be irreparably sacrificed because donor sites generally have poor resilience.

Key-words: grassland restoration, herbaceous species, re-introduction, species translocation, turf translocation.

1.Introduction

Quarry activities are harsh degradations. They fragment landscapes, strongly alter abiotic conditions, and destroy internal species pools (Bradshaw 2000). As a result, the ecological restoration of sites degraded in this way mainly depends on restoring adequate abiotic conditions and dispersing seedsl from surrounding sites (Bradshaw 1997, Campbell et al. 2003, Shu et al. 2005). In such cases, a first step usually consists of returning some soil that contains few or no undesirable species. Following that, restoration usually cannot rely on natural succession, because of the limited potential of seed dispersal, which is severely handicapped as a result of landscape fragmentation (Ash et al. 1994, Bakker et al. 1996, Bradshaw 1997, Bakker and Berendse 1999, Shu et al. 2005, Kiehl 2010), and/or because environmental conditions are unfavorable to seedling establishment (Ash et al. 1994, Yuan et al. 2006). Active dispersion is therefore needed to accelerate grassland colonization by target species (Hutchings & Booth 1996, Bischoff 2002, Kiehl et al. 2010, Chapter 3).

Depending on the level of degradation, restoration interventions may include seed addition (Cooper & MacDonald 2000, Turner et al. 2006, Kirmer et al. 2012, Ballesteros et al. 2012), native species transplantation (Ash et al. 1994, Fattorini 2001, Krautzer & Wittmann 2006, Menges et al. 2008, Kiehl et al. 2010, Godefroid et al. 2011, Soliveres et al. 2012), or turf or rhizome transfer (Ash et al 1994, Cooper & MacDonald 2000). When sowing mixtures of seeds (Poschlod et al. 1998, Hölzel & Otte 2003, Jongepierová et al. 2007, Kiehl et al. 2010, Baasch et al. 2012) fails to improve natural dispersion processes (Chapter 3), the latter reintroduction methods are used, although they are usually more expensive (Kirmer et al. 2009).

Transplantation can be an effective method of reintroduction (Fattorini 2001, Krautzer & Wittmann 2006, Menges et al. 2008, Kiehl et al. 2010, Godefroid et al. 2011), and is often more effective than seeding as it bypasses the vulnerable stages of germination (Maschinski & Wright 2006, Guerrant & Kaye 2007, Menges 2008). Restoration projects commonly use transplantation of native trees (Durigan & Silveira 1999), shrub seedlings (Soliveres et al. 2012) and/or perennial grasses (May et al. 1982, Cooper & McDonald 2000, Mottl et al. 2006). Reintroduction aims to establish a species in an area which was once part of its historical range, but from which it has either been extirpated or become extinct. On the other hand, translocation is the deliberate and mediated movement of wild individuals or populations from one part of their range to another (IUCN 1998). Species translocation occurs within two contexts, which do not necessarily imply one another: 1) in attempting to save rare and endangered species (Milton et al. 1999, Maschinski & Wright 2006, Guerrant Jr. & Kaye 2007), and 2) in attempting to restore populations or communities (Fattorini 2001). The main advantage of species translocation is that translocated plants reproduce and recruit more rapidly than seeded plants: the chance to establish a self-sustaining population is, as a result, greater (Godefroid et al. 2011). However, studies have already shown that some plant species are difficult to reintroduce and are therefore not suited to restoration (Fahselt 2007, Menges 2008, Godefroid et al. 2010); disturbances provide new environmental conditions, to which even some native species are not adapted, especially in the case of strong degradation (Yuan et al. 2006, Negreiros et al. 2011). In this context, other reintroduction methods must be tested.

Community translocation, also known as habitat translocation, involves the removal of an assemblage of species from one site and the attempt to establish it as a functioning community in another, receptor site (Bullock 1998). Community translocation was developed primarily in Britain, and was originally intended to move, out of harm’s way, communities that would otherwise have been completely destroyed by civil engineering or excavation projects (Bullock 1998, Good et al. 1999, Milton et al. 1999, Bruelheide & Flintrop 2000, Butt et al. 2003, Trueman et al. 2007, Box et al 2011). Maintaining the entire original community intact, without damage, is unrealistic, and this is why such projects have often focused on preserving the main features of the communities while allowing some limited damage (Bullock 1998, Bruelheide & Flintrop 2000, Trueman et al. 2007). In fact, plant communities are modified when they are translocated (Bruelheide 2003, Klimes et al. 2010, Trueman et al. 2007, Box et al. 2011, Pywell et al. 2011), e.g. grass cover tends to increase while forb cover tends to fall (Conlin & Ebersole 2001, Bay & Ebersole 2006, Trueman et al. 2007). Community translocation thus does not guarantee to maintain the spatial vegetation mosaic, which seems to be a more complicated goal to achieve (Bruelheide & Flintrop 2000).

Derived from community translocation, turf translocation’s goal is to restore species-rich plant communities, with the aim of maximizing the final number of species in the resulting community. This method has proven successful in many grassland types (Pywell et al. 1995, Conlin & Ebersole 2001, Bay & Ebersole 2006, Kidd et al. 2006, Klimes et al. 2010, Pywell et al. 2011, Aradottir 2012): turfs are suitable for rapid establishment in damaged areas (Krautzer & Wittmann 2006) and plant survival is usually high (Pywell et al. 2011). Small turfs are sufficient for introducing some species (Kidd et al. 2006, Klimes et al. 2010, Aradottir 2012) provided those turfs can act as a species source from which new colonization occurs (Reis et al. 2003, Klimes et al. 2010). In addition, other factors, such as vegetation type, can influence translocation success; for example, dry grasslands seem to transfer more successfully (Bullock et al. 1998, Trueman et al. 2007, Pywell et al. 2011) than wet meadows, and this has to do with the particular hydrological patterns associated with such systems.

While several methods of restoring temperate grasslands are demonstrably efficient and well documented (Kiehl et al. 2010), well-researched techniques for restoring tropical grasslands are scarce. C*ampos rupestres*, one physiognomy of the Cerrado (Brazilian savanna), are species-rich grasslands (Giulietti et al. 1997, Echternacht et al. 2011), established on quartzite-derived soils, found at altitudes of between 800m and 2000m, and covering around 130 000km^2 of total area (Barbosa 2012). They are constraint ecosystems occurring in shallow, extremely nutrient-poor, and highly acidic soils (Benites et al. 2007, Chapter 1). They occur in a region that is attractive for mining activities; thus, they are highly threatened (Klink & Machado 2005, Hoekstra et al. 2005). Although currently mandatory, environmental recovery practices have been only partially effective in Brazil (Neri & Sanchez 2010).

Because hay transfer proved to be an inconclusive method of restoring *campos rupestres* (Chapter 3), and since some important Cyperaceae and Poaceae species seeds showed low viability and germinability (Chapter 4), in the present work we opt for translocating individuals of native *campo rupestre* species along with vegetation turfs from reference areas (donor sites) to degraded areas (receptor sites). Our objective is to assess the effectiveness of these two restoration methods in ensuring that the desired range of species is introduced and that problems affecting seedling establishment are overcome. We have evaluated 1) the feasibility of translocating selected native species (survival and growth) and relative impact of nutrient supply and transplantation period on their survival; 2) the feasibility of translocating vegetation turfs and the comparative effects of turf size, turf origin, and degraded substrate type on translocation success (as measured by the number of surviving translocated individuals and species); 3) the resilience of grasslands from which translocated turfs were drawn in order to assess the destructive impact of the technique.

2.Material and Methods

2.1. Study area

Our study area is located in the southern portion of the Espinhaço Range, approximately 100 km northeast of Belo Horizonte, in the state of Minas Gerais, in the Environmental Protected Area (*Area de Proteção Ambiental* in Portuguese) of Morro da Pedreira, buffer zone to the Serra do Cipó National Park. There, the climate is classified as Cwb (C: warm temperate, w: dry winter, b: warm summer) according to the Köppen's system. It is markedly seasonal, with a warm rainy season and a cool dry one. The mean annual precipitation is 1622 mm and the annual temperature is 21.2°C (Madeira & Fernandes 1999). The sandy and the stony grasslands, which are the main herbaceous physiognomies of *campos rupestres*, are species-rich grasslands, dominated primarily by Poaceae, Cyperaceae and Velloziaceae (Chapter 1). Most of the species are perennial and resprouter.

Two degraded sites were selected for our experiments. Studies had reported the presence of degraded areas in the region as early as 1996 (Negreiros et al. 2011), but the overall start of degradation may actually date back to 1980. In 2002, a new disturbance occurred when highway MG010 was asphalted. Degraded areas found along the road were exploited for gravel and/or were used to park machines. When the road was complete, the degraded areas left behind represented two kinds of substrate: degraded sandy substrate and degraded stony substrate.

Small quarries are common in the region and their creation leas to vegetation being destroyed and soils being disturbed. Even when exploitation stops, soils are not entirely restituted, and they may be heavily contaminated by construction debris (Figure 16).

2.2. Species translocation

In the first experiment, four grasses, two sedges, and two Velloziaceae all having a high dominance index in *campos rupestres* were chosen (Chapter 1): *Tatianyx arnacites, Mesosetum exaratum, Homolepsis longispicula, Paspaslum erianthum, Lagenocarpus rigidus* subsp*. tenuifolius, Rhynchospora riedeliana, Vellozia resinosa*, and *Vellozia* *epidendroides*. Twenty similar-size individuals of each species were collected, with soil (around 10cm deep), in *campo rupestre* donor sites and transplanted to a degraded area with a sandy substrate (hereafter named degraded sandy substrate - DSa) in March 2011 (Experiment 1A, Figure 39). Of the 20 individuals, 10 were selected to receive an artificial nutrient supply (NPK: 10.10.10). As a control, 10 additional individuals of each species were translocated to an adjacent pristine area hereafter referred to as the reference sandy grassland (Sa); five of these individuals received the artificial nutrients. In order to test the impact of the period of transplantation, new translocations were carried out in November 2011 (Experiment 1B, Figure 39). Ten individuals of each species were collected from donor grasslands and five were transplanted to the DSa and five to the Sa without fertilization.

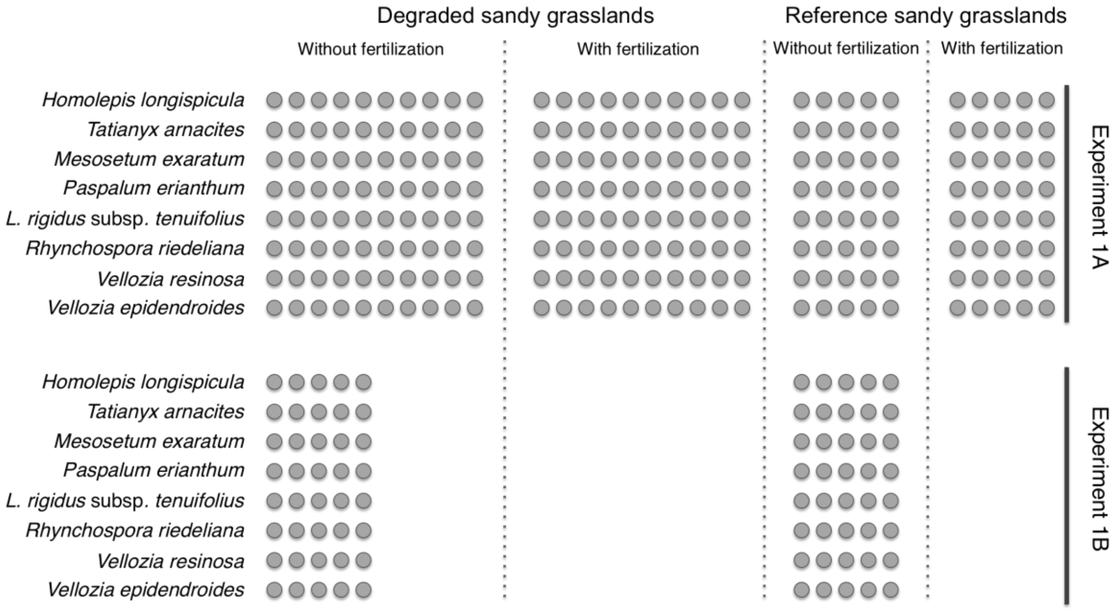

Figure 39: Experimental design of species translocation. Experiment 1A was carried out in March 2011 at the end of the rainy season, while Experiment 1B was carried out in November 2011 at the beginning of the rainy season.

Survival was recorded for each individual in March 2011 (T0) (the date of transplantation), June 2011 (T3), December 2011 (T9) and March 2012 (T12), in the first experiment. For the second experiment, survival was recorded in November 2011 (the date of transplantation) and again three months later in February 2012. In addition, on each date, growth was charted by measuring, in each individual, the height, the number of green leaves, and the presence of inflorescence which we use to assess the sustainability of the species in the restored area by considering its reproductive ability. The Relative Growth Rate (RGR) was calculated for height and defined as: RGR= (Ln h_2 – Ln h_1) / (t_2 – t_1) where h_i is the height in metres at time t_i in weeks.

2.3. Turf transfer

To check whether translocation is a possible method of restoring the two *campo rupestre* grassland types, we transferred soil-vegetation turfs from two donor reference grasslands (i.e. a sandy (Sa) and a stony grassland (St)) to two kinds of degraded areas, one having a degraded sandy substrate (DSa), and the other, a stony substrate (DSt)). The degraded receptor sites (DSa and DSt) were located less than 1 km from the donor sites. The soil of the receptor sites was excavated to create beds of an appropriate depth to accomodate the turfs. In the first experiment (Experiment 2A, Figure 40), turfs from donor reference sandy grasslands (hereafter referred as TSa) were transferred to DSa in March 2011, using two different 10-cm-deep turf sizes: 40x40cm and 20x20cm, each spaced by 20 cm. Four replicates of eight turfs of each size were set up. In the second experiment (Experiment 2B, Figure 40), 10-cm deep 20x20cm turfs were transferred from the donor reference sandy (TSa) and stony (hereafter referred as TSt) grasslands to DSt (receptor site). Four replicates of eight turfs each were set up. Turfs were watered twice per week during the first month.

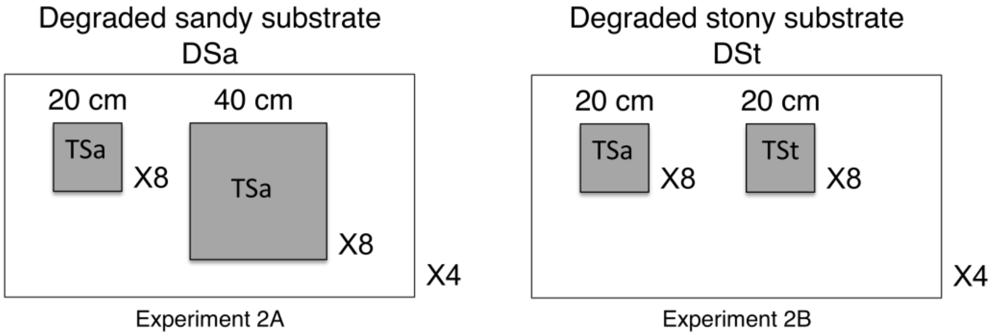

Figure 40: Experimental design of turf translocation carried out in March 2011 at the end of the rainy season. Experiment 2A was carried out in degraded sandy substrate DSa, while Experiment 2B was carried out in degraded stony substrate DSt.

Vegetation surveys were carried out on March 2011 (T0) (the date of transfer), June 2011 (T3), December 2011 (T9) and May 2012 (T14). On each date, we recorded a list of species observed on each turf, their respective number of individuals, and their respective percent cover. In addition, we monitored the vegetation recovery on the two donor reference sites on each quadrat where turf was removed on May 2012. In St, there were 32 20x20cm quadrats and in Sa there were 32 40x40cm quadrats and 32 20x20cm quadrats. For each quadrat the species list with respective number of individuals were recorded.

2.4. Statistical analysis

2.4.1. Species translocation

To understand the influence of substrate type and nutrient supply on survival, GLM procedures using binomial errors and logit link functions were run, with survival (1 or 0) as the response variable and substrate type and nutrient supply as explicative variables. For all GLM, site effects were removed using the *offset* component of the GLM procedure; *offset* component allows including an *a-priori* known component in the linear predictor during fitting (using the R package stats) (Crawley 2007). The impact of translocation period and substrate type on survival were also assessed using the same GLM method with translocation period and substrate as explicative variables.

Due to high mortality, statistical analyses were not carried out for *Lagenocarpus rigidus* subsp*. tenuifolius, Rhynchospora riedeliana, Mesosetum exaratum, Homolepis longispicula, Vellosia resinosa* and *Vellozia Epidendroides*. For *Paspalum erianthum,* two-way ANOVA was used to evaluate the effect of substrate type and nutrient supply on height RGR between T0 and T14. Normality and homoscedasticity assumptions were checked and a square root transformation was applied (Sokal & Rohlf 1998). In addition, the effect of substrate type and nutrient supply on the number of new leaves was tested by GLM procedures using a poisson distribution and log link function. We also used a GLM with a poisson distribution and log link function to test the effect of substrate type and nutrient supply on the number of *lost* leaves in *T. arnacites*.

2.4.2. Turf translocation

In order to assess the impact of turf size, turf origin, translocation substrate, and time on the percentage of vegetation, a generalized linear mixed model (LMER) with a quasibinomial distribution was used, treating sites and replicates as random effects. In order to assess the impact of turf size, turf origin, substrate type, and time on the number of individuals or species occurring by turf, we used another generalized linear model having a poisson distribution, with sites and replicates once again treated as random effects. Species were classified into three plant forms: graminoids (Cyperaceae, Iridaceae, Poaceae and Xyridaceae), forbs (including Eriocaulaceae, Velloziaceae, Amaranthaceae, some Asteraceae and other forbs), and subshrubs (including Melastomataceae and some Asteraceae). The same analyses were used to study the impact of turf size, turf origin, substrate type, and time on the number of individuals in each plant form. The relationship between turf size, time, and the proportion of surviving individuals was assessed using a generalized linear mixed model with a binomial distribution and sites and replicates treated as random effects.

The effect of turf size on vegetation percentage recovery was assessed using a generalized linear mixed model employing a quasibinomial distribution and taking sites and replicates as random effects. Finally, a generalized linear mixed model with a poisson distribution and with sites and replicate taken as random effects was used to analyze the effects of substrate on the number of colonizing seedlings.

3.Results

3.1.Species translocation

3.1.1.Effect of substrate type (natural VS. degraded substrate) and nutrient supply

The first survey of species translocation was realized in June 2011 (T3) and showed a high mortality among translocated individuals. There was an overall negative effect of nutrient supply on survival (z=3.10, p<0.01), whereas substrate type of the translocation (i.e. on Sa or DSa) did not impact individual survival (z=1.78, p=0.08). At the species level, neither nutrient nor substrate type had a significant effect on survival (Table 22). *Homolepis longispicula*, *Rhynchospora riedeliana*, *Vellozia epidendroides* and *Vellozia resinosa* registered the highest mortality, with an upper limit of only 40% of individuals surviving the first 3 months following translocation. In some cases, no individuals survived (Table 22). Among the other species, *Lagenocarpus rigidus* subsp. *tenuifolius,* and *Mesosetum exaratum* registered a moderate survival rate, higher than 60% in some cases (i.e. in Sa with nutrient and in DSa without added nutrients), but just exceeding 20% in the case of translocation to DSa with added nutrients (Table 22). Finally, 3 months after their translocation, individuals of *Paspalum erianthum* and *Tatianyx arnacites* recorded high survivability (>80%), no matter the treatment (Table 22).

Table 22: Number of individuals translocated in March 2011 (T0) and still surviving 3 months later in June 2011 (T3) with percent survival. Individuals were translocated to a degraded sandy area (DSa) and to a reference sandy grassland (RSa), broken into two groups, one with and added nutrient supply (N) and one without (n). To test the effect of nutrient supply and substrate type, GLM procedures were run with a binomial family distribution and logit link function. ns: non significant.

Time	T0				T3				GLM procedures on T3 data		
Treatment	DSa/N	DSa/n	RSa/N	RSa/n	DSa/N	DSa/n	RSa/N	RSa/n	Nutrient	Substrate	Interaction
Homolepis longispicula	10	10	5	5	1 (10%)	0 (0%)	1 (20%)	2 (40%)	0.005 ^{ns}	0.390 ^{ns}	0.005 ^{ns}
Lagenocarpus rigidus	10	10	5	5	2 (20%)	6 (60%)	3 (60%)	2 (40%)	1.830 ^{ns}	1.300 ^{ns}	-1.580 ^{ns}
Mesosetum exaratum	10	10	5	5	0 (0%)	7 (70%)	4 (80%)	3 (60%)	0.006 ^{ns}	0.006 ^{ns}	-0.006 ^{ns}
Paspalum erianthum	10	10	5	5	10 (100%)	10 (100%)	5 (100%)	5 (100%)	0.001 ^{ns}	0.001 ^{ns}	0.001^{ns}
Rhynchospora riedeliana	10	10	5	5	1 (10%)	2 (20%)	0 (0%)	2 (40%)	0.630 ^{ns}	0.006 ^{ns}	0.006 ^{ns}
Tatianyx arnacites	10	10	5	5	8 (80%)	10 (100%)	5 (100%)	5 (100%)	0.003 ^{ns}	0.002 ^{ns}	0.002 ^{ns}
Vellozia epidendroides	10	10	5	5	0 (0%)	4 (40%)	0 (0%)	0 (0%)	0.004 ^{ns}	0.001 ^{ns}	0.002 ^{ns}
Vellozia resinosa	10	10	5	5	0 (0%)	2 (20%)	0 (0%)	0 (0%)	0.003 ^{ns}	0.001 ^{ns}	0.002 ^{ns}

By December 2011 (T9), added nutrients were still having an overall negative effect on individual survival (z=1.96, p<0.05), though the significance of the effect had subsided by March 2012 (T12) (z=1.82, p=0.068). At T9 and at T12, substrate type did not have effect on individual survival (p>0.1). Between T9 and T12, mortality was low, only *Mesosetum exaratum* suffered a dead individual (Table 23). At T12, one year after the translocation, *Lagenocarpus rigidus* subsp. *tenuifolius* survived well (i.e. 60%) on DSa without added nutrients, but survival was low (<10%) with added nutrients indicating a negative effect of added nutrients on this species (z=1.065, p<0.05) (Table 23). For *Mesosetum exaratum* the pattern was similar, with only 30% of individuals translocated to DSa without added nutrients surviving at T12 (Table 23). *Tatianyx arnacites* individuals, which had survived well in the first 3 months, recorded survival only on DSa at T9 and T12 (between 50% and 60%); all individuals translocated to Sa died (Table 23). *Paspalum erianthum* was the only species to survive very well one year after the translocation; s only 2 individuals died on Sa (Table 23).

Table 23: Number and percentage survival of translocated individuals in December 2011 (T9) and in March 2011 (T12). Individuals were translocated to a degraded sandy area (DSa), and to a reference sandy grassland (RSa) broken into two groups, one with an added nutrient supply (N) and one without (n). To test the effect of nutrient supply and substrate type, GLM procedures were run on data recorded in March 2012, with a binomial family distribution and logit link function. ns: non significant.

