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Degradation and invasibility of subtropical grasslands in Southern Brazil

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Für meine Eltern

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Summary

Grasslands cover 41% of all terrestrial biomes. They have on the one hand an enormous value for humanity through providing a large number of ecosystem functions and services, but are on the other hand extremely threatened by several factors. The main threats to grassland systems are changes of land use and the invasion of non-native organisms. Land-use changes include many different components from changes in grassland management to losses due to conversion to other land use or the regeneration after abandonment of other land uses. This PhD thesis aims to analyze the consequences of degradation, both concerning land-use changes and invasion by non-native species, and to develop strategies for the conservation and restoration of grasslands, using a highland region of Southern Brazil as an example. The region is suffering from ongoing land-use changes, and the role of non-native plant species for these changes is still largely unknown. Grassy biomes have been neglected by nature conservation in Brazil to date and therefore comprehensive strategies to ensure the survival of these ecosystems are missing.

The first main study of the PhD thesis describes a framework for grassland degradation and restoration that integrates different forms of land use and thresholds between degradation stages. Grassland that is in equilibrium with management is considered as the reference by this framework. The first form of degradation is caused by changes in management type or intensity. The model assumes that this kind of change does not go beyond a self recovery threshold, indicating that by means of re-introducing the original management, the grassland will recover to its original form. The second form of degradation is the conversion of the grassland to a different land use, e.g. a plantation of exotic trees, which leads to a complete change of ecosystems structure and processes. The model further assumes that after this type of land use is abandoned, a development to a strongly degraded stage of grassland is possible. This development, however, will reach a second threshold, the restoration threshold that can only be overcome by extensive measures, e.g. soil melioration. Results from spatial

analyses using remote sensing data showed, that while loss of grassland itself can be detected, qualitative conclusions about the different degradation stages of grassland can only be made based on field data.

The second main study of the PhD thesis reports on a major field survey over two years that quantified abiotic and biotic changes in the study region caused by the different forms of grassland degradation described in the conceptual framework. To achieve this aim vegetation and soil data were collected in five different land-use types that represent different stages of the conceptual model. Permanent grassland that is managed by burning and grazing served as a reference. Two types of management changes were used to quantify the first type of degradation, i.e. a grassland that is not (or at very low frequency) burned and not (or in very low intensity) grazed, and in contrast a grassland with very intensive management including fertilization and over-sowing with non-native species. For the case that grassland is converted and afterwards abandoned, also two different land-use types were examined: areas that had undergone a period as agricultural field including fertilization, deep tillage, and in most cases over-sowing with non-native species; and areas that had experienced a period of use as pine plantation that was then logged. The here collected data allowed a quantification to which degree the different land-use types caused degradation. It could be shown that the reduction in management intensity led to a structurally different grassland that maintained many typical grassland species but showed decreases in species numbers. Intensive grassland on the other hand, not only showed strong deviations concerning biotic components but also concerning abiotic factors. For both types it is not clear whether they have reached or crossed the self-recovery threshold. In order to assess this, experiments that re-introduce traditional management to these areas would need to be conducted. Both areas that have experienced conversion to other land uses show marked changes in species composition in comparison to the reference. In addition, areas under agriculture also show strong abiotic deviations, similar to intensive grassland. The examined areas were of different age but no effect of time since abandonment of other land use could be determined. This is an indication that these areas might have reached the afore mentioned restoration threshold after which measures will be necessary to create reference grassland conditions. Further experiments are necessary to determine which restoration measures would be best suited to improve these secondary grasslands.

If restoration measures have to be conducted, these also need to account for the presence of non-native species in the different land-use types. As not all non-native species are considered problematic and management is not feasible for every species, a tool to rank these species is necessary. It is important to conduct this ranking on a regional scale to derive adequate management strategies. Optimally this ranking would encompass an assessment of impacts of the different species. These assessments are however time intensive and management does often not have this time to reach decisions. As an alternative, a decision tree is presented in the third main study of the PhD thesis, that uses species distribution data to rank them as 'spreading', 'establishing' or 'sporadic'. The corresponding management suggestions indicate whether a species is in need for active management, e.g. eradication, or intensive or light monitoring. Distribution data for all non-native species were extracted from the vegetation dataset collected during the field survey and species were ranked according to the decision tree. The results were compared with a national list, where many species that have been identified during the ranking were not present. These findings emphasize that restoration on a regional scale also needs non-native species assessments on a regional scale to integrate these adequately into management strategies.