Time	T9				T12				GLM procedures on T12 data		
Treatment	DSa/N	DSa/n	RSa/N	RSa/n	DSa/N	DSa/n	RSa/N	RSa/n	Nutrient	Substrat	Interaction
Homolepis longispicula	1 (10%)	0 (0%)	0 (0%)	1 (20%)	1 (10%)	0 (0%)	0 (0%)	1 (20%)	0.003 ^{ns}	-0.002 ^{ns}	0.004 ^{ns}
Lagenocarpus rigidus	1 (10%)	6 (60%)	0 (0%)	0 (0%)	1 (10%)	6 (60%)	0 (0%)	0 (0%)	2.065 *	-0.004 ^{ns}	0.001 ^{ns}
Mesosetum exaratum	0 (0%)	4 (40%)	0 (0%)	0 (0%)	0 (0%)	3 (30%)	0 (0%)	0 (0%)	0.004 ^{ns}	0.001 ^{ns}	-0.002 ^{ns}
Paspalum erianthum	10 (100%)	10 (100%)	5 (100%)	3 (60%)	10 (100%)	10 (100%)	5 (100%)	3 (60%)	0.001 ^{ns}	0.001 ^{ns}	-0.001 ^{ns}
Rhynchospora riedeliana	1 (10%)	1 (10%)	0 (0%)	0 (0%)	1 (10%)	1 (10%)	0 (0%)	0 (0%)	0.001 ^{ns}	-0.004 ^{ns}	-0.001 ^{ns}
Tatianyx arnacites	5 (50%)	6 (60%)	0 (0%)	0 (0%)	5 (50%)	6 (60%)	0 (0%)	0 (0%)	0.290 ^{ns}	0.004 ^{ns}	0.001 ^{ns}
Vellozia epidendroides	0 (0%)	2 (20%)	1 (20%)	0 (0%)	0 (0%)	2 (20%)	1 (20%)	0 (0%)	0.003 ^{ns}	0.003 ^{ns}	-0.004 ^{ns}
Vellozia resinosa	0 (0%)	1 (10%)	0 (0%)	0 (0%)	0 (0%)	1 (10%)	0 (0%)	0 (0%)	0.002 ^{ns}	0.001 ^{ns}	-0.001 ^{ns}

3.1.2. Effect of the translocation period

Transplantation at the end of the rainy season (March 2011) tended to be more successful than at the beginning (p=0.06), with the exception of Velloziaceae (Table 24), whatever the substrate type (p=0.72). When translocation occurred in November 2011, *Homolepis longispicula, Lagenocarpus rigidus, Mesosetum exaratum, Rhynchospora riedeliana* and *Tatianyx arnacites* showed low survival (<40%) (Table 24); on the contrary *Vellozia epidendroides* and *Vellozia resinosa,* which barely survived on Sa, had moderate survival on DSa (Table 24). Finally, only *Paspalum erianthum* survived as well (>80%) as in the first experiment.

Table 24: Number and percentage of surviving translocated individuals 3 months after the translocation, in June 2011 for individuals translocated in March 2011 and in February 2012 for individuals translocated November 2011. Individuals were translocated to a degraded sandy area (DSa) and to a reference sandy grassland (RSa) without added nutrients. 10 individuals for each species were translocated to DSa in March 2011, and for the other treatments, 5 individuals per species were translocated. To test the effect of the period of transplantation and substrate type GLM procedures were run with a binomial family distribution and logit link function. ns: non significant.

Date of transplantation	mars-11	mars-11	11-nov	11-nov	GLM procedures	
Substrate type	DSa	RSa	DSa	RSa	Date	Substrate
Homolepis longispicula	0 (0%)	2 (40%)	0 (0%)	0 (0%)	-0.002 ns	-0.001 ns
Lagenocarpus rigidus	6 (60%)	2 (40%)	0 (0%)	2 (40%)	-0.001 ns	0.006 ns
Mesosetum exaratum	7 (70%)	3 (60%)	0 (0%)	1 (20%)	-0.960 ns	0.006 ns
Paspalum erianthum	10 (100%)	5 (100%)	5 (100%)	4 (80%)	-0.002 ns	-0.001 ns
Rhynchospora riedeliana	2 (20%)	2 (40%)	0 (0%)	0 (0%)	-0.004 ns	0.001 ns
Tatianyx arnacites	10 (100%)	5 (100%)	2 (40%)	2 (40%)	-0.003 ns	0.001 ns
Vellozia epidendroides	4 (40%)	0 (0%)	5 (100%)	2 (40%)	0.004 ns	0.001 ns
Vellozia resinosa	2 (20%)	0 (0%)	3 (60%)	0 (0%)	0.001 ns	0.001 ns

3.1.3. At the species level: cases of *Paspalum erianthum* and *Tatianyx arnacites*

Substrate type and nutrient supply did not have a statistically significant effect on the height relative growth rate (RGR) between March 2011 and March 2012 of *Paspalum erianthum* (F=0.64, p= 0.42 for substrate type and F=0.05, p=0.82 for nutrient supply). However, there was an impact of the substrate on the number of new leaves: individuals translocated to DSa showed higher numbers of new leaves (z=-2.67, p<0.01), whereas nutrient supply had no effect on new leaf production (z=0.70, p=0.48). Moreover, on the DSa, 10 individuals out of 20 produced flowers 14 months after translocation, while only 1 individual out of 10 produced flowers in the reference area.

For *Tatianyx arnacites,* there was an impact of substrate type and nutrient supply on leaf loss, with individuals translocated to Sa showing lower leaf loss (z=-6.26, p<0.001). Moreover, whereas nutrient supply appeared to decrease leaf loss on Sa, it actually increased leaf loss on DSa (z=4.04, p<0.001).

3.2. Turf transplantation

At T0 on the degraded sandy area (DSa), we translocated 39 species using 40x40cm turfs and 32 species using 20x20cm turfs, both from the reference sandy grasslands

(TSa). At T0, on the stony degraded area (DSt), 30 species were translocated using 20x20cm tufs from the reference sandy grassalnds (TSa) and 31 species using 20x20cm turfs from the reference stony grasslands (TSt). The percent cover of vegetation decreased with time no matter the treatment (z=-5.83, p<0.001) and was higher on TSa (z=-9.59, p<0.001), higher on bigger turfs (i.e. 40x40cm) (z=32.04, p<0.001), and higher on DSa (z=14.33, p<0.001) and ((Figure 41).

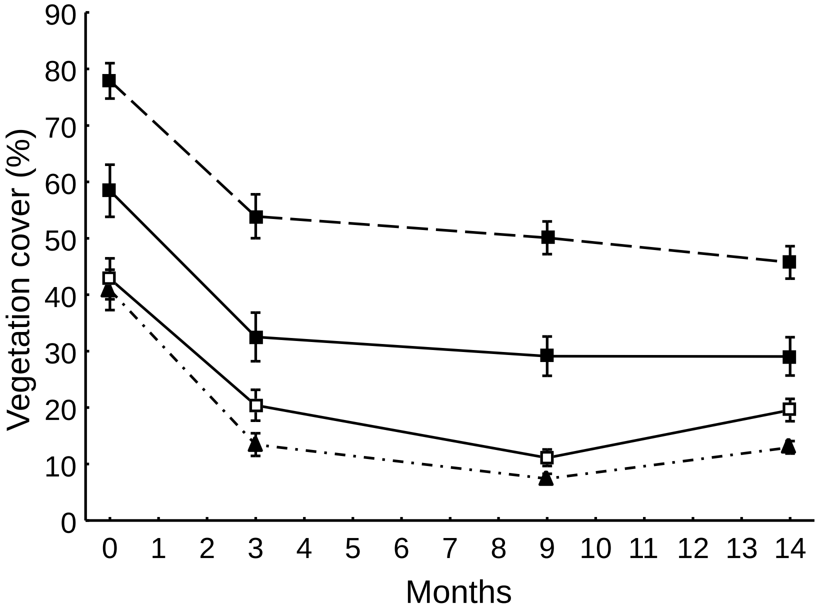

Figure 41: Average vegetation cover (%) (mean ± standard error) on 40x40cm TSa (black squares with dashed line), on 20x20cm TSa (black squares with solid line) translocated in DSa and on 20x20cm TSt (black triangles and dashed line) and TSa (open squares and solid line) translocated in DSt over time (in months).

3.2.1.Effects of the turf size

This experiment was carried out on degraded sandy areas (DSa), and as expected, at T0 significantly more individuals were translocated using 40x40cm turfs (103.4 ± 4.0 individuals in 40x40cm turf and 32.4 ± 2.6 in 20x20cm turf, z=32.61, p<0.001, Figure 42a). The number of individuals decreased during the first three months on both kinds of turf (z=-4.67, p<0.001), however, after that, the proportion of surviving individuals (compared to the number of individuals transplanted at T0) remained stable at around 67% of surviving individuals on 40x40cm turfs and 70% of surviving individuals on 20x20cm turfs (values in May 2012, T14, z=0.74, p=0.45, Figure 42a). The number of individuals remained higher on bigger turfs (z=37.29, p<0.001) at T14 (Figure 42a). The number of species present on each turf was higher on 40x40cm turf (z=7.32, p<0.001) and did not vary significantly with time (z=-1.70, p=0.08, Figure 42b).

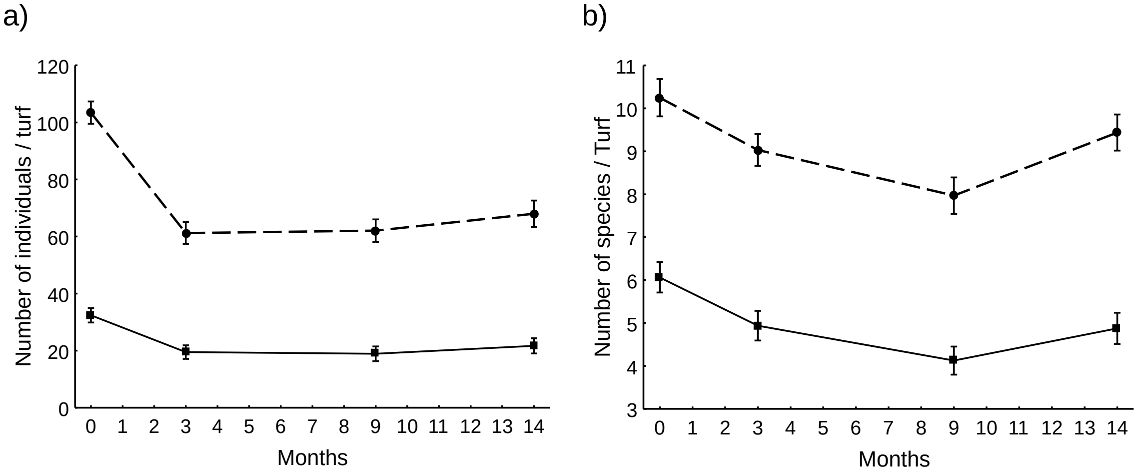

Figure 42: a) Average number of individuals and b) plant species richness in 40x40cm (dashed lines) or 20x20cm (solid line) translocated turfs in DSa over time (in months). Means within size were significantly different in May 2012 (T 14) (P <0.001) in both number of individuals and species richness.

Between March 2011 (T0) and May 2012 (T14), graminoids, which represented the majority of translocated individuals, decreased (Table 25). 40x40cm turfs allowed to translocate more graminoids (Table 25). The same number of forbs was translocated onto 40x40cm turfs and 20x20cm turfs (p=0.4), and the number remaining decreased significantly with time (z=-2.26, p<0.01, Table 4). Few sub-shrubs occurred on translocated turfs whatever turf size, this did not vary with time (Table 25).

Table 25: Average number of individuals in 20x20cm and 40x40cm turfs translocated to degraded sandy substrate at T0 and T14 according to plant form: graminoids, forbs and sub-shrubs. Results of the LMER procedures are shown.

	T0		T14				
	20x20cm	40x40cm	20x20cm	40x40cm	Size	Time	Interaction
Graminoids	30.6 ± 2.7	101.6 ± 3.9	20.7 ± 2.7	66.8 ± 4.7	32.94 ***	-3.43 ***	0.01 ns
Forbs	1.4 ± 0.6	1.2 ± 0.3	0.6 ± 0.2	0.8 ± 0.3	-0.75 ns	-2.26 **	1.28 ns
Sub-shrubs	0.4 ± 0.2	0.6 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	1.20 ns	0.30 ns	-0.65 ns

3.2.2.Effects of the turf origin

This experiment was carried out on degraded stony substrate (DSt), and we noted that the origin of the turf had an impact on the number of individuals (z=3.86, p <0.001), and so did time (z= -5.47, p<0.001), as did the combination of the two (z=-5.22, p<0.001) (Figure 43). At T0, there was a higher number of individuals in turfs from stony grasslands (TSt) (22.7 ± 2.0 individuals) than in turfs from sandy grasslands (TSa) (19.6 ± 1.8 individuals) (z=-3.18, p<0.01); between the three first months, the number of individuals decreased drastically (z=-12.28, p<0.001) and became similar between the two kinds of turf at T3 (9.2 ± 2.4 individuals in TSt and 7.8 ± 1.0 individuals in TSa, z=1.79, p=0.07, Figure 43a). Latter, between T9 and T14, the number of individuals increased in both kinds of turf (z=4.33, p<0.001) and TSa became denser than TSt (12.7 ± 1.1 individuals in TSa and 10.0 ± 0.6 individuals in TSt, z=-3.18, p<0.001, Figure 43a). On the other hand, the number of species present on each turf was slightly higher in TSa than in TSt (5.1 ± 0.3 species in TSa and 4.4 ± 0.2 species in TSt, z=-1.95, p=0.05) and did not vary with time (z=0.5, p=0.61, Figure 43b).

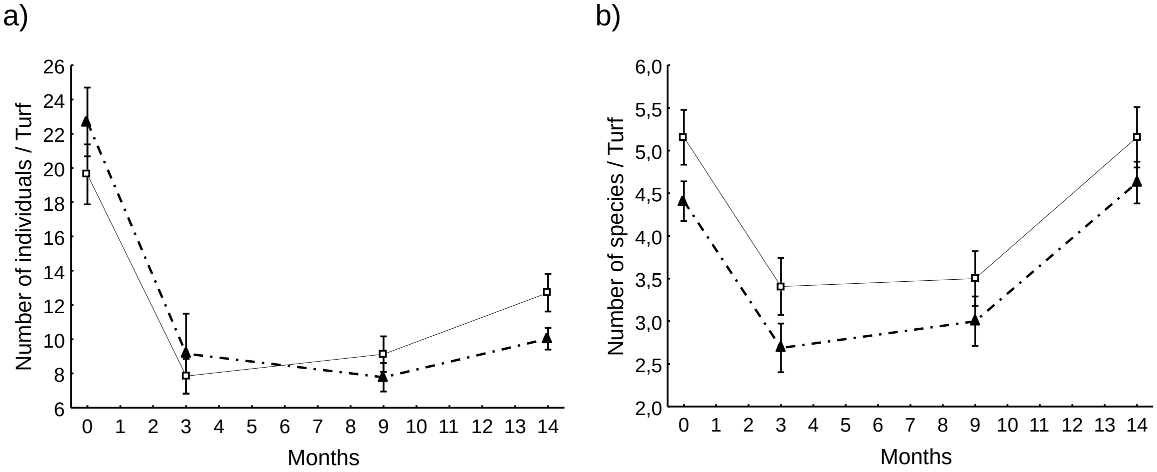

Figure 43: a) Average number of individuals and b) plant species richness in 20x20cm TSt (dashed lines) and TSa (solid line) translocated in DSt over time (in months). Means within origin of turfs were similar in May 2012 (T 14) (P >0.05) in both number of individuals and species richness.

At T0, more graminoids were observed in TSa than in TSt (p<0.01, Table 26). Graminoids decreased with time (p<0.001), more drastically in TSt than in TSa (p<0.05, Table 26). On the contrary, more forbs were observed in TSt than in TSa at the beginning of the translocation (T0). Forb number did not decrease in TSa, but it did decrease drastically in TSt (p<0.001, Table 26), especially Velloziaceae and Eriocaulaceae species. There was no difference in sub-shrub number between TSa and TSt at T0, and their number increased with time in both kinds of turfs (Table 26).

Table 26: Average number of individuals in 20x20cm turfs from sandy grasslands (TSa) and stony grasslands (TSt), translocated on degraded stony substrate at T0 and T14 according to plant form: graminoids, forbs and sub-shrubs. Results of the LMER procedures are shown.

	T0		T14				
	TSa	TSt	TSa	TSt	Origin	Time	Interaction
Graminoids	19.0 ± 1.7	16.1 ± 1.7	11.6 ± 1.1	7.9 ± 0.5	-2.77 **	-7.52 ***	-2.22 *
Forbs	0.5 ± 0.2	6.5 ± 1.3	0.5 ± 0.1	1.1 ± 0.4	9.86 **	0.001 ns	-4.40 ***
Sub-shrubs	0.1 ± 0.1	0.1 ± 0.1	0.6 ± 0.2	1.0 ± 0.3	0.001 ns	3.02 **	0.52 ns

3.2.3.Effects of the substrate of the degraded area.

The substrate of the degraded area had an impact on the number of translocated individuals (z=-4.00, p <0.001), as did time (z= -7.48, p<0.001), whitout interaction between both (z=-0.01, p=0.99, Figure 44a). At T0, there were more individuals on turfs transplanted to degraded sandy substrates (DSa) (32.4 ± 2.6 individuals) than degraded stony substrates (DSt) (19.6 ± 1.8individuals, z=-4.78, p<0.001, Fig. Figure 44a). During the first three months, the number of individuals by turf decreased (z=-10.03, p<0.001) on both kinds of substrate (Figure 44a). Latter, between T9 and T14 the number of individuals increased in both degraded areas (z=2.46, p=0.01); the number of individuals in turfs translocated on DSa remained higher (21.7 ± 2.7 individuals) than on turfs translocated on DSt (12.7 ± 1.1 individuals, z=-4.04, p<0.001, Figure 44a). At T0, there was no difference in species richness between the two kinds of substrate where translocation occurred (z=-1.52, p=0.12, Fig. Figure 44b). The number of species did not vary on turf translocated to DSt over time (z=0.50, p=0.6), but decreased slightly on turf translocated to DSa with time (z=-2.29, p=0.021, Figure 44b).

At the beginning of the experiment (T0), turfs translocated to DSa had a higher number of graminoids than turfs translocated to DSt (p<0.001, Table 27), and this number decreased with time in both degraded substrates. The same number of forbs were translocated to the two degraded substrates (p=0.09) and this decreased with time (p<0.001, Table 27). The number of sub-shrubs decreased only on turfs translocated to DSa, but it remained stable on turfs translocated to DSt (p<0.001, Table 27).

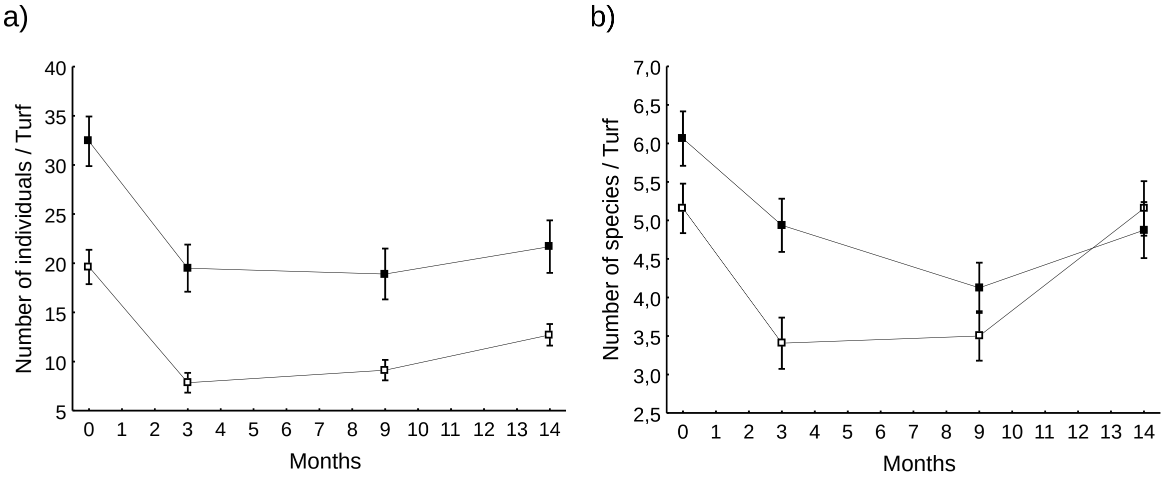

Figure 44: a) Average number of individuals and b) plant species richness in 20x20cm TSa transplanted in DSa (full squares) and in DSt (open squares) over time (in months). Means within each substrate were significantly different in May 2012 (T 14) in number of individuals (P <0.001) but similar in species richness (p=0.6).

Table 27: Average number of individuals in 20x20cm turfs from sandy grasslands translocated to degraded sandy substrate (DSa) and degraded stony substrate (DSt) at T0 and T14 according to plant form: graminoids, forbs and sub-shrubs. Results of the LMER procedures are shown.

	T0		T14				
	DSa	DSt	DSa	DSt	Substrate	Time	Interaction
Graminoids	30.6 ± 2.7	19.1 ± 1.7	20.6 ± 2.7	11.6 ± 1.1	-4.32 ***	-7.78 ***	-1.24 ns
Forbs	5.5 ± 0.4	4.7 ± 0.3	4.4 ± 0.3	4.4 ± 0.3	-1.68 ns	-2.97 **	1.77 ns
Sub-shrubs	1.4 ± 0.6	0.5 ± 0.2	0.7 ± 0.2	0.5 ± 0.1	-1.12 ns	-0.19 ns	2.74 **

3.2.4.Reference grassland regeneration

The regeneration rate of donor grasslands from which turfs were drawn is very low. More than one year after turf removal (14 months), only a few individuals recolonized the sampled areas. On sandy donor grasslands, 2.78 ± 0.58 seedlings were recorded on 20x20cm quadrats (representing 1.20% ± 0.34% of the quadrat) and 5.03 ± 0.66 seedlings on 40x40cm quadrats (representing 1.70% ± 0.44% of the quadrat); vegetation percent cover recovery did not vary with turf size (z=-7.80, p>0.05). On stony donor grasslands, 1.40 ± 0.22 seedlings were registered on 20x20cm quadrats, which is significantly lower than on sandy donor grasslands (z=-1.81, p<0.06). Species that recolonized the most significantly are *Rhynchospora riedeliana* (97 seedlings), *Rhynchospora consanguinea* (68 seedlings), *Rhynchospora tenuis* subsp. *austro-brasiliensis* (48 seedlings) and *Lavoisiera cariophyllea* (11 seedlings).

4.Discussion

Natural succession can be relied upon for some restoration projects (Prach & Pysek 2001, Vieira et al. 2006), however the restoration or rehabilitation of highly degraded areas (e.g. by mining or civil engineering), is more challenging, and sometimes requires species introduction. In our case, a large proportion of species (i.e. seven out of eight) showed high mortality, indicating that they are particularly difficult to translocate. Information on transplantation failure is scarce, but some studies have reported that plant species can be difficult to reintroduce (Pavlik 1996, Menges 2008, Godefroid et al. 2011). The selected species were expected to be suitable candidates for reintroduction because they present some traits, such as vegetative reproduction, which is common in such environments (Figueira 1998, Hoffmann 1998, Coelho et al. 2006, Coelho et al. 2007, Figueira & Del Sarto 2007, Fidelis et al. 2010), and this should favor the success of plant translocation in the long-term, ensuring species' expansion in the area (Farnsworth 2007, Pywell et al. 2007).

However, establishment is a crucial step, and some stress-tolerant species, such as our *campo rupestre* species, perform badly (Pywell et al. 2007). Individuals of *Tatianyx arnacites* survived but they tended to wilt (i.e. loose leaves). Only one species, *Paspalum erianthum,* was able to survive and grow. In addition, some individuals reproduced, producing flowers, which is, in the context of ecosystem restoration, the ultimate goal and a key measure of the fate of reintroduction (Fahselt 2007, Menges et al. 2008, Godefroid et al. 2011). *Paspalum erianthum* is a grass widely distributed from North to South America and probably has higher adaptation abilities (Farnsworth 2007) than other species which have narrower distributions and therefore higher specialization. As a result, we have been able to show that it is possible to transplant some native herbaceous species onto degraded areas.

Mortality was particularly high during the first months, which are fundamental for plant establishment. Desiccation has been cited as an important factor causing mortality in reintroduction experiments (Godefroid et al. 2011, Soliveres et al. 2012). However the plant translocation that was done at the beginning of the wet season did not increase species survival: even though individuals were less water-stressed compared to those translocated at the end of the dry season, they tended to suffer more the effects of translocation. On the other hand, herbaceous savanna species accumulate carbohydrates during the wet season as part of their mechanism for coping with drought (Batalha & Martins 2004) and are thus potentially more resistant to stressful situations, such as translocation, at the end of the wet season.

In addition, in our case, translocation in sandy reference grasslands, where environmental conditions are potentially suitable, did not improve translocated species' survival, which underscores the point that limited or unsuitable soil conditions in degraded areas is not the unique reason for failure (Maunder 1992, Bottin et al. 2007). We also noted a negative effect of nutrient supply on plant survival; this result is not in agreement with Negreiros et al. (2009) who demonstrated that despite the fact that *campo rupestre* species are adapted to low nutritional quality soils (Benites et al. 2007, Chapter 1), shrub seedlings developed well with high fertility substrate conditions, but this tendency can sometimes be reversed in the face of competition (Buisson 2005).

Our results suggest that more than site conditions or water supply, translocation itself damages individuals. Indeed, establishment of adult plants following translocation can be considered problematic due to the unavoidable disturbance of the root system (Milton et al. 1999, Fahselt 2007). Clonal reproduction was demonstrated for some species of Eriocaulaceae in *campos rupestres* (Coelho et al. 2007, Figueira & Del Sarto 2007), but we suspect that it is present in many other species such as Cyperaceae, Velloziaceae or Poaceae. Because root connections are what underly clonal reproduction, it appears likely that root damage is probably fatal. It is worth recalling that these species are characterized by a high habitat specificity (Chapter 1, 3), a vulnerability that was exacerbated by root damage. Together, these effects may have hampered their establishment (Farnsworth 2007, Pywell et al. 2007).

Although seedling transplantation has been already highlighted as a successful method of restoring alpine vegetation (Fattorini, 2001), seeds and seedlings are also more susceptible to environmental hazards (Urbanska & Chambers 2002). As in previous studies (Conlin & Ebersole 2001, Bay & Ebersole 2006), our results demonstrate that turf translocation is effective in introducing herbaceous species in highly damaged mountain grasslands, as evidenced by the numerous native species surviving more than a year after translocation. Compared to hay transfer (Chapter 3) or to individual translocation at the same locale, the transfer of *campo rupestre* turfs is the most effective restoration method we studied. Even though turf transplantation allowed the introduction of various species, plant composition in the turf changed over course of the first year (Bullock 1998, Bruelheide 2003, Klimes et al. 2010, Trueman et al. 2007, Box et al. 2011, Pywell 2011). The decrease in individuals especially during the three first months reflected the “trauma” associated with translocation. Because the natural rate species turn-over in *campos rupestres* is quite low due to a preponderance of perennial species, we consider these initial changes to be the result of the translocation. Nonetheless, in many turfs, species richness was maintained over time. This response to translocation (i.e. strong initial decline in individuals) was observed on all turfs, independently of the turf size, receptor site substrate, or turf origin.

As bigger turf allowed the introduction of an initially larger pool of individuals/species, and considering the important initial loss, we suggest that the use of bigger turfs can guarantee better translocation success. In our case, turf size did not appear to have an impact on translocation success between the different plant-forms. Although it has been reported that sub-shrubs are more sensitive to small turf than grasses (Aradottir 2012), in *campos rupestres,* sub-shrubs are scattered on donor grasslands and their translocation is thus limited to a few individuals, even when bigger turfs are used. Nevertheless, response to translocation might vary between plant-forms (Conlin & Ebersole 2001, Bay & Ebersole 2006, Trueman et al. 2007). Graminoids, especially Poaceae and Cyperaceae, which are dominant on *campos rupestres* (Chapter 1), are the most well-represented among the species we translocated, especially on turf from sandy grasslands; they thus suffer the most drastic population reductions following translocation. The introduction of forbs was globally ensured by using turf from stony grasslands, but they showed a high mortality, especially Velloziaceae and Eriocaulaceae, which are characteristic to *campos rupestres*. The origin of turfs did not appear to have an effect on translocation success (i.e. as measured by the number of individuals or species) until our final survey; turfs from sandy grasslands tended to regenerate with new individuals, both from *campos rupestres* and from the surrounding degraded areas, more rapidly than turfs from stony grasslands.

We did not found any sign of colonization outside the turfs whatever the turf size, the turf origin or the substrate; although small turfs have already been underlined as an efficient species source useful to initiate colonization (Klimes et al. 2010), it was already reported that species do not always spread up (Kardol et al. 2009). Successful establishment outside the turf can be precluded by differences in chemical and physical soil properties between the donor and the receptor site (Pywell et al. 2007). Moreover, changes and expansion of the vegetation to fill in adjacent areas occur on the long-term (Kidd et al. 2006). For example, Trueman et al. (2007) showed that species density gradually declined on the translocated turf for the first four years after translocation but recovered in the fifth year. Short-term observations of plant establishment are not sufficient (Pywell et al. 2011) and our experiment will have to be monitored on the longer-term.

An interesting result is that turfs can be establish on different kinds of soil even if soil characteristics of the receptor site are often limiting factors to establishment (Pywell et al. 1995, Bullock 1998), On the other hand, degraded site substrate may impact the implementation of translocation: turf translocation was more complicated on degraded stony substrate due to the high quantity of little rocks complicating excavation. Conserving the integrity of the turfs was in such case more difficult, resulting in lower number of transplants.

So far, our results showed that turf translocation is possible to introduce native *campos rupestres* species in degraded areas*.* This approach had also the benefit of translocating key functional components of the soil microbial community, and the above- and below-ground invertebrate community (Pywell et al. 2011). However it is an expensive method (Kirmer et al. 2009, Pywell et al. 2011) and the regeneration of both donor sites is really low and damages almost irreversible. For all these reasons, *campo rupestre* translocation should only be considered as a mean of habitat rescue, in circumstances when complete habitat destruction is otherwise unavoidable.

5.Conclusion

The translocation of native herbaceous species with the aim of restoring *campos rupestres* is clearly very complicated. In our experiments, only one species, the grass *Paspalum erianthum,* survived, grew, and produced flowers, indicating promising long-term viability of this species upon translocation. As for the other species, the mortality rate was disappointingly high, and probably resulted from the trauma of transplantation and the root damage it probably inflicted. We found a similar effect in turf translocation where there was an important decrease, followed by immediate stabilization, in the number of individuals during the first months. We suppose that these plants, being perennial and reproducing primarily vegetatively, are constructed such that damage to their root system is probably fatal. In spite of this, turf translocation has proven to be an effective method for reintroducing native herbaceous species to degraded areas. Long-term monitoring will be necessary to find out if turfs can actually act as species sources. Turf translocation should only be used with the understanding that the extant plant communities from which donor material is drawn will be irreparably sacrificed, because donor sites generally have poor resilience, and thus,should only be used when communities are planned on being completely destroyed.

General Discussion

The basic objective of this thesis was to improve the understanding of the functioning of *campos rupestres*: by defining what species compose *campos rupestres* and how they are structured; and by assessing their dynamics i.e. the seasonal changes in reproduction at community level and the resilience of communities after human disturbances.

The applied goal of this thesis project was to conduct the scientific studies necessary to find the most efficient method to restore these diverse and endangered communities.

In this discussion, I aim to answer the three questions set in the introduction: what do we want to restore? ; Are *campos rupestres* resilient to a strong disturbance? ; And, can we restore *campos rupestres*? I have therefore drawn the main conclusion of this study and have highlighted how these results contribute to ecological theory and/or to ecological restoration.

1.What do we want to restore?

1.1. Composition and structure of herbaceous communities of campos rupestres

Defining the reference ecosystem in a restoration project is fundamental to set goals, to monitor restoration processes and to assess success (SER 2004). *Campos rupestres* are peculiar tropical mountain grasslands and the main vegetation formation encountered along the Espinhaço range. The choice of the reference ecosystem is therefore obvious; we set the *campos rupestres* as the reference because 1) there are the main vegetation formation still encountered on the intact surrounding areas, which suggest that it is the pre-disturbance state (Choi et al. 2008, Buisson 2011); 2) of the high biodiversity and endemism they host, hence their conservation value; and, 3) like other mountain ecosystems, they provide valuable ecosystem services, such as water purification, medicinal plants, recreational services, etc. (MEA 2005)

Campos rupestres are usually described as a more or less continuous herbaceous stratum with small sclerophyllous evergreen shrubs and subshrubs, subjected to environmental constraints, such as seasonal drought, fire, high insulation, high temperatures and high radiations (Giulietti et al. 1997). In **chapter 1** we demonstrated that rather than a homogeneous herbaceous stratum, *campos rupestres* are composed of a mosaic of communities, formed by at least two kinds of grasslands. The large majority of species are perennial (**chapter 1 & 2**) and resprouters (chapter 1 & personal observation after a fire). Each grassland-type is characterized by its own vegetation (Giulietti et al. 1997, Conceição & Pirani 2007), while the main species are common to both grasslands, such as *Tatianyx arnacites, Mesosetum exaratum, Homolepis longispicula, Paspalum erianthum, Lagenocarpus rigidus* subsp. *tenuifolius, Rhynchospora consanguinea, Rhynchospora riedeliana, Bulbostylis paradoxa, Paepalanthus geniculatus, Syngonanthus cipoensis, Vellozia epidendroides, Xyris melanopoda, Xyris obtusiuscula* or *Xyris pilosa* among others. However, each species occurs at various density and/or frequency depending on the grasslands, emphasizing a larger niche in one or the other grassland. On the other hand, some species are restricted to one grassland-type, underlining their narrower niche. We thus argue that species assemblages in *campos rupestres* are non-random, but constrained by abiotic and/or biotic factors.

A part of the heterogeneity of plant composition both between and within the sandy and stony grasslands can be attributed to the high level of endemism at local scale or at the scale of Espinhaço Range: 12% of species are micro-endemic (Serra do Cipó), 12% are endemic from the Espinhaço range in Minas Gerais and 10% are found only along the Espinhaço Range. Corroborating with that, 39 % of species are confined to the *campos rupestres*, while 14% of species are in common with the cerrado and 19% are also found in other biomes. Then even if *campos rupestres* can be included into the Cerrado (as mentioned in the introduction), it remains that these ecosystems are a truly unique physiognomy.

Because there is considerable local diversity in the different *campos rupestres* along the Espinhaço Range (Echternacht et al. 2011), it is difficult to clearly define them based on a list of species. However, within all Espinhaço Range, many species show morphological convergence and their functioning is thus most probably similar (Giulietti et al. 1997, Alves & Kolbek 2010). Within a restoration context, we therefore argue that what we show in this thesis about the *campos rupestres* of the Serra do Cipó (in term of functioning and dynamics) is also true for other *campos rupestres* in the Espinhaço Range.

1.2. From the regional species pool to the external species pool: patterns of reproduction in campos rupestres

In **chapter 2,** we have highlighted the variety of phenological strategies occurring in *campos rupestres*, which underline that, beyond species diversity, *campos rupestres* also harbor a diversity of ecological strategies among the herbaceous flora. Flowering patterns of the herbaceous flora of the *campos rupestres* are related to seasonal climate variations: the reproduction of many species are confined to the rainy season; these species should therefore be strongly impacted by climate change (Werneck et al. 2012). In addition, other species reproduce during the transition from the rainy to the dry season or during the dry season. Consequently, dissemination occurs both during the rainy or the dry season, which implies different germination and establishment strategies. A relationship between seed dispersal and seedling establishment has already been showed in Neotropical savannas for woody species (Salazar et al. 2011, Silveira et al. 2012): most seeds dispersed in the wet season are non-dormant (Salazar et al. 2011), but we might expect that seeds produced during the rainy season and dispersing at the end of it (period of transition with the dry season) to have dormancy (Silveira et al. 2012).

We have also shown a large diversity of reproduction frequency. Some species adopted a continuous reproduction, producing seeds almost all year long; other species reproduce sporadically, others regularly every year, others reproduce only one year out of two. Finally some species were not observed reproducing during our two-year survey, among these some dominant species, such as *Tatianyx arnacites, Mesosetum exaratum, Homolepis longispicula, Paspalum pectinatum, Bulbostilys paradoxa,* or *Bulbostylis emmerichiae*. This indirectly illustrates how *campos rupestres* are constrained ecosystems subjected to disturbances: indeed, *campos rupestres* are nutrient poor ecosystems and stress-tolerant species are often long-lived clonal species (Bekker et al. 1997; Chang et al. 2001; Matus et al. 2005, Coelho et al. 2006, 2007, Figueira & Del Sarto 2007).

Finally according to the phenological study, Cyperaceae, Xyridaceae, Ericaulaceae, Melastomataceae and other sub-shrubs mainly ensure seed production in *campos rupestres*, whereas Poaceae, an important family, produces very few seeds. **Chapter 2** stresses that, if spontaneous succession occurs in *campos rupestres*, the low or irregular seed production of some species is a strong limiting factor.

2.Plant community dynamics after disturbance

2.1. Regeneration after a natural disturbance

Plant establishment in *campo rupestre* reference grasslands from the seed bank is limited (**Chapter 3** & Appendix 4): seed banks are poor in species and in seeds in comparison to other habitats, such as nearby gallery forests (Medina and Fernandes 2007), Cerrado (Salazar et al. 2011) or other tropical savannas (Perez and Santiago 2001). The ability to form a seed bank varies in *campos rupestres*: while some species appear not to form seed banks (Velten & Garcia 2007), others may form only a small persistent seed bank (Velten & Garcia 2007, Giorni 2009, Silveira 2011). Bekker et al. (1997) already noted that species associated with poor nutrient conditions were relatively scarce in the seed bank. It was also suggested that increasing habitat disturbance always selects for increased seed persistence (Hölzel & Otte 2004), but it is not the case in *campos rupestres,* where fire is the main disturbance and where seed persistence were not demonstrated.

Indeed, in the Cerrado, in response to fire, vegetative reproduction is a frequent strategy, much more successful than sexual reproduction (Hoffmann 1998). Fidelis et al. (2010, see also Fidelis 2008) also pointed out the importance of bud banks in tropical grasslands that are subjected to fire, which would replace the seed bank in such communities. This corroborates with our **chapter 4** results: we were not able to find evidence that fire-related cues enhance germination, which suggests that *campos rupestres* species adopt other strategies to establish after fire.

2.2. Campos rupestres are not resilient to a strong disturbance

The main degradation which occurred in this ecosystem in the last decades, was the construction of highway MG-010, followed, in 2002, by its asphalting. The processes created some quarries along the road, which were exploited for gravel and/or were used to stock gravel and/or park machines, destroying *campo rupestre* vegetation. The regeneration of communities subjected to strong disturbances, such as quarries or mining, mainly relies on primary succession, since the entire vegetation is lost, seed bank destroyed and soil completely altered (Bradshaw 2000). However primary succession is known to be slow (Walker and del Moral 2003): its rate depends strongly to the proximity of colonist sources. Thereby surrounding vegetation is a very important factor affecting the process of colonization (Rehounkova & Prach 2006). In our case, we have shown (**Chapter 3**) that eight years after the disturbance, the degraded areas, despite the fact that they are surrounded by pristine *campos rupestres*, presented a vegetation composition quite different from those of reference grasslands and a large surface still had bare ground: we can thus assert that *campos rupestres* are not resilient to strong disturbance. Only some species which occurred on reference grasslands, such as *Mesosetum loliiforme, Marcetia taxifolia, Rhynchospora consanguinea,* can be found in degraded areas with stony substrates. However, ruderal species, such as *Aristida setifolia, Andropogon bicornis* or *Chamaecrista rotundifolia,* are dominant on degraded areas*.* In addition, the different degraded areas harbor quite different vegetation composition one from another. The forces, which promote divergence in primary succession, such as proximity, microsites or priority effects, are strong (Temperton & Zirr 2004, Del Moral et al. 2005, Rehounkova & Prach 2006, Del Moral 2007); several alternative communities can thus develop after this kind of intense disturbance, which, in our case, do not carry or carry only few target species.

The main impact of such strong disturbance was the complete destruction of the seed bank and vegetation (absence of internal species pool) and soils; spontaneous succession from the seed bank is therefore unlikely in degraded areas and only depends on dispersal. Despite soil alteration some *campos rupestres* species are found scattered on the degraded stony areas, along with some ruderal species. This indicates that soil conditions can limit spontaneous regeneration but is not sufficient in itself to explain the low resilience.

2.3. Drivers of plant community recovery

In **Chapter 1**, we have highlighted that *campos rupestres* are a mosaic of at least two communities, but more than the detection of these patterns, it is important to understand the rules or constraints that determine these patterns (Weiher & Keddy 1995). In **Chapter 3,** we have stressed that these two communities are not resilient to strong disturbance. Understanding why these communities are not resilient and what determines their recovery has helped us to define which factors determine the assembly of *campo rupestre* communities. According to the filter model, a niche-based concept which provides a framework to understand plant community assembly (Keddy 1992, Gotelli & McCabe 2002, Temperton & Hobbs 2004, Weiher et al. 2011), each community represents a subset of the regional species pool determined by dispersal, environmental and biotic filters.

In addition, neutral processes can occur alongside niche processes: the regional community assembly is then defined by the complementarity between niche-based processes, evolutionary history, habitat choice and diversification of equivalent species with neutral assembly (Ricklef 2008, Weiher et al. 2011). Indeed, both stochastic processes, such as colonization or extinction rate, and deterministic processes associated with niche processes (particularly important in constraint ecosystems like *campos rupestres*) can be of major importance in structuring natural communities (Chase & Myers 2011). These new approaches to community assembly have acknowledged the important role of dispersal in shaping local assemblages (Ricklef 2008, Vellend 2010, Weiher et al. 2011). As *campos rupestres* are constraint ecosystems we then focus here on deterministic processes associated with niche processes.

2.3.1.Dispersal filter

Dispersal is a key contributor to the regional species pool (Vellend 2010). It is also a barrier to spontaneous recovery in herbaceous systems (Hutchings & Booth 1996 ; Bischoff 2000 ; Kiehl et al. 2010 ; Török et al. 2010 ; Piqueray & Mahy 2011). *Campos rupestres* are complex grasslands (Conceição & Pirani 2005, 2007) with a huge biodiversity, representing a large global species pool, including many endemic species (Alves & Kolbek 1994, Echternacht et al. 2011, **Chapter 1**). *Campos rupestres* are known to be a center of biodiversity especially for Velloziaceae, Eriocaulaceae and Xyridaceae (Giulietti et al. 1987, Mello-Silva 1995, Wanderley 2011). Endemism is usually attributed to the fragmentation of populations, which promotes genetic differentiation, and therefore the evolution of new species, often with a very limited distribution (Alves & Kolbek 1994, Giulietti et al. 1997, Jesus et al. 2001, 2009). The large amount of endemic species in *campos rupestres* implies dispersal limitation since it is a prerequisite for allopatric speciation (Coyne and Orr 2004).

We did not study dispersion *per se*, but according to the literature, anemochory and autochory are the two main seed dispersal syndromes in *campos rupestres,* followed by zoochory (Faria Jr. & Santos 2006, Conceição et al. 2007a, Dutra et al. 2009, Fonseca et al. 2012, Lima et al. 2013). However these studies usually inferred seed dispersal modes from morphological traits of the seeds which might be misleading (Tackenberg et al. 2003). Indeed many species commonly defined as wind dispersed, have, in fact, low wind dispersal potential (Tackenberg et al. 2003). In grasslands, seed release height and vegetation height are more fundamental to determine seed dispersal distances (Soons et al. 2004, Thomson et al. 2011) than seed mass, which has been long considered as an important factor for dispersal over long distances. This is supported by the fact that many *campo rupestre* species invest in stalk length (Bazzaz et al. 2000), especially Eriocaulaceae, Xyridaceae, Asteraceae or Amaranthaceae (Le Stradic, unpublished data). Zoochory seems to be the most important dispersal way concerning woody Cerrado species (Leal & Oliveira 1998, Batalha & Martins 2004, Arbelaez & Parrado-Rosselli 2005, Lima et al. 2013), so we can hypothesize that zoochory can be an important mode in the rocky outcrops of *campos rupestres,* but much less in the open areas, such as sandy and stony grasslands. We did not find studies which reported hydrochory, while the importance of water as a dispersal mechanism in *campos rupestres* should not be underestimated: sandy grasslands are regularly flooded during the rainy season and sedges seeds are known to be buoyant (Leck & Schutz 2005).

Actually, in *campos rupestres,* the dispersal remains a black box, only few studies dealt with this aspect (Fonseca et al. 2012, Lima et al. 2013); and there is no study about seed rain for example. Restoration ecology can, however, provide some answers. Indeed, in case of strong degradation the entire seed bank is removed and thus no longer occurs on the degraded areas (**Chapter 3**). The availability of propagules in the surroundings and their dispersion is therefore the only way to ensure seed supply and initiate vegetation recovery (Bradshaw 1997, Campbell et al. 2003, Shu et al. 2005). In our case, seed banks did not recompose with *campo rupestre* target species *via* dispersion from reference grasslands; seed bank composition in degraded areas is quite different from those encountered in the reference grasslands and mainly composed of ruderal species. One species, *Mesosetum loliiforme*, largely present on the degraded seed bank is also encountered on reference grasslands. This native grass is found in Brazil on natural pastures and is one of the main forage species (Pott 1982). This species 1) reproduces every year, while other Poaceae on *campos rupestres* do not and 2) forms a seed bank on the degraded areas. These two characteristics are favorable to colonize new areas and this species was common on some stony degraded areas. On the other hand, characteristic species of *campos rupestres,* such as *Tatianyx arnacites* or *Rhynchospora riedeliana* for example, are not found in the degraded seed bank while they were found in those of reference grasslands: they are able to form seed bank but probably did not reach to the degraded areas.