In the final discussion of the PhD thesis the results from both, the assessment of degradation by land use and the ranking of non-native species, were combined. Based on this, measureable goals for restoration were defined and management strategies developed. These strategies include suggestions, how restoration of reference grasslands can be achieved on areas that have undergone some other form of land use and how conservation of reference grasslands in areas that have suffered degradation by management changes could be accomplished.

Zusammenfassung

Grasländer bedecken etwa 41% der terrestrischen Erdoberfläche. Sie haben einerseits eine besondere Bedeutung für die Menschheit, da sie wichtige Ökosystemfunktionen und -dienstleistungen bereitstellen, andererseits werden sie durch mehrere Faktoren zunehmend gefährdet. Die Hauptursachen für die Gefährdung von Grasländern sind der steigende Landnutzungswandel und die Invasion nicht-heimischer Arten. Landnutzungswandel umfasst verschiedene Komponenten, wie die Änderung des Graslandmanagements, den Verlust von Graslandfläche durch die Umwandlung in andere Arten von Landnutzung sowie die Regenerierung nach Aufgabe von anderen Landnutzungen. Die vorliegende Dissertation hat das Ziel, die Folgen von Degradierung, sowohl in Hinblick auf Landnutzungswandel als auch auf die Invasion nicht-heimischer Arten, zu untersuchen. Daraus werden Strategien für den Schutz und die Renaturierung einer Graslandregion in Südbrasilien entwickelt. Das Untersuchungsgebiet hat in den letzten Jahren einen sehr starken Landnutzungswandel erfahren und die Rolle nicht-heimischer Arten für diesen Wandel ist noch gänzlich unbekannt. Naturschutz in Brasilien hat Graslandsysteme bisher vernachlässigt und es fehlen daher Methoden, um den Fortbestand dieser Systeme zu gewährleisten.

Die erste Hauptstudie der Dissertation entwickelt daher zunächst ein Modell, das verschiedene Formen von Degradierung, Renaturierung und Schwellenwerte zwischen verschiedenen Degradationsstadien beinhaltet. Grasländer, die durch Management in einem Gleichgewicht gehalten werden, werden in diesem Modell als Referenzsysteme betrachtet. Eine erste Form der Degradierung wird durch Änderungen der Art oder Intensität des Managements verursacht. Das Modell geht davon aus, dass diese Art der Degradierung dabei einen Schwellenwert für die eigenständige Erholung nicht überschreitet. Dies bedeutet, dass eine Rückführung zum eigentlichen Management zu einer Wiederherstellung des Systems aus sich selbst heraus führen kann. Die zweite Form der Degradierung ist dagegen eine Umwandlung der Grasländer in eine andere

Form der Landnutzung, z.B. eine Aufforstung mit nicht-heimischen Baumarten. Dies hat eine komplette Veränderung der Standortbedingungen zur Folge. Das Modell geht davon aus, dass sich das System bei Aufgabe dieser neuen Landnutzung zu einer stark degradierten Form eines Graslandes zurückentwickeln kann. Diese Entwicklung geht jedoch nur bis zu einem zweiten Schwellenwert, dem Renaturierungs-Schwellenwert, der nur durch besondere Maßnahmen wie beispielsweise Bodenverbesserung, überwunden werden kann. Eine räumliche Analyse von Fernerkundungsdaten in der Untersuchungsregion zeigt, dass es möglich ist, den Verlust von Grasländern auf diese Weise darzustellen. Die verschiedenen Formen der Degradierung von Grasländern können so aber nicht abgebildet werden, sondern bedürfen vielmehr umfassenden Feldstudien.