Therefore, as no target species was encountered on the degraded seed bank after eight years, we hypothesize that dispersion is the first barrier to the resilience of strongly disturbed *campos rupestres.* In addition, each degraded area is characterized by its own species composition (**Chapter 3**), we then supposed that landscape factors, especially the proximity of seed sources, are important factors to determine plant composition at the beginning of the succession (Del Moral et al. 2005) in *campo rupestre* degraded areas. For example, degraded sites DSt2 and DSt3, which are directly surrounded by pristine *campos rupestres*, also recorded some *campo rupestre* species among the spontaneous vegetation. In the same way, we also note that DSa2, DSa3 and DSt1, which are close together, presented some similarities in vegetation composition, mainly ensured by ruderal species, probably because colonization is ensured by the same species source (ruderal species already present on the degraded areas and the along the road).

2.3.2.Environmental filter

Campos rupestres are commonly defined as constraint ecosystems, due to the dry season (water shortage lasts around 5 months), strong wind during the dry season, high daily temperature oscillations, intense irradiation (UV) (Giulietti et al. 1997). Abiotic filter is therefore expected to be a strong constraint structuring *campo rupestre* communities. Indeed, **chapter 1** stresses the relationship between environmental conditions (i.e. both granulometry and chemical properties of the soil) and vegetation composition: abiotic filter has been shown to play an important role in defining and circumscribing each community, confining some species to one or the other habitat. Both grasslands occurred in the same area, side-by-side, separated by just a few centimeters; at local scale, dispersion alone cannot explain observed patterns. During the rainy season, stony grasslands are drier than sandy grasslands: since they are usually located on slope, water runs off, and they are more impacted by water erosion and never experience temporary flooding (Vitta 1995). We also show that soil composition varies between both grasslands, maybe as a consequence of this local topography and drainage.

The importance of abiotic conditions has also been reported in **Chapter 3**. We have shown that local site characteristics and the type of substrate are important to determine primary succession (Rehounkova & Prach 2006): the degraded stony substrate seems more appropriate to spontaneous recovery, potentially due to the microsites created by stones. Soil alteration was one of the main consequences of degradation (Negreiros et al. 2011), when exploitation/road asphalting stopped, soils are not restituted entirely and construction debris may be added resulting in a highly altered soil. Thus, after road building, degraded areas presented several kinds of substrate: degraded sandy substrate, degraded stony substrate or degraded latosol substrate. All degraded soils present lower nitrogen content and tend to be less acidic than reference grasslands. Areas with degraded stony and sandy substrates tend to have lower phosphorus and organic carbon contents, on the contrary latosol degraded areas have higher phosphorus, higher pH and higher magnesium and calcium contents.

Usually environmental filter leads to a convergence of traits that are required to survive in a particular environment (under-dispersion): even if species composition differs, species that coexist are more similar than expected (Weiher & Keddy 1995, Weiher et al. 2011). This was observed by Giulietti et al. (1987) in *campos rupestres* where there is a morphological convergence between species. On the contrary, the biotic filter tends to cause trait over-dispersion in order to limit similarity and avoid niche overlapping (Weiher et al. 2011).

2.3.3.Biotic factors

Biotic filters, such as competition or facilitation are poorly studied in *campos rupestres* (Guilherme 2011). The competition strategy is unlikely because the habitat is stressful, species are thus preferentially stress tolerant first (Grime 1977). On sandy grasslands, where substrate is not partly composed by quartzitic stones, the vegetation is denser; we thus hypothesize more competition on this kind of grasslands. Only one study dealt with facilitation in *campos rupestres* and it did not highlight this kind of intra-specific interaction despite the fact that *campos rupestres* are potentially favorable to it (Guilherme 2011).

In addition, despite local differentiation and limited dispersal of many species, generating high endemism in *campos rupestres*, geographic isolation alone cannot explain population differentiation (Jesus et al. 2001, 2009), suggesting action of other evolutive forces beyond gene flow, such as localized pollinator behavior for example.

3.Can we restore *campos rupestres*?

Three kinds of restoration interventions were tested in order to initiate and accelerate the recovery of *campo rupestre* vegetation in degraded areas (Kielh et al. 2010, Godefroid et al. 2011, Pywell et al 2011). We used the filter model as a framework to set up restoration experiments and to determine what factors constraint community assembly. In the first experiment, we manipulated the dispersal filter, bringing *campo rupestre* seeds into a degraded area. Following our results, we examined the germination behavior of fifteen herbaceous species. In the second experiment, we translocated eight native species in order to overcome the dispersal filter and the germination, a critical phase for establishing in the degraded areas, and in order to improve environmental conditions bringing together soil and translocated plant. Finally, we translocated vegetation turfs: we aimed to bring to the degraded areas i) a pool of target species, ii) soil of the reference ecosystem and iii) possible associated microorganisms (Carvalho et al. 2012), therefore overcoming the dispersal, the abiotic filters and part of the biotic filter. Assessing the performance of multiple approaches is useful for testing multiple hypotheses, quickly expands the restoration toolbox in case of success, while restoration failure is also very instructive to learn about the inability of some techniques and to adapt new ones (Hilderbrand 2005).

Hay transfer is a useful technique to increase seed supply in grasslands which recorded notable success in Europe in various kinds of habitats (Patzelt et al. 2001, Hölzel & Otte 2003, Riley et al. 2004, Kiehl & Wagner 2006, Donath et al. 2007, Edwards et al. 2007, Klimkowska et al. 2009, Coiffait-Gombault et al. 2011, Baasch et al. 2012). In North America, Graf & Rochefort (2008) reported that hay transfer was less successful than in Europe probably due to the questionable viability of reintroduced seeds. Similarly, in tropical grasslands, the method failed completely, even if hay contained lots of seeds (**Chapter 3**). The large majority of observed seedlings emerging in degraded areas are ruderal non-target species which colonized on their own. Failure can be explained by i) failure in seed germination (i.e. seed dormancy, unviable seeds, unfavorable germination conditions) and/or ii) unfavorable site conditions leading to poor seedling establishment. Our regular monitoring of germination has never revealed seedling emergence either on degraded areas or in greenhouse. We therefore hypothesize, like Graf & Rochefort (2008), that hay transfer failure is primarily due to germination issues rather than establishment limitation. We then conclude that, although dispersal is a limiting factor for vegetation establishment, poor seed quality and germination are additional ones.

In order to verify this, we have carried out germination tests on 15 herbaceous native species (**Chapter 4**). Velloziaceae and Xyridaceae species have high germination, corroborating the results of other studies (Abreu & Garcia 2005, Garcia et al. 2007). On the contrary, some Cyperaceae, Poaceae and Asteraceae species record extremely low or null germination. Among these species three groups can be distinguished, species with a lot of embryoless seeds: *Richterago arenaria, Rhynchospora ciliolata, Lagenocarpus alboniger*, species with many unviable seeds: *Echinolaena inflexa* for example, and species presenting physiologically dormant seeds: *Lagenocarpus rigidus subsp. tenuifolius, Rhynchospora consanguinea or Rhynchospora riedeliana.* While collected hay was mainly composed of Cyperaceae and Poaceae seeds, embryoless seeds, low seed viability and dormancy can explain why this restoration technique has failed. Hay also contained Xyridaceae but maybe this small seeds were taken away by water runoff or wind, or the hand-vacuum equipment was not an efficient manner to collect large amount of these seeds, or seeds did not manage to germinate. On the other hand, we suppose that Velloziaceae were not present on the hay, because they do not produce lot of fruits and usually irregularly (**Chapter 2**).

Finding how to break dormancy could be key to extend restoration project and improve vegetation establishment in disturbed areas. Whereas we expected a significant relationship between fire effects and germination, we found little evidence that fire related cues enhance germination of *campo rupestre* species, whether they have non-dormant or dormant seeds, suggesting that germination is not a preferential way to regenerate after fire. However, fire stimulates flowering of some resprouter species in *campo rupestre* (Neves et al. 2011, Conceição & Orr 2012, personal observation), among which Poaceae and Cyperaceae species, which are then able to resprout rapidly and produce seeds with high germination percent. These species were never observed flowering during the two years of the phenological surveys, while they are abundant in *campos rupestres.* We therefore suggest that the ultimate goal of producing seeds might be to disperse rather than to recover.

Since dominant *campo rupestre* species do not produce fruit or have low germinability, we choose to translocate adult species rather than transplant seedlings grown from seeds in greenhouses (**Chapter 5**). Among the eight species translocated, just one, *Paspalum erianthum*, survived, grew and reproduced. Reporting failure is rare; reasons for failure are thus poorly discussed. Some studies have reported that species translocation can be hard to achieve for some species (Milton et al. 1999, Menges 2008, Godefroid et al. 2011). *Paspalum erianthum* is a grass widely distributed from North to South America and probably has higher adaptation abilities since common species have lower habitat specialization (Farnsworth 2007). On the other hand, the other species have narrower distribution usually restricted to Espinhaço Range, except *Homolepis longispicula* found all over Brazil (Forzza et al. 2010), and probably suffer from inadequate habitat. Native species transplantation was already pointed out as an efficient method to re-introduce species in degraded areas (Fattorini 2001, Soliveres et al. 2012), but some other studies underlined the variable success associated with this method especially because success is usually context-dependent (e.g. herbivory, disturbance, competition) (Ash et al. 1994, Milton et al. 1999, Menges 2008, Godefroid et al. 2011). Maybe it is possible to improve translocation success by placing microclimate shelters to minimize transplanting stress (Milton et al. 1999), however we hypothesize that root damage is too great and hampers greatly translocation success, more than environmental constraints. Establishment is a crucial step and stress-tolerant species, such as *campo rupestre* species, perform badly (Pywell et al. 2007). In future studies, using seedling transplantation (obtained in greenhouse from seeds) can also reduce root damage compared to adult translocation and then improve re-introduction success, but this is currently hampered by limited knowledge about herbaceous species germination.

Finally, we **translocated vegetation turfs** which allow the reintroduction of numerous species, such as *Tatianyx arnacites, Homolepis longispicula, Lagenocarpus rigidus* subsp. *tenuifolius*, dominant and characteristic *campo rupestre* species, for which the individual translocation failed. Species richness in these turfs decreased greatly just after translocation and was therefore quite lower to that observed in pristine areas on the same surface. Some endemic species, such as *Syngonanthus cipoensis*, survived and occurred on translocated turfs more than one year after the transplantation. This method is therefore the most successful we tested: we overcome the risk and uncertainties associated with establishing the vegetation from seeds (hay transfer) and reduce problems related to root damages (except for species located at the turf edges). Despite the presence of a highly invasive species, such as *Melinis repens,* on the area*,* this one was not found on turf yet. Long-term monitoring will permit to answer if this method is actually efficient to restore degraded *campos rupestres*, if turfs are able to sustain on degraded areas; turf translocation is known to help to restore grassland communities on the long-term (Pywell et al. 2011). So far, the vegetation has not spread outside the turfs to fill in adjacent areas, and this might need much more time (Kidd et al. 2006). However this technique was also highly destructive and donor grasslands are poorly resilient, that is why turf translocation should be considered only when habitat destruction is unavoidable, as a “rescue” measure. Nevertheless, some private areas of *campos rupestres* are already threatened to be destroyed by mining or quarrying enterprise and reclamation, rehabilitation or restoration are required by laws. In such cases, we recommend planning turf transfer in order to save a part of *campo rupestre* species instead of losing them. Soil transfer of the degraded grasslands can also be conceivable in order to improve the edaphic conditions of the degraded areas and then facilitate native plant establishment in association with other restoration methods (seeding / seedling transplantation).

4.From restoration ecology to community ecology

As presented in the introduction, restoration ecology can be useful to answer some theoretical questions in community ecology and improve understanding of community assembly. Several factors are responsible for the low resilience of *campos rupestres* following strong disturbance. The resilience is first limited by the phenology of some species, inclusive dominant species, which did not produce seeds during the two-year survey (**Chapter 2,** Figure 45), and thus did not supply the external species pool. We also hypothesize that the dispersal of main species of *campos rupestres* is limited*,* because few target species were encountered and only on some degraded areas; moreover no target species were found on the degraded seed bank (**Chapter 3,** Figure 45). However, while we could have overcome dispersal filter using hay transfer, target species of *campos rupestres* did not establish in degraded areas, which imply that limited dispersal alone cannot explain why vegetation did not recover on these areas

(**Chapter 3,** Figure 45**).** There are thus two hypotheses: germination failure and/or harsh environmental conditions impeding seedling establishment. Germination issues are another limiting factor to the recovery of *campos rupestres* (**Chapter 4,** Figure 45): some species had a high germinability while others presented embryoless, unviable seeds or dormant seeds. Finally *campos rupestres* are a mosaic of physiognomies defined by soil and topography among other, characterized by poor nutrient soil and harsh environmental conditions (**Chapter 1,** Figure 45); the abiotic filter constrains therefore vegetation assembly. A lot of species are confined to such environment and occur exclusively on *campos rupestres*; vegetation establishment in degraded areas where soils are really altered is thus unlikely. Species translocation failed to provide information about a possible limitation due to abiotic filter, because root damages were probably more fateful than inappropriate environmental conditions in such experiment (**Chapter 5,** Figure 45). Resilience of *campos rupestres* after strong disturbance is complex: we obtain the most convincing results, in terms of restoration, using turf translocation, a technique which allows to overcome dispersal filter, to modify the abiotic conditions, to overcome the critical germination step and potentially to bring into the degraded areas associated microorganisms (Carvalho et al. 2012) (**Chapter 5,** Figure 45).

Our result highlights that, while stochastic processes are important to determine patterns of species composition, deterministic processes associated with niche processes are of major importance in structuring natural communities at local scale in *campos rupestres* (Chase & Myers 2011).

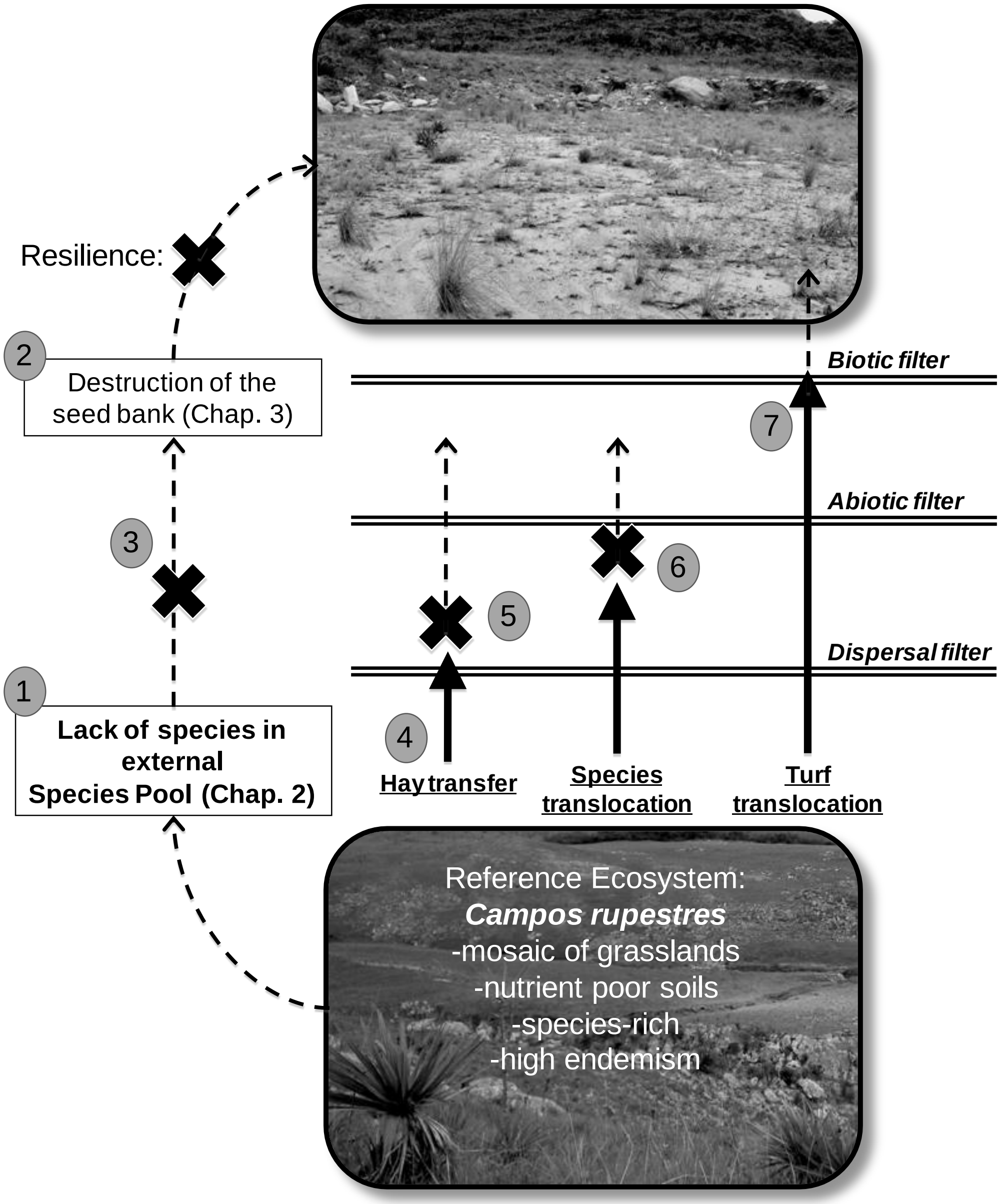

Figure 45: Main insights of the thesis. 1) Phenological survey allows showing that some species did not reproduce regularly and then are absent from the external species pool which can probably colonize degraded areas; 2) Spontaneous succession from the seed bank is unlikely because it was completely removed during the disturbance; 3) Dispersal limitation did not allow the seed bank re-composition; 4) Hay transfer, which allows overcoming the dispersal filter, was not efficient to initiate vegetation establishment on degraded areas; 5) Some species among them Poaceae & Cyperaceae failed to germinate, other germinated well like Xyridaceae or Velloziaceae but were not able to establish on degraded areas, due to unfavorable germination conditions or because hay did not contain these species; 6) Probable root damages impede species establishment, just one species *Paspalum erianthum* was reintroduce on degraded areas; 7) turf translocation was the most successful restoration method allowing to introduce native species on degraded areas, but it was also the technique which most impacted the reference grasslands.

Main considerations of this thesis

Before presenting possible perspectives, I am going to sum up the main conclusions of this research:

a) Concerning **community ecology:**

-**Chapter 1** has confirmed that *campos rupestres* are species-rich grasslands, composed by different communities due to topography and soil properties;

-**Chapter 2** has showed the variety of phenological patterns occurring on *campos rupestres* and has underlined that some species do not reproduce sexually regularly*;*

-**Chapter 3** has highlighted that *campos rupestres* are nor resilient to strong anthropogenic disturbance; *campo rupestre* seed bank is poor in seeds and species, regeneration from seed bank is thus unlikely; dispersal limitation do not allow recomposing the seed bank of degraded areas;

-**Chapter 3** has showed that dispersal limitation is not the only limiting factor to *campo rupestre* regeneration;

-**Chapter 4** has emphasized that germination behaviors vary among herbaceous species: some of them germinate well, others present dormancy or unviable seeds.

-**Chapter 4** has highlighted that fire-related cues do not enhance germination of *campo rupestre* species, despite the fact that it is a fire-prone environement;

-**Chapter 5** has confirmed the strong relationship between soil and vegetation in *campos rupestres.*

b) Concerning **restoration ecology**

-**Chapter 3** has showed that overcoming dispersion technique is not efficient *in campo rupestres*; highly altered soils and germination limitation seems the most limiting factors (**Chapter 4**);

-**Chapter 5** has underlined that species translocation is risky and not successful for the majority of native species;

-**Chapter 5** has found that the best manner to restore degraded *campos rupestres* is turf translocation;

-**Chapter 5** has confirmed that this technique must be used only when habitat destruction is already planned, as a “rescue” measure due to the low resilience of destructed *campos rupestres*.

c) Concerning **ecological restoration**

-In case of unavoidable degradation, we suggest to proceed with a “rescue” program including translocation of vegetation turf destroyed or at least to conserve topsoil.

-These techniques can be associated with the transplantation of woody species (Le Stradic et al. 2008).

Perspectives

1.To increase studies at large scale and use functional traits

New species are found regularly on *campos rupestres*, thus not all the species composing them are known; and this is a barrier for understanding how the system works. However, it seems important to improve research in order to understand processes generating biodiversity, structuring communities and allowing the coexistence of species, especially at large scales (e.g. Echternacht et al. 2011); studies on *campos rupestres* cannot be limited solely to species lists. McGill et al. (2008) argue that community ecology should be re-built using general traits, overcoming barrier linked to species list (Lawton 1999, Simberloff 2004), and bringing general patterns to community ecology. Indeed the use of functional traits is becoming more and more common in community ecology (Cadotte et al., 2011). Then developing researches on functional traits at the scale of the Espinhaço Range will allow drawing some general patterns in *campos rupestres,* because they allow comparisons between different regions and scales (Lavorel et al. 2002, Westoby & Whright 2006). They are also a useful tool to better define potential ecosystem services associated with *campos rupestres* (Lavorel et al. 2011). In addition, other functionnal aspects, such as dormancy, sclerophylly, water-economy, light harvesting, temperature control, architectural convergence, dispersal (fundamental factor shaping the communities), etc. are poorly known and need more studies. Their long evolutionary history is another aspect which still needs to be investigated.

Here, we have initiated work in order to detect whether some abiotic factors (soil properties) impact community structure. Like Agrawal et al. (2007), we argue that increasing the number of quantitative experimental designs is essential to quantify the magnitude of effects of abiotic and biotic factors, such as competition, facilitation or nutrient availability, and in order to define well their relative importance. Currently, researches on biotic interaction are almost nonexistent, especially concerning positive interactions, such as plant-plant facilitation, despite the fact that these interactions can be useful in restoration (Padilla & Pugnaire 2006).

2.Effect of fire on reproductive phenology

Although *campos rupestres* are a fire-prone environment, few studies deal with this subject, partly because legislation complicates the implementation of fire study. We show here that some species, including some dominant Poaceae, did not reproduce sexually during our two-year survey. However, in August 2011, a fire occurred on Serra do Cipó, and just after (some days), some species flowered among which *Bulbostylis paradoxa* (Figure 46a). A few months after, almost all individuals of species like *Tatianyx arnacites* or *Homolepis longispicula* flowered as well (Figure 46b). It was already reported that fire stimulates flowering of *campos rupestres* species (Munhoz & Felfili 2005, Neves et al. 2011, Conceição & Orr 2012). Then it should be interesting to compare phenological patterns before and after fire, to underline whether species are enhanced by fire to produce flower and fruits. This study should also be realized in association with germination studies. We showed in this thesis that some seeds produced just after fire had a high germinability; however more species need to be tested to draw more global patterns. It is also interesting to assess if such seeds with high germinability can be used to restore degraded areas.