In der zweiten Hauptstudie der Dissertation wurde eine umfangreiche Felduntersuchung über zwei Jahre mit dem Ziel durchgeführt, abiotische und biotische Veränderungen der verschiedenen Degradierungsformen des Graslands in der Untersuchungsregion zu quantifizieren. Dazu wurden Vegetationsaufnahmen und Bodenuntersuchungen in fünf unterschiedlichen Landnutzungstypen durchgeführt, die die im Modell unterschiedenen Degradierungsstufen repräsentieren. Als Referenzgrasländer wurden gebrannte und beweidete, natürliche Grasländer festgelegt. Um die erste Form von Degradierung darzustellen, wurden zwei Grasländer mit Änderungen des Managements betrachtet: Grasländer, in denen die regelmäßige Bewirtschaftung mit Brennen und Beweidung verringert wurde und im Gegensatz dazu, sehr intensiv bewirtschaftete Grasländer, die gedüngt und mit nicht-heimischen Futterpflanzen eingesät wurden. Als Beispiele für die zweite Form von Degradierung wurden ebenfalls zwei verschiedene Flächentypen ausgewählt: Flächen, die als Acker genutzt wurden und dabei Bodenbearbeitung, Düngung und ebenfalls Einsaat von Futterpflanzen ausgesetzt waren, und Flächen, die als Kiefernplantage bewirtschaftet, vor kurzem allerdings abgeholzt wurden. Die hier erhobenen Daten erlauben eine Quantifizierung, zu welchem Grad die verschiedenen Landnutzungen zu einer Degradierung geführt haben. Eine Verringerung der Managementintensität hat im Graslandsystem zu strukturellen Veränderungen und einem Verlust von Pflanzenarten geführt. Intensiv bewirtschaftete Grasländer zeigten neben biotischen auch starke abiotische Veränderungen. Für beide Typen ist jedoch nicht geklärt, ob sie einen Schwellenwert erreicht oder möglicherweise überschritten haben. Um dies zu klären, müssten Experimente durchgeführt werden, bei denen das ursprüngliche Management auf den Flächen wiedereingeführt wird. Beide Flächentypen, die eine Umwandlung zu anderen Landnutzungen erfahren haben, zeigten starke Veränderungen in der Artenzusammensetzung. Zusätzlich wiesen ehemalige Äcker auch abiotische Veränderungen auf ähnlich denen unter intensivem Management. Obwohl die verschiedenen Flächen ein unterschiedliches Alter hatten, konnte kein Effekt der Zeit seit Aufgabe der Nutzung ermittelt werden. Dies deutet darauf hin, dass diese Flächen den Renaturierungs-Schwellenwert erreicht haben und Maßnahmen erforderlich sind, um hier wieder ein Referenzgrasland zu etablieren. Weiterführende Experimente sind auch hier notwendig, um Methoden zu bestimmen, die für die Renaturierung dieser Flächen am besten geeignet wären.

Bei der Planung von Renaturierungsmaßnahmen muss außerdem berücksichtigt werden, ob nicht-heimische Arten auf den verschiedenen Flächentypen vorhanden sind. Da nicht alle diese Arten ein problematisches Verhalten zeigen, und ein Management nicht für alle Arten durchgeführt werden kann, ist ein Werkzeug zur Klassifizierung dieser Arten notwendig. Diese sollte auf einer regionalen Skala erfolgen, um adäquate Managementstrategien zu entwickeln. Im besten Fall würde eine solche Klassifizierung auch Auswirkungen der einzelnen Arten berücksichtigen. Die Ermittlung von Auswirkungen ist jedoch sehr zeitaufwändig und Managemententscheidungen müssen oft schon nach kurzer Zeit gefällt werden. Als Alternative wird in der dritten Hauptstudie der Dissertation daher ein Entscheidungsbaum vorgestellt, der Verbreitungsinformationen der einzelnen Arten benutzt und diese als ‚sich ausbreitend', ‚sich etablierend' und ‚sporadisch vorkommend' klassifiziert. Die dazugehörigen Empfehlungen für das Management zeigen, ob eine Art aktives Management, z.B. Bekämpfung, intensive oder nur leichte Überwachung benötigt. Verbreitungsdaten für alle nicht-heimischen Arten wurden aus dem Vegetationsdatensatz der vorherigen Studie entnommen. Der Vergleich der Ergebnisse mit nationalen Artenlisten nicht-heimischer Arten zeigt, dass viele dieser Arten nicht auf Listen höherer Ordnung vorhanden sind. Dies macht deutlich, dass Renaturierung auf der regionalen Ebene auch regionale Verbreitungsdaten benötigt, um sinnvolle Maßnahmen bezüglich des Umgangs mit nicht-heimischen Arten zu beschließen.