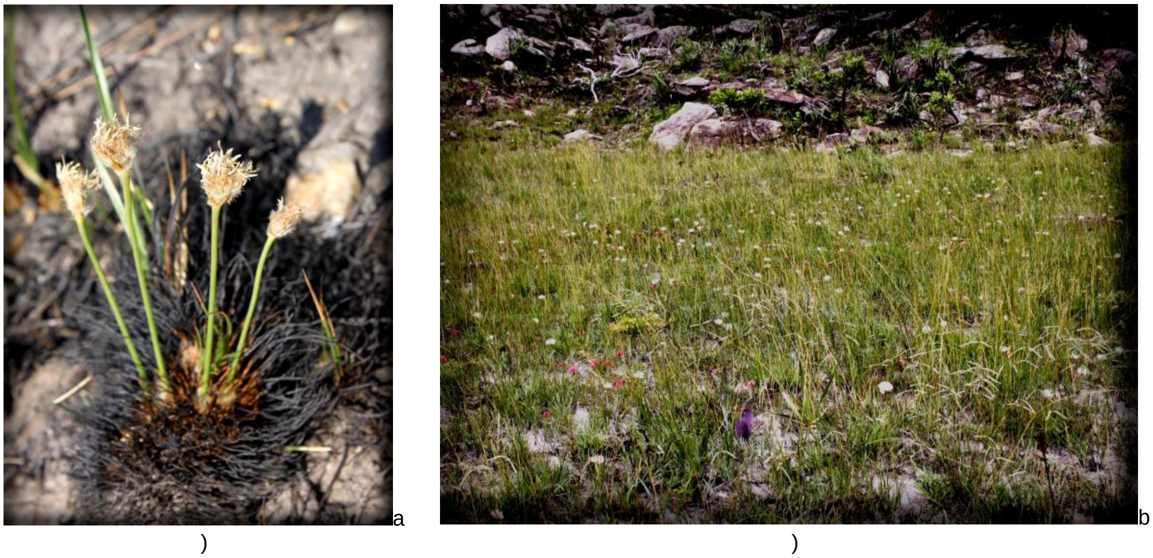

Figure 46: a) *Bulbostylis paradoxa* flowering a few days after a fire, and b) on sandy grasslands, lot of species flowering after a fire. (Photos S. Le Stradic)

3.Understanding regeneration after natural disturbance

Understanding how natural processes operate following natural disturbances allows us to use these processes to restore highly disturbed sites (Prach & Hobbs 2008, Polster 2009, Prach & Walker 2011). In *campos rupestres*, fire is the most frequent disturbance and some studies have already demonstrated that these grasslands are particularly resilient to fire (Neves et Conceição 2010, Hernandez 2012). In August 2011, one of our study sites burnt and, five months after fire, vegetation cover and density in both sandy and stony grasslands have quite similar value to those before fire (Hernandez 2012) (Figure 47). In fire-prone environment, species can (1) resist to fire, conserving a part of their aboveground biomass, (2) resprout, recovering after fire *via* vegetative regeneration and (3) germinate from the seed bank or from newly dispersed seeds (Hoffmann 1998, Keeley & Fotheringham 2000, Pausas et al. 2004, Bond & Keeley 2005). Fire stimulated germination was not encountered in this thesis but we studied few species and therefore other species have to be tested. Moreover, in the Cerrado, in response to fire (one of the most frequent disturbance), vegetative reproduction is a frequent strategy, much more successful than sexual reproduction (Hoffmann 1998). In *campos rupestres*, hemicryptophyte species are largely dominant, also suggesting a selection pressure by fire in these kinds of tropical grasslands: hemicrytophyte species are able to re-grow from underground buds and organs which remain viable after fire (Coutinho 1990). Fidelis et al. (2010) pointed out the importance of the bud bank in tropical and subtropical grasslands subjected to fire, which replace the seed bank in such communities. A bud bank study could therefore be the next step to understand how *campos rupestres* overcome natural disturbances, such as fire, and use this knowledge to restore them. Finally it is important to incorporate the management of natural disturbances, such as fire, as a tool in restoration (Fuhlendorf & Engle 2004) and its potential use (e.g. to enhance sexual or vegetative reproduction of transplanted species) should be assessed.

Figure 47: Resilience of sandy grasslands after a fire a) in September 2011: one week after a fire, and b) in January 2012: four month and a half after a fire.

4. Germination

We have demonstrated in Chapter 3 & 4 that germination issues limit restoration using simple techniques, such as seeding or hay transfer, mainly because some species produce unviable or dormant seeds. Fire-related cues did not enhance germination and did not break dormancy of dormant seeds. Further studies are therefore needed to understand seed dormancy, how this trait evolved and how it is possible to break dormancy.

5. Looking for new restoration techniques

As shown in the present thesis, the most successful method to introduce native species on degraded areas was also the most destructive one, which limits its application. In such a context, it is currently important to look for new methods to propagate plants, such as rhizome transplant (Cooper & MacDonald 2000) or tissue culture (Kock 2007). This latter is a costly and difficult propagation method,only used when there are biological barriers to other methods, such as in *campos rupestres*. This method should be developed for a species in which sexual reproduction issues were identified in the previous studies, since plants produced by tissue culture are often species that invest energy into underground biomass to ensure survival. However the development of tissue culture methods is a very slow process and it can take several years to learn how to produce some species in mass (Kock 2007).

Conclusion

Campos rupestres harbour a great biodiversity and provide valuable services for human well-being including cultural, spiritual and recreational ones. Unfortunately they are extremely threatened by land-use changes, as mining, quarrying, road construction or unplanned development. Our results allow a better understanding of a part of the history of these peculiar grasslands. However, current knowledge did not allow the development of an efficient technique to restore them. In the words of Robert et al. (2009) “our planet’s future may depend on the maturation of the young discipline of ecological restoration”, nevertheless, for the moment, concerning campos rupestres, the preservation of pristine areas should be emphasize and prioritize due to the difficulty to restore them

General view of *campos rupestres.* Photo credit S. Le Stradic

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Appendix Chapter 1

Appendix 1: Plant list. Life forms (Raunkiaer (1904) modified by Mueller-Dombois and Ellenberg (1974)): He: Hemicryptophyte, CH: Chamaephyte, NA: Nanophanerophyte, HL: Hemicryptophytic Liana, GE: Geophyte, TH: Therophyte. Plant forms: F: Forbs, G: Graminoids, Ss: Sub-shrub, S: Shrub, L: Liana, Fe: Fern. Habitats in Brazil (Giulietti et al. 1987, Forzza et al. 2010): CR: campos rupestres, AG: altitude grassland, Ce: cerrado, Ca: Caatinga, AtR: Atlantic rainforest, AmR: Amazon rainforest, WG: wet grassland. Distribution range (Giulietti et al. 1987, Forzza et al. 2010, database SpeciesLink): (a) Serra do Cipó, (b) Espinhço range in the state of Minas Gerais, (c) Espinhaço Range, (d) State of Minas Gerais, (e) Brasil, (f) Wide distribution. IUCN status (Fundação Biodiversitas para o Estado de Minas Gerais (Mendonça and Lins 2000)): VU: Vulnerable, CR: Critical, EN: Endangered. Life cycle: A: annuals and P: perennials. R: species observed resprouting after fire, empty cells mean no observation of the species in the burnt area.

Species	Author	Life form	Plant form	Habitats in Brazil	Distribution range	IUCN	Life-cycle	Resprouters post-fire	Presence in sandy grasslands	Presence in stony grasslands	Mean IVI in sandy grasslands	Mean IVI in stony grasslands	Mean Relative Dominance in sandy grasslands (%)	Mean Relative Dominance in stony grasslands (%)
Amaranthaceae									X	X				
Gomphrena incana	Mart.	HE	F	CR	d		P	R	X	X	0.276	0.640	0.063	0.235
Gomphrena scapigera	Mart.	HE	F	CR, AG	d		P	R	X	X	2.214	0.037	0.433	0.006
Pfaffia denudata	(Moq.) Kuntze	HE	F	CR, AG	e		P	-	X	X	0.107	0.010	0.010	0.001
Apocynaceae									X	X				
Hemipogon hemipogonoides	(Malme) Rapini	HE	F	CR	d		P	R	X	X	0.106	0.016	0.011	0.003
Minaria ditassoides	(Silveira) T.U.P.Konno & Rapini	HE	Ss	CR	d		P	R	X	X	0.039	0.194	0.006	0.025
Oxypetalum cf montanum		HL	L				P	-	X		0.012	-	0.002	-
Apocynaceae sp1		HE	F				P	-	X		0.012	-	0.002	-
Apocynaceae sp2		HE	F				P	-		X	-	0.068	-	0.014
Apocynaceae sp3		HE	F				P	-		X	-	0.024	-	0.016
Apocynaceae sp4		HE	F				P	-		X	-	0.009	-	0.002

Species	Author	Life form	Plant form	Habitats in Brazil	Distribution range	IUCN	Life-cycle	Resprouters post-fire	Presence in sandy grasslands	Presence in stony grasslands	Mean IVI in sandy grasslands	Mean IVI in stony grasslands	Mean Relative Dominance in sandy grasslands (%)	Mean Relative Dominance in stony grasslands (%)
Asteraceae									X	X				
Calea coronopifolia	Sch.Bip. ex Krasch.	HE	Ss	CR	d		P	R	X		0.083	-	0.022	-
Echinocoryne schwenkiaefolia	(Mart. ex Mart.) H.Rob.	HE	Ss	Ce	d		P	-	X		0.012	-	0.002	-
Inulopsis scaposa	(DC.) O. Hoffm.	HE	F	Ce, AtR	e		P	R	X	X	0.407	0.234	0.087	0.030
Lepidaploa sp.		HE	Ss				P	-	X		0.012	-	0.002	-
Lessingianthus linearifolius	(Less.) H.Rob.	HE	Ss	Ce	c		P	R	X	X	0.035	0.127	0.005	0.018
Lessingianthus psilophyllus	(DC.) H.Rob.	HE	Ss	Ce	e		P	R	X	X	0.619	0.149	0.079	0.021
Lychnophora joliana	Semir & Leitão (unresolved name)	NA	Ss				P	R		X	-	0.032	-	0.013
Lychnophora passerina	(Mart. ex DC.) Gardner	NA	Ss	CR	c	VU	P	-	X	X	0.030	0.010	-	-
Lychnophora rupestris	Semir & Leitão (unresolved name)	NA	Ss	CR	a		P	R		X	-	0.034	-	0.014
Minasia sp		HE	F	CR	a		P	-		X	-	0.170	-	0.070
Porophyllum angustissimum	Gardner	HE	Ss	Ce	e		P	R	X	X	0.074	0.081	0.020	0.023
Prestelia eriopus	Sch.Bip.	HE	F	CR	a	CR	P	R		X	-	1.887	-	0.596
Richterago arenaria	(Baker) Roque	HE	F	CR	b	VU	P	R	X	X	1.517	1.909	0.380	0.584
Richterago polymorpha	(Less.) Cabrera	HE	F	CR	d	EN	P	R	X		0.270	-	0.133	-
Richterago polyphylla	(Baker) Cabrera	HE	Ss	CR	b	CR	P	R	X	X	0.046	0.915	0.004	0.182
Richterago revoluta	Leitão Filho	HE	F	CR	b		P	R	X	X	0.061	0.008	0.002	0.001
Trichogonia hirtiflora	(DC.) Sch.Bip. ex Baker	HE	Ss	CR	b		P	-		X	-	0.008	-	0.002
Asteraceae sp1		CH	F				P	-	X		0.012	-	0.002	-
Asteraceae sp2		HE	Ss				P	R	X		0.015	-	0.002	-
Bignoniaceae									X					
Jacaranda racemosa	Cham.	CH	Ss	CR	d	EN	P	R	X		0.124	-	0.050	-
Bromeliaceae										X				
Encholirium heloisae	(L.B.Sm.) Forzza & Wand.	HE	F	CR	a	CR	P	-		X	-	0.008	-	0.001

Species	Author	Life form	Plant form	Habitats in Brazil	Distribution range	IUCN	Life-cycle	Resprouters post-fire	Presence in sandy grasslands	Presence in stony grasslands	Mean IVI in sandy grasslands	Mean IVI in stony grasslands	Mean Relative Dominance in sandy grasslands (%)	Mean Relative Dominance in stony grasslands (%)
Convolvulaceae									X	X				
Evolvulus lithospremoides var.lithospermoides	Mart.	HE	F	Ce	e		P	R	X	X	0.012	0.026	0.002	0.003
Ipomoea aff procumbens	Mart. ex Choisy	HE	Ss	CR	a		P	R	X	X	0.067	0.066	0.009	0.010
Ipomoea serpens	Meisn.	HL	L	CR	d		P	-	X		0.083	-	0.006	-
Cyperaceae									X	X				
Bulbostylis cf capillaris	(L.) C.B.Clarke	HE	G		f		P	-		X	-	0.915	-	0.122
Bulbostylis conifera	(Kunth) C.B.Clarke	HE	G		f		P	-		X	-	0.311	-	0.060
Bulbostylis eleocharoides	Kral & M.T. Strong	HE	G		f		P	R	X		0.014	-	0.002	-
Bulbostylis emmerichiae	T.Koyama	HE	G	Ce	f	EN	P	R	X	X	5.382	0.233	1.066	0.031
Bulbostylis lombardii	Kral & M.T.Strong	HE	G	CR, Ce	a	EN	P	R	X	X	0.109	2.932	0.040	0.713
Bulbostylis paradoxa	(Spreng.) Lindm.	HE	G		f		P	R	X	X	2.206	2.713	1.092	1.149
Bulbostylis scabra	(J.Presl & C.Presl) C.B.Clarke	HE	G		f		P	-	X	X	0.124	0.042	0.059	0.006
Bulbostylis sp1		HE	G				P	-		X	-	0.286	-	0.029
Bulbostylis sp2		HE	G				P	-		X	-	0.008	-	0.001
Lagenocarpus alboniger	(A.St.-Hil.) C.B.Clarke	HE	G	CR	c		P	R	X	X	0.905	3.690	0.579	2.259
Lagenocarpus velutinus	Nees	HE	G	CR	b		P	R	X		1.084	-	0.612	-
Lagenocarpus tenuifolius	(Boeck.) C.B.Clarke	HE	G	CR	c		P	R	X	X	1.730	14.936	1.187	8.908
Lagenocarpus rigidus subsp. tenuifolius	(Kunth) Nees subsp. *tenuifolius* (Boeck.) T.Koyama & Maguire	HE	G	CR	c		P	R	X	X	20.716	5.029	12.833	2.692
Rhynchospora ciliolata	Boeck.	HE	G	CR	c		P	R	X	X	2.000	0.143	1.226	0.060
Rhynchospora consanguinea	(Kunth) Boeck.	HE	G	CR, Ce	e		P	R	X	X	8.072	4.295	0.481	0.154
Rhynchospora emaciata	(Nees) Boeck.	HE	G		f		P	-	X	X	0.078	0.380	0.007	0.048
Rhynchospora globosa	(Kunth) Roem. & Schult.	HE	G		f		P	-	X	X	0.169	0.432	0.022	0.071
Rhynchospora patuligluma	Lindm.	HE	G	Ce	e		P	R	X		2.292	-	0.307	-
Rhynchospora pilosa	(Kunth) Boeck.	HE	G		f		P	-	X		0.139	-	0.041	-

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Rhynchospora recurvata	(Nees) Steud.	HE	G	CR, Ce	c		P	-		X	-	0.219	-	0.112
Rhynchospora riedeliana	C.B. Clarke	HE	G		c		P	R	X	X	9.443	4.315	3.806	1.445
Rhynchospora tenuis	Link	HE	G		f		P	R	X	X	1.128	0.014	0.319	0.001
Rhynchospora tenuis subsp austro-brasiliensis	subsp. *austrobrasiliensis* T. Koyama	HE	G		f		P	R	X	X	11.329	4.634	2.497	0.790
Rynchospora terminalis	(Nees) Steud.	HE	G	Ce	e		P	R	X	X	6.271	5.994	1.483	1.339
Rhynchospora sp1	*(Kunth) Boeck.*	HE	G		f		P	R	X	X	1.297	0.840	0.667	0.303
Rhynchospora sp2		HE	G				P	-		X	-	0.017	-	0.001
Scleria cuyabensis	Pilg.	HE	G	CR	e		P	R	X		0.379	-	0.101	-
Scleria hirtella	Sw.	HE	G		f		P	R	X	X	0.661	0.179	0.033	0.013
Scleria stricta	Kunth	HE	G	AtR	e		P	R		X	-	0.899	-	0.398
Cyperaceae sp1		HE	G				P	-	X		0.051	-	0.017	-
Cyperaceae sp2		HE	G				P	-	X		0.088	-	0.018	-
Cyperaceae sp3		HE	G				P	-	X		0.504	-	0.156	-
Cyperaceae sp4		HE	G				P	-	X	X	0.766	0.739	0.238	0.185
Dicotyledone									X	X				
Dicotyledon 1		HE	Ss				P	-	X		0.011	-	0.002	-
Dicotyledon 2		HE	F				P	-	X		0.022	-	0.002	-
Dicotyledon 3		HE	Ss				P	-		X	-	0.008	-	0.002
Dicotyledon 4		HE	Ss				P	-	X		0.012	-	0.002	-
Dicotyledon 5		HE	Ss				P	-	X		0.012	-	0.002	-
Dicotyledon 6		HE	Ss				P	-		X	-	0.014	-	0.001
Dioscoreaceae									X	X				
Dioscorea debilis	Uline ex R.Knuth	HL	L	CR	c		P	-		X	-	0.018	-	0.003
Dioscorea stenophylla	Uline	HL	L	Ce	c		P	-	X	X	0.047	0.256	0.007	0.017
Droseracea									X	X				
Drosera montana var. hirtella	A. St.-Hil.	HE	F	Ce, Ca, AtR	e		P	-	X		0.012	-	0.002	-

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Drosera montana var. montana	A. St.-Hil.	HE	F	Ce, Ca, AtR	e		P	-	X	X	0.559	0.520	0.045	0.066
Drosera quartzicola	Rivadavia & Gonella	HE	F	CR	a	CR	P	-	X	X	-	0.131	-	0.013
Ericaceae									X	X				
Agarista duartei	(Sleumer) Judd	HE	Ss	CR	a		P	R	X	X	0.053	0.028	0.023	0.003
Gaylussacia riedelii	Meisn.	HE	Ss	CR	a		P	R		X	-	0.272	-	0.091
Eriocaulaceae									X	X				
Leiothrix crassifolia	(Bong.) Ruhland	HE	F	CR	b		P	R	X	X	2.384	0.121	0.738	0.023
Leiothrix curvifolia	(Bong.) Ruhland	HE	F	CR	b		P	-	X	X	0.014	1.682	0.002	0.189
Paepalanthus chlorocephalus	Silveira	HE	F	CR	a		P	R	X	X	0.136	0.249	0.059	0.076
Paepalanthus geniculatus	Kunth	HE	F				P	R	X	X	2.544	2.232	0.662	0.520
Paepalanthus macrocephalus	(Bong.) Koern.	HE	F				P	-		X	-	0.144	-	0.045
Paepalanthus nigrescens	Silveira	HE	F	CR	b		P	R		X	-	2.267	-	0.544
Paepalanthus paulinus	Ruhland	HE	F				P	-	X	X	0.017	0.242	0.002	0.041
Paepalanthus pubescens	Koern.	HE	F				P	-	X		0.086	-	0.025	-
Paepalanthus sp1		HE	F				P	-		X	-	0.008	-	0.002
Syngonanthus aciphyllus	Ruhland	HE	F			EN	P	-		X	-	0.021	-	0.002
Syngonanthus anthemidiflorus	(Bong.) Ruhland	HE	F	CR	b		P	-	X	X	0.701	0.042	0.067	0.005
Syngonanthus cipoensis	Ruhland	HE	F	CR	a		P	R	X	X	4.211	1.039	1.152	0.262
Syngonanthus circinnatus	(Bong.) Ruhland	HE	F	CR	a	EN	P	-		X	-	0.156	-	0.003
Syngonanthus gracilis	(Bong.) Ruhland	HE	F		f		P	-		X	-	-	-	-
Syngonanthus vernonioides var. vernonioides	(Kunth) Ruhland	HE	F	CR	d		P	R	X	X	0.201	1.479	0.013	0.038
Euphorbiaceae									X	X				
Croton timandroides	Müll. Arg.	HE	Ss	Ce, Ca	e		P	-	X	X	0.029	0.002	0.002	-

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Phyllanthus choretroides	Müll.Arg.	HE	Ss	CR	d		P	-	X	X	0.247	0.009	0.132	0.002
Sebastiana ditassoides	(Didr.) M. Arg.	HE	Ss	Ce	e		P	R	X	X	0.329	1.040	0.092	0.312
Fabaceae									X	X				
Calliandra linearis	Benth.	CH	Ss	CR	a		P	R	X	X	3.617	2.129	1.379	0.848
Chamaecrista desvauxii var. langsdorffii	(Collad.) Killip *var. langsdorffii* (Kunth ex Vogel) H.S. Irwin & Barneby	CH	Ss	Ce	e		P	R	X	X	0.163	0.107	0.062	0.021
Chamaecrista ochnacea var. purpurascens	(Vogel) H.S.Irwin & Barneby *var. purpurascens* (Benth.) H. S. Irwin & Barneby	CH	Ss	CR	b		P	R	X	X	0.051	0.392	0.021	0.166
Chamaecrista papillata	H.S.Irwin & Barneby	CH	Ss	CR	d		P	R	X	X	0.178	0.306	0.140	0.182
Gentianaceae									X	X				
Curtia diffusa	(Mart.) Cham.	TH	F	CR	b		A	-	X	X	0.115	0.032	0.007	0.002
Iridaceae									X	X				
Pseudotrimezia cipoana	Ravenna	GE	F	CR	a	VU	P	R	X	X	0.641	2.718	0.041	0.097
Sisyrinchium vaginatum	Spreng.	GE	F	CR, AG	f		P	R	X	X	0.135	0.042	0.030	0.006
Trimezia juncifolia	(Klatt) Benth. & Hook. f.	GE	F	Ce	e		P	R	X	X	0.731	0.375	0.065	0.045
Trimezia fistulosa var. fistulosa	Foster	GE	F	CR	a	VU	P	R		X	-	0.146	-	0.031
Trimezia truncata	Ravenna	GE	F	CR	c		P	R	X	X	0.021	0.086	0.002	0.016
Lamiaceae							P		X	X				
Eriope arenaria	Harley	HE	Ss	CR	b		P	R	X	X	0.444	0.239	0.080	0.088
Hyptis complicata	A.St.-Hil. ex Benth.	HE	Ss				P	-		X	-	0.107	-	0.058
Hyptis sp1		HE	Ss				P	-		X	-	0.020	-	0.003
Lentibulariaceae									X	X				
Utricularia laciniata	A. St.-Hil. & Girard	TH	F	CR, WG	c		A	-		X	-	0.050	-	0.009

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Utricularia pusilla	Vahl.	TH	F	Ce, Ca, AmR, AtR	e		A	-	X	X	1.155	0.029	0.033	0.001
Loganiaceae										X				
Spigelia aceifolia	Woodson	HE	F	CR	a	EN	P	R		X	-	0.022	-	0.003
Lythraceae									X	X				
Cuphea ericoides var. ericoides	Cham. & Schlechtd	HE	Ss	CR, Ca	c		P	R	X	X	0.181	0.008	0.025	0.002
Diplusodon ciliiflorus	*Koehne*	CH	Ss	CR	b		P	-	X		0.012	-	0.002	-
Diplusodon orbicularis	Koehne	CH	Ss	CR	a	VU	P	R	X	X	0.517	3.941	0.094	1.003
Malpighiaceae									X	X				
Banisteriopsis campestris	(A.Juss.) Little	CH	S	Ce, Ca	e		P	R	X	X	0.343	0.065	0.275	0.042
Byrsonima cipoensis	Mamede	CH	S	CR	a		P	R	X	X	0.085	0.010	0.075	0.001
Byrsonima cydoniifolia	A. Juss.	HE	S	Ce	e		P	-		X	-	0.022	-	0.015
Byrsonima dealbata	Griseb.	HE	S	CR	c		P	R		X	-	0.053	-	0.042
Camarea axillaris	A. St.-Hil.	HE	F	CR	c		P	-		X	-	0.030	-	0.015
Tetrapteryx microphylla	(A.Juss.) Nied	CH	S	Ce, Ca	e		P	R		X	-	0.293	-	0.231
Malpighiaceae sp 1		CH	S				P	-		X	-	0.023	-	0.014
Melastomataceae							P		X	X				
Cambessedesia hilariana	DC.	HE	Ss	Ce	e		P	-	X		0.039	-	0.019	-
Cambessedesia semidecandra	A.B.Martins	HE	Ss	CR	a		P	R	X	X	0.586	0.019	0.225	0.003
Chaetostoma armatum	(Spreng.) Cogn.	CH	Ss	Ce	e		P	-	X		0.014	-	0.002	-
Lavoisiera caryophyllea	A.St.-Hil. ex Naudin.	CH	S	CR	a		P	R	X	X	0.133	0.823	0.012	0.040
Lavoisiera confertiflora	Rich. ex Naudin.	CH	S	CR	b		P	R	X	X	0.263	0.058	0.052	0.031
Marcetia acerosa	DC.	CH	S	CR	b	EN	P	R		X	-	1.436	-	0.658
Marcetia taxifolia	(A.St.-Hil.) DC.	CH	S	Ce, Ca, AmR, AtR	e		P	R		X	-	0.500	-	0.303

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Microlicia juniperina	A.St.-Hil.	HE	Ss	CR	d		P	-		X	-	0.049	-	0.006
Microlicia multicaulis	Mart. ex Naudin.	HE	Ss	CR	d		P	R	X	X	0.163	0.215	0.059	0.044
Siphantera arenaria	(DC.) Cogn.	HE	F	CR	b		P	R		X	-	0.357	-	0.079
Orchidaceae									X	X				
Cyrtopodium parviflorum	Lindl.	GE	F	Ce, Ca, AtR	f		P	R		X	-	0.016	-	0.002
Epistephium sclerophyllum	Lindl.	GE	F	Ce, Ca, AmR	f		P	R		X	-	0.015	-	0.002
Orchid no id							A	-			0.445	0.141	0.040	0.021
Orobanchaceae									X	X				
Agalinis brachyphylla	(Cham. & Schltdl.) D'Arcy	HE	Ss	CR	d		P	R		X	-	0.159	-	0.016
Buchnera palustris	(Aubl.) Spreng.	HE	F	Ce, Ca, WG, AmR	f		A	-	X		0.047	-	0.007	-
Poaceae									X	X				
Andropogon brasiliensis	A.Zanin & Longhi-Wagner	HE	G	Ce	d		P	R		X	0.022	0.766	0.002	0.273
Andropogon carinatus	Nees	HE	G	Ce	f		P	R		X	-	1.313	-	0.376
Andropogon cf ingratus		HE	G				P	-		X	-	1.313	-	0.438
Andropogon macrothrix	Trin.	HE	G	CR, AG	f		P	R		X	-	0.496	-	0.197
Anthaenantia lanata	(Kunth) Benth.	HE	G	Ce, AmR, AtR	f		P	R	X	X	1.136	0.086	0.359	0.024
Apochloa cipoense	(Renvoize & Sendulsky) Zuloaga & Morrone	HE	G	CR	d		P	-	X	X	0.281	1.068	0.096	0.273
Apochloa sp1		HE	G				P	-		X	-	0.204	-	0.054
Ctenium brevispicatum	Smith	HE	G	Ce	e		P	R	X	X	0.888	1.569	0.535	0.506
Aristida torta	(Nees) Kunth	HE	G	Ce, Ca, AmR	f		P	-	X	X	0.312	0.292	0.087	0.051

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Aulonemia effusa	(Hack.) McClure	HE	G	Ce, Ca	e	VU	P	R		X	-	0.054	-	0.017
Axonopus brasiliense	(Spreng.) Kuhlm.	HE	G	Ce, Ca, AmR, AtR	f		P	R	X		0.043	-	0.002	-
Axonopus fastigiatus	(Nees ex Trin.) Kuhlm.	HE	G	Ce, Ca, AtR	e		P	R		X	-	0.703	-	0.224
Axonopus cf fissifolius		HE	G	Ce, Ca, AmR, AtR	f		P	-		X	-	0.023	-	0.001
Echinolaena inflexa	(Poir.) Chase	HE	G	Ce, Ca, AmR, AtR	f		P	R	X	X	1.174	0.250	0.407	0.062
Homolepis longispicula	(Döll) Chase	HE	G	Ce	e		P	R	X	X	37.323	14.706	12.350	4.809
Mesosetum exaratum	(Trin.) Chase	HE	G	CR	b	VU	P	R	X	X	16.195	43.169	6.194	14.660
Mesosetum loliiforme	(Hochst.) Chase	HE	G	Ce, Ca, WG, AmR, AtR	f		P	R	X	X	1.382	0.588	0.473	0.188
Panicum cyanescens	Nees	HE	G	Ce, Ca, AmR, AtR	f		P	R	X	X	4.419	0.529	1.122	0.167
Paspalum erianthum	Nees ex Trin.	HE	G	Ce, Ca, AtR	f		P	R	X	X	29.986	11.676	7.356	2.242
Paspalum guttatum	Trin.	HE	G	Ce, AtR	e		P	-		X	-	0.010	-	0.002
Paspalum hyalinum	Nees ex Trin.	HE	G	Ce, Ca, AmR, AtR	f		P	-	X		2.924	-	0.706	-
Paspalum pectinatum	Nees ex Trin.	HE	G	Ce, AmR, AtR	f		P	R	X	X	0.438	3.566	0.247	1.727

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Paspalum polyphyllum	Nees	HE	G	Ce, Ca, AmR, AtR	f		P	-		X	-	0.004	-	-
Paspalum sp1		HE	G				P	-	X		0.042	-	0.002	-
Schizachyrium sanguineum	(Retz.) Alston	HE	G	Ce, Ca	f		P	R		X	-	1.227	-	0.487
Schizachyrium tenerum	Nees	HE	G	Ce, AtR	f		P	R	X	X	3.144	6.628	0.803	1.576
Schizachyrium sp		HE	G				P	-	X		0.608	-	0.158	-
Sporobolus sp		HE	G				P	-	X	X	0.101	0.081	0.021	0.031
Tatianyx arnacites	(Trin.) Zuloaga & Soderstr.	HE	G	CR	c		P	R	X	X	40.237	28.943	17.690	12.825
Trachypogon spicatus	(L.f.) Kuntze	HE	G	Ce, Ca, AmR, AtR	f		P	R	X	X	6.521	10.810	2.604	4.051
Poaceae sp1		HE	G				P	-	X		0.498	-	0.203	-
Poaceae sp2		HE	G				P	-		X	-	0.023	-	0.001
Poaceae sp3		HE	G				P	-	X		0.058	-	0.003	-
Poaceae sp4		HE	G				P	R	X	X	3.963	4.632	1.103	1.309
Poaceae sp5		HE	G				P	-	X		0.012	-	0.002	-
Polygalaceae								-	X	X				
Polygala apparicioi	*Brade*	TH	F	CR	a		A	R	X		0.012	-	0.002	-
Polygala celosioides	Mart. ex A.W.Benn.	TH	F	Ce, AmR, AtR	f		A	-	X		0.150	-	0.014	-
Polygala cneorum	A.St.-Hil.	HE	Ss	Ce, AtR	e		P	R	X		0.045	-	0.004	-
Polygala glochidiata	Kunth.	TH	F	Ce, Ca, AmR, AtR	f		A	-	X		0.306	-	0.026	-
Polygala hebeclada var. hebeclada	DC.	HE	F	Ce, AtR	e		P	-	X		0.013	-	0.002	-

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Polygala hirsuta	A. St.-Hil & Moq.	HE	F	Ce, Ca, AtR	e		P	-	X		0.021	-	0.002	-
Polygala paniculata	L.	TH	F	Ce, Ca, AmR, AtR	f		A	-	X		0.024	-	0.004	-
Polygala sp1		HE	F				P	-		X	-	0.008	-	0.002
Polygonaceae									X	X				
Coccoloba cereifera	Schwacke	CH	S	CR	a	CR	P	R	X	X	0.203	0.174	0.135	0.097
Pterydaceae										X				
Pellaea cymbiformis	J.Prado	HE	Fe	*CR*	b	*CR*	P	R		X	-	0.335	-	0.075
Rapateaceae									X					
Cephalostemon riedelianus	Koern.	HE	G	CR	b		P	R	X		0.118	-	0.085	-
Rubiaceae									X	X				
Declieuxia fruticosa	(Willd. ex Roem. & Schult.) Kuntze	HE	Ss	Ce, Ca, AmR, AtR	f		P	-		X	-	0.031	-	0.005
Declieuxia gracilis	J.H.Kirkbr.	HE	F	CR	a		P	-		X	-	0.008	-	0.002
Declieuxia irwinii	J.H.Kirkbr.	HE	F	CR	a		P	R	X		0.043	-	0.004	-
Galianthe peruviana	(Pers.) E.L.Cabral	HE	Ss	Ce	f		P	R		X	-	0.666	-	0.106
Santalaceae									X	X				
Thesium brasiliense	A.DC.	HE	Ss	CR	e		P	R	X	X	0.248	0.360	0.044	0.060
Turneraceae									X	X				
Turnera cipoensis	Arbo	HE	F	CR	a		P	R	X	X	0.585	0.251	0.050	0.035
Velloziaceae									X	X				
Barbacenia blackii	L.B.Sm.	HE	F	CR	a		P	R		X	-	0.798	-	0.360
Barbacenia flava	Mart. ex Schult. & Schult.f.	NA	Ss	CR	d		P	R	X	X	0.343	0.794	0.284	0.565
Barbacenia sp1		HE	F				P	-		X	-	0.161	-	0.068

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Vellozia albiflora	Pohl	HE	F	Ce, Ca, AtR	e		P	R		X	-	1.284	-	0.487
Vellozia caruncularis	Mart. ex Seub.	HE	F	CR	b		P	R	X	X	0.544	9.369	0.384	6.133
Vellozia epidendroïdes	Mart. ex Schult. & Schult.f.	HE	F	CR	b		P	R	X	X	7.721	5.761	4.435	2.712
Vellozia resinosa	Mart.	HE	F	Ce	d		P	R	X	X	0.115	12.401	0.090	8.780
Vellozia sp		HE	F				P	-	X		0.072	-	0.038	-
Verbenaceae									X	X				
Lippia florida	Cham.	HE	Ss	Ce	b		P	-		X	-	0.021	-	0.001
Stachytarpheta procumbens	Moldenke	HE	Ss	Ce	b	EN	P	R	X	X	0.013	0.010	0.002	0.001
Vochysiaceae									X	X				
Vochysia elliptica var. elliptica	Mart.	CH	Ss	Ce	c		P	R		X	-	0.029	-	0.003
Vochysia pygmaea	Bong.	CH	Ss	CR	b	VU	P	R	X	X	0.276	1.135	0.119	0.462
Xyridaceae									X	X				
Xyris asperula	Mart.	HE	G	CR, Ce	e		P	R	X		0.803	-	0.076	-
Xyris blepharophylla	Mart.	HE	G	CR	c	VU	P	-	X	X	1.113	-	0.166	-
Xyris calostachys	Poulsen	HE	G	CR	b		P	-	X		0.034	-	0.002	-
Xyris glaucescens	Malme	HE	G	CR	c		P	R	X	X	0.332	0.142	0.043	0.009
Xyris graminosa	Pohl ex Mart.	HE	G	CR	d		P	R	X		0.066	-	0.020	-
Xyris hilariana	Malme	HE	G	CR	d		P	-	X	X	0.270	1.529	0.024	0.103
Xyris hymenachme var. blanchetiana	Malme	HE	G	CR	c		P	R	X	X	0.456	0.125	0.032	0.004
Xyris insignis	L.A.Nilsson	HE	G	CR	b		P	-	X		0.612	-	0.065	-
Xyris itatiayensis	(Malme) Wand. & Sajo	HE	G	CR	b		P	-	X	X	0.137	0.803	0.005	0.132
Xyris melanopoda	L.B.Sm. & Downs	HE	G	CR	a		P	R	X	X	0.730	4.009	0.133	0.638
Xyris minarum	Seub.	HE	G	CR	d		P	R	X	X	0.155	14.340	0.007	0.808
Xyris nubigena	Kunth	HE	G	CR	c		P	R	X	X	11.044	1.094	2.632	0.158
Xyris obtusiuscula	L.A.Nilsson	HE	G	CR, AG	e		P	R	X	X	5.453	11.255	1.250	1.206

Species	Author	Life form	Plant form	Habitats in Brazil	Distribution range	IUCN	Life-cycle	Resprouters post-fire	Presence in sandy grasslands	Presence in stony grasslands	Mean IVI in sandy grasslands	Mean IVI in stony grasslands	Mean Relative Dominance in sandy grasslands (%)	Mean Relative Dominance in stony grasslands (%)
Xyris pilosa	Kunth	HE	G	CR	a		P	R	X	X	1.736	7.267	0.390	1.068
Xyris subsetigera	Malme	HE	G	CR	c		P	-	X	X	2.112	0.238	0.311	0.017
Xyris tenella	Kunth	HE	G	Ce, AG	f		P	R	X	X	1.834	2.938	0.162	0.160
Xyris tortula	Mart.	HE	G	Ce	e		P	R	X	X	4.760	0.009	0.334	0.002
Xyris sp1		HE	G				P	-	X		0.633	-	0.056	-
Xyris sp2		HE	G				P	-	X	X	0.023	0.036	0.004	0.001
Xyris sp3		HE	G				P	-	X		0.246	-	0.038	-

Appendix Chapter 2

Appendix 2: List of the 31 main species used to compare sandy and stony grasslands. Life forms (Raunkiaer (1934) modified by Mueller-Dombois & Ellenberg (1974)): He: Hemicryptophyte, CH: Chamaephyte, HL: Hemicryptophytic Liana, GE: Geophyte. Plant forms: F: Forbs, G: Graminoids, Ss: Sub-shrub, L: Liana. IVI values from Chapter 1. All species are perennial.

		Family	Life form	Plant form	Mean IVI in sandy grasslands	Mean IVI in stony grasslands
Richterago arenaria	(Baker) Roque	Asteraceae	HE	F	1.517	1.909
Lagenocarpus alboniger	(A.St.-Hil.) C.B.Clarke	Cyperaceae	HE	G	0.905	3.690
Lagenocarpus tenuifolius	(Boeck.) C.B.Clarke	Cyperaceae	HE	G	1.730	14.936
Lagenocarpus rigidus subsp. *tenuifolius*	(Kunth) Nees subsp. *tenuifolius* (Boeck.) T.Koyama & Maguire	Cyperaceae	HE	G	20.716	5.029
Rhynchospora consanguinea	(Kunth) Boeck.	Cyperaceae	HE	G	8.072	4.295
Rhynchospora riedeliana	C.B. Clarke	Cyperaceae	HE	G	9.443	4.315
Rhynchospora sp1		Cyperaceae	HE	G	1.297	0.840
Rhynchospora tenuis	Link	Cyperaceae	HE	G	1.128	0.014
Rhynchospora tenuis subsp austro-brasiliensis	subsp. *austrobrasiliensis* T. Koyama	Cyperaceae	HE	G	11.329	4.634
Rhynchospora terminalis	(Nees) Steud.	Cyperaceae	HE	G	6.271	5.994
Dioscorea stenophylla	Uline	Dioscoreaceae	HL	L	0.047	0.256
Drosera montana	A. St.-Hil.	Droseraceae	HE	F	0.559	0.520
Paepalanthus geniculatus	Kunth	Eriocaulaceae	HE	F	2.544	2.232
Syngonanthus cipoensis	Ruhland	Eriocaulaceae	HE	F	4.211	1.039
Syngonanthus vernonioides	(Kunth) Ruhland	Eriocaulaceae	HE	F	0.201	1.479
Sebastiana ditassoides	(Didr.) M. Arg.	Euphorbiaceae	HE	Ss	0.329	1.040
Pseudotrimezia cipoana	Ravenna	Iridaceae	GE	F	0.641	2.718
Sisyrinchium vaginatum	Spreng.	Iridaceae	GE	F	0.135	0.042
Mesosetum loliiforme	(Hochst.) Chase	Poaceae	HE	G	1.382	0.588
Panicum cyanescens	Nees	Poaceae	HE	G	4.419	0.529
Thesium brasiliense	A.DC.	Santalaceae	HE	Ss	0.248	0.360
Vellozia epidendroides	Mart. ex Schult. & Schult.f.	Velloziaceae	HE	F	7.721	5.761
Vochysia pygmaea	Bong.	Vochysiaceae	CH	Ss	0.276	1.135
Xyris blanchetiana	Malme	Xyridaceae	HE	G	0.456	0.125
Xyris hilariana	Malme	Xyridaceae	HE	G	0.270	1.529
Xyris itatiayensis	(Malme) Wand. & Sajo	Xyridaceae	HE	G	0.137	0.803
Xyris melanopoda	L.B.Sm. & Downs	Xyridaceae	HE	G	0.730	4.009
Xyris nubigena	Kunth	Xyridaceae	HE	G	11.044	1.094
Xyris obtusiuscula	L.A.Nilsson	Xyridaceae	HE	G	5.453	11.255
Xyris pilosa	Kunth	Xyridaceae	HE	G	1.736	7.267
Xyris tenella	Kunth	Xyridaceae	HE	G	1.834	2.938

Appendix 3: List of species participating or not in the reproductive phenology with their habitat occurrences (Sandy (Sa) or Stony (St) grasslands), the frequency of reproductive events, the timing and the duration of flowering (Fl.), fruiting (Fr.) and dissemination (Diss.). C: continual, SB: sub-annual, A: annual, SP: supra-annual. R: rainy season, RD: transition rainy to dry season, D: dry season, DR: transition dry to rainy season. S: short cycle (< 2 months), L: long cycle (> 2 months). When data are different between both grasslands, values are separated with a "/".

Species participating in phenology	Author	Family	Occurrence		Frequency		Timing			Duration		
			Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Gomphrena scapigera	Mart.	Amaranthaceae	X		SP		R			S		
Pfaffia denudata	(Moq.) Kuntze	Amaranthaceae	X		SP		D			S		
Hemipogon hatschbachii	(Fontella & Marquete) Rapini	Apocynaceae	X		SP		D		D	S		S
Hemipogon hemipogonoides	(Malme) Rapini	Apocynaceae	X	X	A	SP	R	D	RD	S	L	S
Minaria ditassoides	(Silveira) T.U.P.Konno & Rapini	Apocynaceae		X		SP	D		D	S		S
Asteraceae sp1		Asteraceae	X	X	SB	SB	R&D					
Echinocoryne schwenkiaefolia	(Mart. ex Mart.) H.Rob.	Asteraceae	X		SP		D	D	D	L	L	S
Lessingianthus linearifolius	(Less.) H.Rob.	Asteraceae	X	X	A	A	D	D	D	L	L	S/L
Lessingianthus psilophyllus	(DC.) H.Rob.	Asteraceae	X	X	A	SP	D	D	DR	L/S	L/S	L/S
Lychnophora passerina	(Mart. ex DC.) Gardner	Asteraceae	X		SP		DR	R	R	S	S	S
Porophyllum angustissimum	Gardner	Asteraceae	X	X	SP	SP	D	D	DR	L	L/S	L
Richterago arenaria	(Baker) Roque	Asteraceae	X	X	A	A	D	D	RD	L	L	L

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Richterago polymorpha	(Less.) Cabrera	Asteraceae	X		SP		R	R	R	S	S	S
Richterago polyphylla	(Baker) Cabrera	Asteraceae	X	X	SP	A	DR	R	R	L	L	S/L
Richterago revoluta	Leitão Filho	Asteraceae	X		SP		D	D	R	S	S	S
Trichogonia hirtiflora	(DC.) Sch.Bip. ex Baker	Asteraceae		X		SP	R		R	S		S
Jacaranda racemosa	Cham.	Bignoniaceae	X		SP		R			S		
Ipomoea aff procumbens	Mart. ex Choisy	Convolvulaceae		X		SP	R		D	S		S
Ipomoea serpens	Meisn.	Convolvulaceae	X		A		R	RD	D	S	S	S
Bulbostylis capillaris	(L.) C.B.Clarke	Cyperaceae		X		A	R	R	R	L	S	L
Bulbostylis conifera	(Kunth) C.B.Clarke	Cyperaceae		X		A	R	R	R	S	S	L
Bulbostylis eleocharoides	Kral & M.T. Strong	Cyperaceae	X		A		R	R	D	S	L	S
Bulbostylis emmerichiae	T.Koyama	Cyperaceae	X	X	SP	SP	R	R	R	S	S	S
Bulbostylis junciformis	(Kunth) C.B.Clarke	Cyperaceae		X		A	R	R	R	S	S	L
Bulbostylis lombardii	Kral & M.T.Strong	Cyperaceae		X		A	DR	R	R	L	L	L
Lagenocarpus alboniger	(A.St.-Hil.) C.B.Clarke	Cyperaceae	X	X	A	A	RD/R	D	DR	L	L	L
Lagenocarpus rigidus subsp. tenuifolius	(Kunth) Nees subsp. tenuifolius (Boeck.) T.Koyama & Maguire	Cyperaceae	X	X	C	C	C					
Lagenocarpus tenuifolius	(Boeck.) C.B.Clarke	Cyperaceae	X	X	C	C	C					
Lagenocarpus velutinus	Nees	Cyperaceae	X		SP		D	D		S	S	
Rhynchospora ciliolata	Boeck.	Cyperaceae	X	X	C	C	C					
Rhynchospora consanguinea	(Kunth) Boeck.	Cyperaceae	X	X	A	A	R	R	R	S	L	S
Rhynchospora emaciata	(Nees) Boeck.	Cyperaceae	X	X	A	A	R	R	R	S	L	S

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Rhynchospora patuligluma	Lindm.	Cyperaceae	X	X	A	SP	DR	R	R	S	L	S
Rhynchospora pilosa	(Kunth) Boeck.	Cyperaceae	X		C		C					
Rhynchospora recurvata	(Nees) Steud.	Cyperaceae		X		A	DR	R	R	S	S	S
Rhynchospora riedeliana	C.B. Clarke	Cyperaceae	X	X	C	C	C					
Rhynchospora sp1		Cyperaceae	X	X	A	A	DR	R	R	L	L	L
Rhynchospora tenuis	Link	Cyperaceae	X	X	A	SP	R	R	D	L	L	L
Rhynchospora tenuis subsp austro-brasiliensis	subsp. austrobrasiliensis T. Koyama	Cyperaceae	X	X	A	A	R	R	DR/R	L	L	L
Rhynchospora terminalis	(Nees) Steud.	Cyperaceae	X	X	A	C	R/C	R/C	DR	L	L	L
Scleria cuyabensis	Pilg.	Cyperaceae	X		SP		R	R	R	S	S	S
Scleria hirtella	Sw.	Cyperaceae	X		A		R	R	RD	S	S	S
Scleria stricta	Kunth	Cyperaceae		X		A	R	R	R	S	S	S
Dioscorea stenophylla	Uline	Dioscoreaceae	X	X	A	A	R	R	R	L	L	S
Drosera hirtella	A. St.-Hil.	Droseraceae	X		A		RD	D	D	L	S	S
Drosera montana	A. St.-Hil.	Droseraceae	X	X	A	A	R	R	R	L	S	L
Drosera quartzicola	Rivadavia & Gonella	Droseraceae		X		A	R	R	R	S	S	S
Leiothrix crassifolia	(Bong.) Ruhland	Eriocaulaceae	X	X	A	A	R	D	DR	S	L	L/S
Leiothrix curvifolia	(Bong.) Ruhland	Eriocaulaceae		X		A	R	D	DR	L	L	L
Paepalanthus chlorocephalus	Silveira	Eriocaulaceae	X	X	A	A	RD	D	DR	L	L	S
Paepalanthus geniculatus	Kunth	Eriocaulaceae	X	X	A	A	R	R	RD	L	L	L
Paepalanthus nigrescens	Silveira	Eriocaulaceae		X		A	RD	R	R	L	L	L
Paepalanthus paulinus	Ruhland	Eriocaulaceae		X		A	D	D	D	L	L	L
Syngonanthus anthemidiflorus	(Bong.) Ruhland	Eriocaulaceae	X	X	A	A	RD	D	DR	L	L	L

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Syngonanthus cipoensis	Ruhland	Eriocaulaceae	X	X	A	A	D	DR	R	L	L	S
Syngonanthus circinnatus	(Bong.) Ruhland	Eriocaulaceae		X		SP	D	D	R	L	S	S
Syngonanthus gracilis	(Bong.) Ruhland	Eriocaulaceae	X		SP		D	D	DR	L	L	L
Syngonanthus vernonioides var. vernonioides	(Kunth) Ruhland	Eriocaulaceae	X	X	A	A	D	D	DR	L	L	L
Phyllanthus choretroides	Müll.Arg.	Euphorbiaceae	X		A		R	D	D	L	L	S
Sebastiana ditassoides	(Didr.) M. Arg.	Euphorbiaceae	X	X	SB	SB						
Calliandra linearis	Benth.	Fabaceae	X		SP		R	R	R	S	S	S
Chamaecrista desvauxii var. langsdorffii	(Collad.) Killip var. langsdorffii (Kunth ex Vogel) H.S. Irwin & Barneby	Fabaceae	X	X	A	SP	R	R	R	S	S	S
Chamaecrista ochnacea var. purpurascens	(Vogel) H.S.Irwin & Barneby var. purpurascens (Benth.) H. S. Irwin & Barneby	Fabaceae		X		A	D	DR	R	S	L	L
Chamaecrista papillata	H.S.Irwin & Barneby	Fabaceae	X		SP		D			S		
Curtia diffusa	(Mart.) Cham.	Gentianaceae	X	X	SP	SP	R	D	D	S	S	S
Pseudotrimezia cipoana	Ravenna	Iridaceae	X	X	A	A	R	R	R	S	S	S
Sisyrinchium vaginatum	Spreng.	Iridaceae	X	X	SP	SP	R	R	R	S	S	S
Trimezia juncifolia	(Klatt) Benth. & Hook. f.	Iridaceae	X	X	A	SP	RD	D	DR	L	L/S	L/S
Trimezia truncata	Ravenna	Iridaceae	X	X	SP	SP	R	R	R	S	S	S
Hyptis sp1		Lamiaceae		X		A	R	R	R	S	S	S

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Utricula laciniata	A. St.-Hil. & Girard	Lentibulariaceae		X		A	R		R	S		S
Utricula pusilla	Vahl.	Lentibulariaceae	X	X	A	A	R		R	L		S
Lignous sp1		Dicotyledon	X		SP		R			S		
Lignous sp2		Dicotyledon		X		SP	R			S		
Cuphea ericoides	Cham. & Schlechtd	Lythraceae	X	X	A	A	RD	R	R	S	L/S	S
Diplusodon orbicularis	Koehne	Lythraceae	X	X	A	A	RD	D	D	S	L	S/L
Tetrapteryx microphylla	(A.Juss.) Nied	Malpighiaceae		X		A	R	RD	D	S	S	S
Cambessedesia hilariana	DC.	Melastomataceae	X		SP		RD	D	D	S	S	S
Cambessedesia semidecandra	A.B.Martins	Melastomataceae	X		A		R	R	R	S	L	L
Chaetostoma armatum	(Spreng.) Cogn.	Melastomataceae	X		SP		R	RD	D	L	L	S
Lavoisiera caryophyllea	A.St.-Hil. ex Naudin.	Melastomataceae	X	X	SP	A	RD	D	D	S	S/L	S
Lavoisiera confertiflora	Rich. ex Naudin.	Melastomataceae	X	X	A	SP	RD	D	DR	L/S	L	L
Marcetia acerosa	DC.	Melastomataceae		X		A	R	RD	RD	S	L	S
Marcetia taxifolia	(A.St.-Hil.) DC.	Melastomataceae	X	X	A	A	D	DR	R	S	L	S
Microlicia multicaulis	Mart. ex Naudin.	Melastomataceae	X	X	A	A	R	RD	D	S	L	L
Siphantera arenaria	(DC.) Cogn.	Melastomataceae		X		A		RD	D		L	S
Buchnera palustris	(Aubl.) Spreng.	Orobanchaceae	X		SP		D	D	D	L	L	L
Agalinis brachyphylla	(Cham. & Schltdl.) D'Arcy	Orobanchaceae		X		A	RD	D	D	S	L	L
Andropogon brasiliensis	A.Zanin & Longhi-Wagner	Poaceae		X		A	R	D	D	S	S	S
Apochloa euprepes	(Renvoize) Zuloaga & Morrone	Poaceae	X	X	A	A	R	R	R	S	S	L
Aristida torta	(Nees) Kunth	Poaceae	X	X	A	A	RD	D	D	S	L	S/L

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Axonopus fastigiatus	(Nees ex Trin.) Kuhlm.	Poaceae		X		A	R		R	S		S
Echinolanea inflexa	(Poir.) Chase	Poaceae	X	X	A	A	R	RD	RD	S	L	L
Homolepsis longispicula	(Döll) Chase	Poaceae	X	X	SP	SP			RD			S
Mesosetum exaratum	(Trin.) Chase	Poaceae	X	X	SP	SP	R	D	R	S	S	S
Mesosetum loliiforme	(Hochst.) Chase	Poaceae	X	X	A	A	R	R	R	S	S	S
Panicum cyanescens	Nees	Poaceae	X	X	A	A	R	R	RD	S	S	L
Paspalum erianthum	Nees ex Trin.	Poaceae		X		SP			R			S
Paspalum hyalinum	Nees ex Trin.	Poaceae	X		A		D	D	DR	L	L	L
Paspalum polyphyllum	Nees	Poaceae		X		A		D	DR		L	S
Schizachyrium sanguineum	(Retz.) Alston	Poaceae		X		A	R	R	R	S	S	S
Schizachyrium tenerum	Nees	Poaceae	X	X	SP	SP	R	R	R	S	S	S
Tatianyx arnacites	(Trin.) Zuloaga & Soderstr.	Poaceae		X		SP	R		R	S		S
Trachypogon spicatus	(L.f.) Kuntze	Poaceae	X	X	SP	A	R	R	R	S	S	S
Polygala apparicioi	Brade	Polygalaceae	X		SB							
Polygala celosioides	Mart. ex A.W.Benn.	Polygalaceae	X		A		D	D	D	L	L	L
Polygala cneorum	A.St.-Hil.	Polygalaceae	X		A		DR	R	R	S	S	S
Polygala glochidiata	Kunth.	Polygalaceae	X		SB							
Polygala paniculata	L.	Polygalaceae	X		SB							
Coccoloba cereifera	Schwacke	Polygonaceae	X		SP		R		R	S		S
Cephalostemon riedeliana	Koern.	Rapataceae	X		A		R	RD	D	L	L	S
Galianthe peruviana	(Pers.) E.L.Cabral	Rubiaceae		X		A	R	RD	D	L	L	L
Thesium brasiliense	A.DC.	Santalaceae	X	X	SB	SB						

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Vellozia caruncularis	Mart. ex Seub.	Velloziaceae		X		SP	D	DR	R	S	L	L
Vellozia epidendroides	Mart. ex Schult. & Schult.f.	Velloziaceae	X	X	A	A	D/R	D/R	DR/RD	L	L	L
Vellozia resinosa	Mart.	Velloziaceae		X		SP		D	DR		L	S
Vochysia pygmaea	Bong.	Vockysiaceae	X	X	A	A	R	RD	D	L	L	L
Xyris asperula	Mart.	Xyridaceae	X		A		R	D	D	L	L	L
Xyris blanchetiana	Malme	Xyridaceae	X	X	A	A	RD	D	DR	L	L	L
Xyris blepharophylla	Malme	Xyridaceae	X	X	A	A	RD	D	DR	L/S	L	L
Xyris glaucescens	Malme	Xyridaceae	X	X	A	A	RD	D	DR	L/S	L	S
Xyris graminosa	Pohl ex Mart.	Xyridaceae	X		A		RD	D	DR	S	L	L
Xyris hilariana	Malme	Xyridaceae	X	X	A	A	RD	D	DR	L	L	L
Xyris insignis	L.A.Nilsson	Xyridaceae	X	X	A	A	RD	D	D	L	L	L
Xyris itatiayensis	(Malme) Wand. & Sajo	Xyridaceae	X	X	A	A	R	RD	D	S	L	S
Xyris longiscapa	L.A.Nilsson	Xyridaceae	X		SP		R	R	R	S	S	S
Xyris melanopoda	L.B.Sm. & Downs	Xyridaceae	X	X	A	A	DR	R	R	L	L	L
Xyris minarum	Seub.	Xyridaceae	X	X	A	A	RD	D	DR	L	L	L
Xyris nubigena	Kunth	Xyridaceae	X	X	A	A	RD	D	DR	L	L	L
Xyris obtusiuscula	L.A.Nilsson	Xyridaceae	X	X	A	A	R	D	DR	L	L	L
Xyris pilosa	Kunth	Xyridaceae	X	X	A	A	RD	D	DR	L	L	L
Xyris sp1		Xyridaceae	X		SP		R	D	DR	L	L	S
Xyris sp2		Xyridaceae	X	X	SP	SP	D	D	D	S/L	L	S
Xyris subsetigera	Malme	Xyridaceae	X	X	A	A	RD	D	D	L/S	L	L
Xyris tenella	Kunth	Xyridaceae	X	X	A	A	D	D	DR	L	L	L
Xyris tortula	Mart.	Xyridaceae	X		A		RD	RD	D	L	S	S

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Species not participating in phenology												
Gomphrena incana	Mart.	Amaranthaceae	X	X								
Apocynaceae sp1		Apocynaceae	X									
Apocynaceae sp2		Apocynaceae	X	X								
Apocynaceae sp3		Apocynaceae		X								
Apocynaceae sp4		Apocynaceae		X								
Oxypetalum cf montanum		Apocynaceae	X									
Asteraceae sp2		Asteraceae	X									
Calea tridactylila	Sch.Bip. ex Krasch.	Asteraceae	X									
Inulopsis scaposa	(DC.) O. Hoffm.	Asteraceae	X	X								
Lepidaploa sp1		Asteraceae	X									
Lychnophora joliana	Semir & Leitão (unresolved name)	Asteraceae		X								
Lychnophora rupestris	Semir & Leitão (unresolved name)	Asteraceae		X								
Minasia cipoensis	Loeuille (unresolved name)	Asteraceae		X								
Prestelia eriopus	Sch.Bip.	Asteraceae		X								
Encholirium heloisae	(L.B.Sm.) Forzza & Wand.	Bromeliaceae		X								
Bulbostylis paradoxa	(Spreng.) Lindm.	Cyperaceae	X	X								
Bulbostylis sp1		Cyperaceae		X								
Cyperaceae sp1		Cyperaceae	X									
Cyperaceae sp2		Cyperaceae	X									
Cyperaceae sp3		Cyperaceae	X	X								

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Rhynchospora globosa	(Kunth) Roem. & Schult.	Cyperaceae	X	X								
Rhynchospora sp2		Cyperaceae		X								
Agarista duartei	(Sleumer) Judd	Ericaceae	X	X								
Gaylussacia riedelii	Meisn.	Ericaceae		X								
Paepalanthus macrocephalus	(Bong.) Koern.	Eriocaulaceae		X								
Paepalanthus pubescens	Koern.	Eriocaulaceae	X									
Croton timandroides	(Didr.) Müll.Arg.,	Euphorbiaceae	X									
Trimezia fistulosa var. fistulosa	Foster	Iridaceae		X								
Eriope arenaria	Harley	Lamiaceae	X	X								
Hyptis sp2		Lamiaceae		X								
Spigelia aceifolia	Woodson	Loganiaceae		X								
Diplusodon ciliiflorus	Koehne	Lythraceae	X									
Banisteriopsis campestris	(A.Juss.) Little	Malpighiaceae	X	X								
Byrsonima cipoensis	Mamede	Malpighiaceae		X								
Byrsonima cydoniifolia	A. Juss.	Malpighiaceae		X								
Byrsonima dealbata	Griseb.	Malpighiaceae		X								
Camarea axillaris		Malpighiaceae		X								
Microlicia juniperina	A.St.-Hil.	Melastomataceae		X								
Epistephium sclerophyllum	Lindl.	Orchidaceae		X								
Andropogon carinatus	Nees	Poaceae		X								
Andropogon cf ingratus		Poaceae		X								
Anthaenantia lanata	(Kunth) Benth.	Poaceae	X	X								
Apochloa sp1		Poaceae		X								

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Aulonemia effusa	(Hack.) McClure	Poaceae		X								
Axonopus brasiliense	(Spreng.) Kuhlm.	Poaceae	X									
Ctenium brevispicatum	J.G. Sm.	Poaceae	X	X								
Paspalum guttatum	Trin.	Poaceae		X								
Paspalum pectinatum	Nees ex Trin.	Poaceae	X	X								
Paspalum sp1		Poaceae	X									
Poaceae sp1		Poaceae	X									
Poaceae sp2		Poaceae		X								
Poaceae sp3		Poaceae	X									
Poaceae sp4		Poaceae	X	X								
Poaceae sp5		Poaceae	X									
Schizachyrium sp1		Poaceae	X									
Sporobolus sp1		Poaceae	X	X								
Polygala hirsuta	A. St.-Hil. & Moq.	Polygalaceae	X									
Polygala sp1		Polygalaceae		X								
Pellaea cymbiformis	J.Prado	Pterydaceae		X								
Declieuxia fruticosa	(Willd. ex Roem. & Schult.) Kuntze	Rubiaceae		X								
Declieuxia irwinii	J.H.Kirkbr.	Rubiaceae	X									
Turnera cipoensis	Arbo	Turneraceae	X	X								
Barbacenia blackii	L.B.Sm.	Velloziaceae		X								
Barbacenia flava	Mart. ex Schult. & Schult.f.	Velloziaceae	X	X								
Barbacenia sp1		Velloziaceae		X								
Vellozia albiflora	Pohl	Velloziaceae		X								

			Occurrence		Frequency		Timing			Duration		
Species participating in phenology	Author	Family	Sa	St	Sa	St	Fl.	Fr.	Diss.	Fl.	Fr.	Diss.
Vellozia sp1		Velloziaceae	X									
Lippia florida	Cham.	Verbenaceae		X								
Stachytarpheta procumbens	Moldenke	Verbenaceae	X	X								
Vochysia elliptica var. elliptica	Mart.	Vochysiaceae		X								
Xyris calostachys	Poulsen	Xyridaceae	X									
Xyris sp3		Xyridaceae	X									
Dicotyledon 1			X									
Dicotyledon 2			X									

Appendix Chapter 3

Appendix 4: Soil seed bank in mountain Neotropical grasslands: seasonal variations and potential to restore degraded areas.

1.Introduction

Ecological restoration is the process of intentionally assisting the recovery of degraded ecosystems in order to repair ecosystem processes, productivity and services, as well as to re-establish biotic integrity (SER 2004). Before implanting a restoration project, the first step is to assess the resilience of the ecosystem in order to identify whether restoration is necessary and to gather potentially useful information to plan restoration. Natural regeneration of plant communities after a given disturbance is important for their conservation and can be an effective strategy for restoration (Leck et al. 1989, Bakker et al. 1996, Aide et al 2000, Sampaio et al 2007). However, the process of natural succession of species-rich grasslands, when highly destroyed, is slow (Bradshaw 1983, Davis et al. 1985, Bradshaw 1997), particularly when there is a lack of seed pool from the seed bank (Bakker et al. 1996). Among the restoration techniques aiming to reintroduce target species on degraded areas, topsoil transposition containing nutrients, organic matter and the seed bank was already noted as an effective technique (Reis et al. 2003, Vieira 2004, Cobbaert et al. 2004, Jakovac 2007). Native seeds from the seed bank are brought through transplanted soil, and edaphic conditions of the degraded area are changed improving environmental condition for plant establishment (Potthoff et al. 2005). However before planning such restoration experiment, a prerequisite is to assess the composition of the seed bank in reference grasslands.

The term "seed bank" is defined as the reserve of viable seeds present in the soil and on the soil surface (Robert 1981).Thompson & Grime (1979) highlighted that the transient and/or persistent seed bank confer to the vegetation the potential to regenerate after a disturbance or to colonize new areas. The ability of plant species to produce seeds which remain viable in the soil (i.e. forming the seed bank) allows them to overcome unfavourable environmental conditions to germinate and establish. It was already demonstrated that seed bank has an important functional role in perennial grassland community as a means for population maintenance and regeneration of many species (Kalamees & Zobel 2002, Pakeman & Small 2005). Moreover, the seed bank plays an important role on determining the trajectory of secondary succession after disturbances

(Pakeman & Small 2005). In European grasslands, viable seeds of characteristic species are often absent from the seed bank due to their low longevity or because of low seed production (Hutchings & Booth 1996, Bekker et al., 1997; Buisson et al. 2006), as a consequence the natural regeneration of these ecosystems is low. In mountain grasslands in South America, Funes et al (2001) verified that the largest number of seeds, and thus the highest potential for regeneration, was found in wetter sites, but then the number decreased progressively from mesic to xeric habitats.

Campos rupestres, are one of the physiognomies of the Cerrado (Brazilian savanna), representing c.a. 130,000km² (Barbosa 2012) found at altitudes of between 800m and 2000m. They are composed of a mosaic of stony and sandy grasslands, that bogs along the streams and scattered rocky outcrops with sclerophyllous evergreen shrubs and sub-shrubs (Chapter 1). *Campos rupestres* are constrained ecosystems with shallow soils, poor in nutrients and highly acidic (Benites et al. 2007, Chapter 1), highly diverse vegetation and one of the highest levels of endemism in Brazil (Giulietti et al. 1997, Echternacht et al. 2011). *Campos rupestres* are still subjected to damage, in particular with mining, quarrying, and civil engineering activities.

The objectives of this work were to evaluate the natural regeneration of *campos rupestres* through seed banks, assessing the seasonal variation (rainy and dry season) in seed quantity and species composition, and the similarity between the seed bank from sandy and stony grasslands. We also discussed the seed bank composition with the above-ground composition.

2. Material and methods

2.1. Study site

Our study area is located in Brazil, in the southern portion of the Espinhaço Range, in the Environmental Protected Area (*Area de Proteção Ambiental* in Portuguese) Morro da Pedreira, buffer zone of the Serra do Cipó National Park (State of Minas Gerais). The climate is classified as Cwb according to the Köppen's system with warm temperate dry winter from May to October and warm rainy summer from November to April. The mean annual precipitation is 1622 mm and the annual temperature is 21.2°C (Madeira & Fernandes 1999).

2.2. Seed bank analysis

Five sites of the two main grassland-types (i.e. sandy and stony grasslands) were selected, and five 1L soil samples were taken at the end of the rainy season (end of March) and five at the end of the dry season (end of September), which is the peak period of fruit production (n = 5 samples × 10 sites × 2 seasons = 100). Each sample consisted of 10 pooled sub-samples, randomly taken at each site, to overcome seed bank heterogeneity. Samples were washed with water on sieves of 4 mm and 200 µm mesh sizes to remove 1) plant fragments and stones and 2) the finest fraction (clay and silt). The remaining soil containing seeds was spread as a thin layer on trays (25cm x 35cm) on compresses placed over a 3 cm thick layer of vermiculite (neutral substrate). Control trays (n=3) (made of compresses over vermiculite) and controls of the finest fraction (n=3) (made of the finest fraction spread out on compresses over vermiculite) were also set in order to 1) make sure that no species could colonize the greenhouse and contaminate samples and 2) make sure that no seed <200 µm may have been lost to sieving. All trays were kept in a greenhouse, regularly moved and watered. Emerging seedlings were identified weekly and removed or replanted in pots for later identification to avoid competition in the trays and emission of allelopathic substances. After one month without germination, each sample was dried and microplowed before starting a second germination period, as this being known to cause more seeds to germinate (Roberts 1981).

2.3. Statistical analysis

To analyse seed bank data, t-tests with separate variance estimates were run to compare mean seed/species number in each sample/site between sandy and stony grasslands during the dry and the rainy season. Then, a dissimilarity matrix using Bray-curtis indices, based on species abundance data was calculated, and an ANOSIM was performed.

3. Results

Seed banks of both sandy and stony grasslands are poor in species and seeds. A higher total number of seeds was observed in sandy grasslands seed bank during the rainy season (Table 1). However, neither grassland-types, nor seasons had a significant effect on the mean number of seeds or species in samples or in sites (Table 1). The seed bank compositions between grassland-types and seasons were similar (ANOSIM R=0.018, p=0.068, Table 2). Frequent species occurring in the seed banks were also species normally found in the vegetation, such as *Tatianyx arnacites, Lagenocarpus rigidus* subsp. *tenuifolius, Rhynchospora riedeliana, Rhynchospora consanguinea* and *Rhynchospora tenuis* subsp. *austro-brasiliensis* (Table 3). However, some species which are common in the *campos rupestres* (i.e. with a high importance value index) such as *Mesosetum exaratum* and *Vellozia spp* were absent from the seed banks (Table 3).

Table 1: Number of germinated seeds and number of species found in the seed bank of the 5 sandy and 5 stony grasslands (5 samples x 5 site x 2 grassland-types x 2 season, n=100). ns: non significant difference. T-tests with separate variance estimates were run. ns: non significant difference.

	Dry season		Rainy season		t-test	
	Sandy grasslands	Stony grasslands	Sandy grasslands	Stony grasslands	Season effect	Grassland type effect
Total number of germinated seeds	118	89	121	102		
Mean number of germinated seeds in each sample (1L)	4.72 ± 0.71	3.56 ± 0.87	4.84 ± 0.95	4.08 ± 0.56	-0.40^{ns}	1.22^{ns}
Mean number of germinated seeds at each site	23.60 ± 5.69	17.80 ± 4.88	24.20 ± 8.87	20.40 ± 2.58	-0.27^{ns}	0.85^{ns}
Mean number of species in each sample (1L)	2.32 ± 0.28	1.92 ± 0.33	2.60 ± 0.45	2.84 ± 0.37	-1.66^{ns}	0.21^{ns}
Mean number of species at each site	7.60 ± 1.21	7.60 ± 1.63	10.20 ± 2.65	10.20 ± 0.73	-1.61^{ns}	0^{ns}

Table 2: Dissimilarity matrix (Bray-curtis indices) of the seed bank composition between grassland-types (sandy and stony grasslands) and seasons (rainy season and dry season) based on abundance data (n=5 samples x 5 sites x 2 grassland-tyes x 2 seasons). St-R: Stony grassland in rainy season, St-D: Stony grassland in dry season, Sa-R: Sandy grassland in rainy season, Sa-D: Sandy grassland in dry season.

	St-R	St-D	Sa-R
St-D	0.6		
Sa-R	0. 7	0.8	
Sa-D	0. 7	0.6	0.7

Table 3: Dominant species in the seed bank from the sandy and stony grasslands and in the established vegetation.

	Species	Total seed number	Seed number in sandy grasslands	Seed number in stony grasslands	Relative Dominance in sandy grasslands (cm^2/m^2)	Relative Dominance in stony grasslands (cm^2/m^2)
Dominant species in the seed bank	*Tatianyx arnacites*	69	40	29	17.7	12.8
	Rhynchospora riedeliana	61	33	28	3.8	1.4
	Rhynchospora consanguinea	58	37	21	0.5	0.2
	Rhynchospora tenuis subsp. austro-brasiliensis	47	27	20	2.5	0.8
	Xyris pilosa	17	1	16	0.4	1.1
	Lagenocarpus rigidus subsp tenuifolius	14	11	3	11.9	2.7
	Lagenocarpus tenuifolius	14		14	2.1	8.9
	Trachypogon spicatus	10	4	6	2.6	4
Dominant species in the vegetation absent or poorly represented in the seed bank	*Mesosetum exaratum*				6.2	14.7
	Homolepsis longispicula				12.4	4.8
	Paspalum erianthum				7.4	2.2
	Vellozia resinosa	2		2	0.1	8.8
	Vellozia epidendroïdes	1	1		4.4	2.7
	Vellozia caruncularis	2		2	0.4	6.1

4.Discussion

Although the natural sandy and stony *campos rupestres* are highly diverse (Chapter 1), their seed banks are poor in seeds and species and do not vary among seasons. Medina and Fernandes (2007) have already pointed out that the seed banks of some herbaceous communities of *campos rupestres* are species poor in comparison to other physiognomies, such as some nearby gallery forests. Seed bank of the Cerrado and other tropical savannas appear to be richer in seeds than those of *campos rupestres* (Perez & Santiago 2001, Salazar et al. 2011). We argue that *campos rupestres* have a weak ability to regenerate from the seed bank due to the absence of transient and/or persistent seed bank (Thompson & Grime 1979, Kalamees & Zobel 2002). The lack of viable seeds of characteristic species in the seed bank, due to their short longevity, has also been demonstrated in European grasslands (Hutchings & Booth 1996, Bekker et al., 1997; Buisson et al. 2006). In consequence, seed bank plays little role in regeneration (Edwards & Crawley 1999, Pakeman & Small 2005) and when dispersal is also limited, the natural regeneration of these ecosystems is low.

First, the low density of emergences can reflect the large quantity of dormant seeds reported before for some *campo rupestre* species (Gomes et al. 2001, Silveira &

Fernandes 2006, Garcia et al. 2011, Silveira et al. 2012). Several other hypotheses can explain the low seed density in the seed bank. Indeed, the ability to form a seed bank seems to vary in *campos rupestres*: while some species appear not to form seed banks (Velten & Garcia 2007), others may form only a small persistent seed bank (Velten & Garcia 2007, Giorni 2009, Silveira 2011).

Bossuyt & Honnay (2008) have found that seed density are low in stable communities which is the case of *campos rupestres* that are supposed to have been stable ecosystems for 20,000 years (Barbosa 2012); indeed it has been suggested that increasing habitat disturbance always selects for increased seed persistence (Hölzel & Otte 2004).

Bekker et al. (1997) have noted that species associated with poor nutrient conditions are relatively scarce in the seed bank. Funes et al. (2001) have found that the largest number of seeds is found in wetter sites and although *campo rupestres* are sometimes flooded in the rainy season, they are subjected to a severe five-month dry season which can lead to unfavorable environmental conditions to seed bank formation (Funes et al. 2001).

In addition, the poverty of the seed bank might also be associated to the low quantity of annuals species (which are obligate seeder) in *campos rupestres* where perennial species are dominant (Chapter 1), although Hölzel & Otte (2004) have found large proportion of perennial species with a strong tendency to accumulate seeds in the soil, in some European grasslands.

Moreover, in the Cerrado, in response to fire (one of the most frequent disturbance), vegetative reproduction is a frequent strategy, much more successful than sexual reproduction (Hoffmann 1998). Fidelis et al. (2010) have also pointed out the importance of the bud banks in tropical grasslands that are subjected to fire, which would replace the seed bank in such communities. Indeed, Pausas & Verdu (2005) have highlighted that species able to resprout almost never evolved to one with persistent propagules, contrary to species unable to resprout. The most serious implication of a poor seed bank is the low capacity of *campos rupestres* to regenerate from the seed bank faced to strong disturbances.

We have found little similarities between the standing vegetation and the seed bank, mainly due to the scarcity of species in the seed bank. It is usually accepted that similarity between seed bank and vegetation are low in stable ecosystems (Bossuyt &

Honnay 2008): without disturbances, germination from the seed bank is not promoted (lack of creation of new microsite). However, if the similarity between seed bank and vegetation decreases with time after the disturbance in forest and wetland ecosystems, this is not always true in grasslands. Indeed, Hopfensperger (2007) has noted that similarity between seed bank and vegetation tends to increase with time since the disturbance in grasslands. C*ampos rupestres* are subjected to regular disturbance (fire), but due to the poverty of the seed bank, we assume that this way is not the preferential manner to regenerate. This could be due to the fact that *campos rupestres* are nutrient poor ecosystems and stress-tolerant species are often long lived clonal species (Bekker et al. 1997; Chang et al. 2001; Matus et al. 2005).

We thus suggest that using topsoil transfer (Reis et al. 2003) to restore *campos rupestres* will have a limited effect due to the poverty of the seed bank although soil transfer could improve the edaphic conditions of the degraded areas and then facilitate native plant establishment. Moreover, topsoil transfer leads to the destruction of the vegetation on the donor site. Therefore, it should only be considered in circumstances when complete habitat destruction is otherwise unavoidable and should be associated with other restoration methods. In addition, Bossuyt & Honnay (2008) have already noted that the absence of target species greatly limit the restoration of target plant communities from the seed bank. In such case, the regeneration of grasslands relies mainly on seed dispersal.

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Appendix Chapter 4

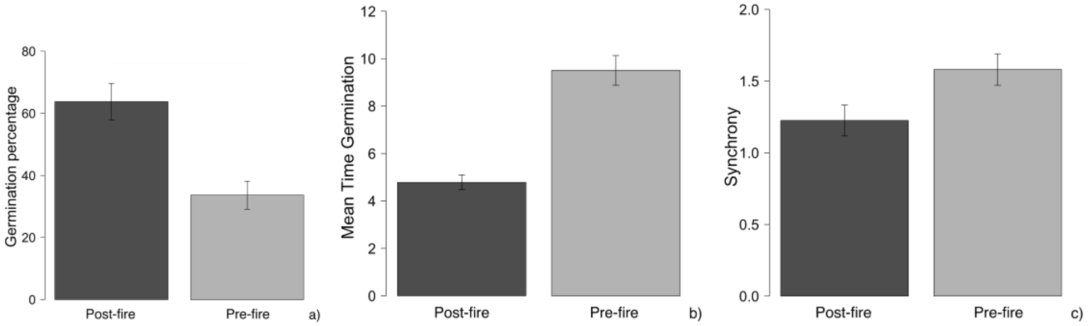
Appendix 5: Life-history traits of the four plant species dispersing seeds after a fire in August 2011.

	Family	Distribution range	Seed dispersal period after fire
Bulbostylis emmerichiae T.Koyama	Cyperaceae	Wide distribution	December 2011
Bulbostylis paradoxa (Spreng.) Lindm.	Cyperaceae	Wide distribution	December 2011
Homolepis longispicula (Döll) Chase	Poaceae	Brazil	January 2012
Paspalum pectinatum Nees ex Trin.	Poaceae	Wide distribution	January 2012

Appendix 6: Phylogenetic reconstruction method. To understand the evolution of seed dormancy in the herbaceous flora of the *campos rupestres*, we built a phylogenetic tree showing relationships among the studied taxa after checking the names against the Missouri Botanical Garden's nomenclatural database (http://www.tropicos.org/Home.aspx). We built a pruned tree with our 15 study species as terminal tips with the aid of Phylomatic:

http://www.phylodiversity.net/phylomatic/.

Species relationships were improved and polytomies were resolved based on available and published data for the taxa relationships.



Appendix 7: a) Average germination percentage (±SE), b) MTG and c) germination synchrony of species with post-fire and pre-fire seed production from the *campos rupestres* of Serra do Cipó, southeastern Brazil. a) GLM procedure with poisson distribution F=4.64, $p<0.05$, b) GLM procedure with gamma distribution f=39.70, $p<0.001$ and c) t-test t=-2.3, $p<0.05$.

Appendix 8: Average seed mass before and after soaking in tap water for 72h, with the increased seed mass percentage (%) for 15 herbaceous species from *campos rupestres* in Southeastern Brazil. Statistics refered to Wilcoxon tests.

Species	Before	After	%	W
Aristida torta	10.95 ± 0.07	11.63 ± 0.22	6.16	0 *
Echinolaena inflexa	39.20 ± 0.87	124.05 ± 6.77	216.45	0 *
Lagenocarpus alboniger	107.82 ± 9.98	189.78 ± 16.26	76.00	0 *
Lagenocarpus rigidus	49.95 ± 2.11	84.07 ± 3.16	68.31	0 *
Lessingianthus linearifolius	30.03 ± 1.27	61.70 ± 1.96	105.49	0 *
Rhynchospora ciliolata	11.47 ± 1.26	17.70 ± 1.24	54.24	0 *
Rhynchospora consanguinea	19.83 ± 0.79	24.60 ± 0.67	24.08	0 *
Rhynchospora riedeliana	19.00 ± 1.38	29.60 ± 0.73	55.79	0 *
Richterago arenaria	38.55 ± 3.28	79.10 ± 5.57	105.9	0 *
Vellozia caruncularis	5.37 ± 0.64	8.23 ± 0.77	53.02	0 *
Vellozia epidendroides	5.03 ± 0.39	6.47 ± 0.57	28.85	1, p=0.057
Vellozia resinosa	14.07 ± 0.80	20.45 ± 1.72	45.29	0 *
Vellozia variabilis	5.25 ± 0.29	7.35 ± 0.22	40.00	0 *
Xyris obtusiuscula	1.87 ± 0.13	2.43 ± 0.11	29.33	0 *
Xyris pilosa	1.87 ± 0.12	2.17 ± 0.11	16.00	0 *

RESUME

Composition, phenologie et restauration de pelouses d'altitude, les campos rupestres - Brésil. Les changements globaux, en particulier les changements d'usage des terres, modifient profondément le fonctionnement des écosystèmes ainsi que la biodiversité et, ont déjà impacté de nombreux services écosystémiques. La disparition de ces écosystèmes souligne la nécessité de préserver les zones intactes, cependant, quand les programmes de conservation sont insuffisants, la restauration des zones détruites ou perturbées peut permettre de venir en appui aux efforts de conservation et de minimiser les dommages. Ce travail a pour objet d'étude les *campos rupestres*, des pelouses néotropicales situées en altitude, faisant partie du Cerrado (savane brésilienne), qui recèlent une importante biodiversité dont un fort taux d'endémisme et qui, comme bien d'autres écosystèmes de montagne, fournissent de précieux services écosystémiques : la filtration de l'eau ou encore des zones de loisir. Ils ont été, et sont encore, grandement affectés par les activités humaines telles que les travaux de génie civil, les carrières ou les mines. Le premier objectif de cette thèse était de décrire l'écosystème de référence, afin de définir clairement un objectif de restauration ainsi que mesurer les progrès et le succès de la restauration. Nous avons montré que les *campos rupestres* sont composés d'au moins deux communautés végétales distinctes (une avec un substrat caillouteux et l'autre avec un substrat sableux), chacune ayant une composition en espèces et une structure particulières ainsi qu'une grande biodiversité. La phénologie reproductive varie au sein des communautés herbacées: la majorité des espèces fleurissent et fructifient pendant la saison des pluies alors que d'autres espèces adoptent différents comportements phénologiques. Tout au long de nos 2 années de suivis phénologiques, certaines espèces dominantes, notamment des Poaceae, n'ont pas été observées en fleur ce qui implique une dispersion limitée de ces espèces vers les zones dégradées. Les communautés végétales de *campos rupestres* ne sont pas résilientes aux fortes perturbations: plusieurs années après, presque aucune des espèces cibles n'ont été trouvées en zones dégradées, les sols ont complètement été modifiés et les banques de graines ne se sont recomposées qu'avec des espèces rudérales non désirées. Selon le modèle des filtres, une communauté résulte d'un pool régional d'espèce sélectionné par un ensemble de filtres : de dispersion, abiotique et biotique. Les interventions de restauration que nous avons mises en place avaient pour but d'agir sur les différents filtres afin de diriger la dynamique des communautés végétales. Nous avons donc, par la suite, mis en place trois protocoles de restauration *in-situ* (le transfert de foin, la translocation d'espèce et la translocation de plaque de végétation) pour restaurer les deux types de communautés de *campos rupestres* identifiées. Le transfert de foin n'a pas permis la restauration des communautés végétales de *campos rupestres* en raison de l'importante altération des sols et, surtout, à cause de la mauvaise qualité des graines. En effet, nos études de germination ont montré que, alors que certaines espèces de Xyridaceae et Velloziaceae germent très bien, certaines espèces dominantes de Poaceae, de Cyperaceae ou d'Asteraceae ont des graines soit vides, soit non viables, soit dormantes ; le semis se révèle alors peu efficace. Par ailleurs, nous n'avons pas mis en évidence d'effet positif du feu sur la germination des espèces de *campos rupestres*. La translocation d'espèces s'avère un succès pour une seule espèce, *Paspalum erianthum*, alors que pour les autres, les dommages causés au niveau des racines lors de la translocation limitent probablement leur survie. Enfin la translocation de plaques de végétation s'avère être la méthode la plus efficace puisque de nombreuses espèces ont ainsi pu être réintroduites en zones dégradées. Cependant, en raison de la faible résilience des *campos rupestres* dans lesquels les plaques de végétation ont été prélevées, cette méthode ne peut être envisagée que pour sauver des habitats dans le cas extrême où la destruction de l'habitat est inévitable. Face à la difficulté de restaurer les *campos rupestres*, leur protection et leur conservation doit être une priorité.

Keywords: banque de graines, Cerrado, écologie des communautés, écologie de la restauration, écosystèmes néotropicaux d'altitude, germination, pelouses, restauration de pelouses, savanes, transfert de foin, transfert de plaque de végétation, translocation, transplantation.

RESUMO

Composição, fenologia e restauração dos campos rupestres – Brasil. As mudanças ambientais globais, principalmente as mudanças de uso da terra, afetam profundamente o funcionamento dos ecossistemas e a biodiversidade e já alteraram muitos serviços ecossistêmicos. Essas perdas enfatizam a necessidade de se preservar ecossistemas intocados; no entanto, quando os programas de conservação não são suficientes, a restauração das áreas que foram destruídas ou perturbadas pode melhorar os esforços de conservação e mitigar os danos. Este trabalho trata dos campos rupestres, campos neotropicais encontrados em altitudes, incluídos no Cerrado, que possuem uma grande biodiversidade com um alto grau de endemismo e, assim como outros ecossistemas de montanhas, fornecem serviços ecossistêmicos valiosos, tais como filtragem da água e áreas de lazer. Eles foram – e ainda estão sendo – impactados por atividades humanas, tais como obras de engenharia civil, pedreiras e minas. O primeiro objetivo do presente trabalho foi descrever o ecossistema de referência, a fim de definir claramente um objetivo de restauração para monitorar o progresso e o sucesso da restauração. Mostramos que campos rupestres são compostos por pelo menos duas comunidades vegetais distintas (campos arenoso e pedregoso), cada uma com composição e estrutura específicas e apresentando grande biodiversidade. Vários padrões fenológicos ocorrem nas comunidades herbáceas de campos rupestres: a maioria das espécies florescem e frutificam durante a estação chuvosa, quando algumas espécies reproduzem durante a estação seca mas outros padrões podem ser observados. Durante o nosso levantantamento fenológico de 2 anos, algumas espécies dominantes de Poaceae, entre outros, não foram observadas reproduzindo, o que implica possibilidades limitadas de dispersão em áreas degradadas. A vegetação de campos rupestres não é resiliente após um grande distúrbio: vários anos depois do distúrbio, espécies nativas quase não são encontradas em áreas degradadas, os solos estão completamente alterados e os bancos de sementes recompõem apenas espécies ruderais. De acordo com o modelo dos filtros, uma comunidade local é o resultado de um conjunto regional de espécies selecionadas por três filtros: um filtro de dispersão, um filtro abiótico e um filtro biótico. A atuação sobre os diferentes filtros para influenciar a comunidade de plantas foi o núcleo de nossas intervenções de restauração. Aplicamos, então, três protocolos de restauração in-situ (a transferência de feno, a translocação de espécies e translocação do placa de vegetação) para restaurar os dois tipos de campos. A transferência de feno não permite a restauração da vegetação de campos rupestres devido à alteração do solo e, principalmente, por causa da baixa qualidade das sementes. De fato, estudos mostram que algumas Xyridaceae e Velloziaceae têm uma germinação alta, enquanto algumas espécies dominantes, como Poaceae, Cyperaceae ou Asteraceae, têm sementes sem embrião, inviáveis ou dormentes, o que torna a semeadura uma técnica pouca eficiente. Não há evidências de que o fogo aumenta a germinação das espécies de campos rupestres. A translocação de espécies foi bem sucedida para apenas uma espécie, *Paspalum erianthum*; para as outras, danos nas raizes provavelmente impediram a sobrevivência. A translocação de placa de vegetação finalmente foi o método mais bem sucedido, uma vez que numerosas espécies foram reintroduzidas em áreas degradadas. No entanto, devido à baixa resiliência dos campos rupestres de onde as placas foram retiradas, a translocação de placa de vegetação apenas pode ser considerada no caso de resgate de habitat, em circunstâncias em que a destruição completa do habitat é inevitável. Face à dificuldade de se restaurar os campos rupestres, a proteção e a conservação dos mesmos deve ser uma prioridade.

Palavras-chave : Banco de semente, Campos rupestres, Cerrado, ecologia da restauração, ecologia das communidade, ecossistema neotropical de montanha, germinação, restauração de campos, savannas, transferência de feno, translocação de placa de vegetação, translocação, transplantação.

ABSTRACT

Composition, phenology and restoration of campo rupestre mountain grasslands - Brazil. Global environmental changes, especially land-use changes, have profound effects on both ecosystem functioning and biodiversity, having already altered many ecosystem services. These losses emphasize the need to preserve what remains; however when conservation programs are not sufficient, restoring areas that have been destroyed or disturbed can improve conservation efforts and mitigate damages. This work focuses on campos rupestres, Neotropical grasslands found at altitudes, which are part of the Cerrado (Brazilian savannas). They host a great biodiversity with a high level of endemism and, like other mountain ecosystems, provide valuable ecosystem services, such as water purification and recreational services. They have been and still are being impacted by human activities, such as civil engineering construction, quarrying or mining. The first objective of this thesis was to describe the reference ecosystem in order to aim for a clear restoration target and to monitor progress and success. We show that campos rupestres are composed of at least two distinct plant communities (i.e. sandy and stony grasslands), each having a specific composition and structure, hosting a great biodiversity. Several phenological patterns occur among the herbaceous communities: the majority of species flowers and fruits appear during the rainy season but other patterns can be observed. During our 2-year survey, some dominant species belonging to Poaceae, among others, were not observed reproducing, which implies limited chances to disperse on degraded areas. Campo rupestre vegetation is not resilient following a strong disturbance: several years after the disturbance, almost no native species are encountered on the degraded areas, soils are completely altered and seed bank recomposes only with non-target ruderal species. According to the filter model, a local community is a subset of the regional species pool determined by a set of dispersal, abiotic and biotic filters. Acting on the different filters to influence the plant community was the core of our restoration interventions. We then applied three in-situ restoration protocols (hay transfer, species translocation and turf translocation) to restore both kinds of grassland. Hay transfer does not allow the restoration of campo rupestre vegetation because of soil alteration and mainly because of poor seed quality. Indeed, germination studies show that, while some Xyridaceae and Velloziaceae have a high germinability, some dominant Poaceae, Cyperaceae or Asteraceae species have embryoless, unviable or dormant seeds, which makes seeding less efficient. There is no evidence that fire-related cues enhance germination in campos rupestres. Species translocation is successful for only one species, Paspalum erianthum; for the others, root damages probably impede survival. Finally, turf translocation is the most successful method, since numerous species are re-introduced on degraded areas. However due to the low resilience of pristine campos rupestres where turfs are taken from, turf translocation can only be considered in the case of habitat rescue, in circumstances when complete habitat destruction is otherwise unavoidable. Face to the difficulty to restore these peculiar grasslands, the protection and the conservation of campos rupestres must be made a high priority.

Keywords: Cerrado, community ecology, germination, grassland restoration, hay transfer, Neotropical mountain ecosystems, restoration ecology, rupestrian fields, rupestrian grasslands, savannas, seed bank, translocation, transplantation, turf transfer.