Im Schlusskapitel der Dissertation werden die Erhebung des Degradierungszustandes der verschiedenen Flächentypen und die Klassifizierung der vorhandenen nicht-heimischen Arten zusammengeführt. Daraus können sowohl die Ziele für die Renaturierung dieser Grasländer abgeleitet werden, als auch Managementstrategien entwickelt werden. Diese Strategien umfassen sowohl Empfehlungen, wie die Renaturierung von Referenzgrasland auf Flächen mit anderer Landnutzung sowie der Schutz von natürlichen Grasländern erreicht werden kann, wenn Managementänderungen zu einer Degradierung geführt haben.

Chapter 1

General Introduction

1.1 Grasslands

Grasslands cover ca. 41% of the land surface, comprising savannas (14%), grassy shrublands (13%), non-woody grasslands (8%) and graminoid tundra (6%); they can be found on every continent, except Antarctica (White et al. 2000; Suttie et al. 2005). These numbers should, however, be treated with care, as there is no generally accepted definition of grasslands. In a wider sense, all ecosystems with grasses dominating the ground cover are considered as 'grassland', while the maximum cover of trees is 10–40% depending on the study (compare Suttie et al. 2005 and Parr et al. 2014). Thus, especially in savannas the boundary between grassland and forest has been debated for a long time (Staver et al. 2011), and the total area of grassland may therefore be underestimated in some regions. Other sources of inaccuracy are that grassland that is grazed with livestock is often treated as agricultural land and grassy biomes are often wrongly classified as deforested land (Veldman et al. 2015b). Table 1 gives an overview of the different types of grasslands and the respective climatic regions where they can be found.

It is further possible to distinguish permanent and secondary grasslands. The former are naturally occurring and are divided based on the factor restricting forest growth into 'edaphic', 'climatic' and 'mesic' grasslands (Veldman et al. 2015a). Mesic grasslands, which are depending for their persistence on disturbance by fire or herbivores, are often wrongly perceived as grasslands that have developed due to anthropogenic land use (Bond and Parr 2010). However, they have to be clearly distinguished from real secondary grasslands that are emerging after other land use, e.g. after clearance of forest or abandonment of croplands. Some studies show that many grasslands are exceptionally species-rich (Wilson et al. 2012), not only in plant species but also, for example in birds (White et al. 2000). However, Noss et al. (2015)

Table 1 Overview of different types of grassland that can be found around the world. The table describes the major climatic region (Köppens climate) and the respective grassland type that can be found therein. Structural and climatic characteristics that can be used to distinguish types from each other are described in the next column. Finally, examples for each grassland type are given but these are not comprehensive. The information is derived from Gibson (2009) as well as Pfadenhauer and Klötzli (2014).

Köppens Climate	Grassland Type	Structural or Climatic Characteristics	Examples
Tropical and humid climates (A)	Savannas	Winter dry season with possible fires; Presence of large grazers; tall tussock grasses, shrubs and low trees	Serengeti and Veld in Africa; Cerrado in Brazil; Australian savannah
Dry climates (B)	Steppe grasslands and deserts	Potential evaporation and transpiration exceed precipitation	
Semi arid climate	Tropical/subtropical semiarid desert and steppe grasslands	low-latitude steppe; hot temperatures	Chaparral; near deserts in Africa and Australia; southern South America; portions of India
	Temperate arid grassland	mid-latitude steppe; cold and dry; low-growing bunch grasses	Near deserts in western Great Plains; China/Mongolia; Russian steppe
Arid climate	Deserts	sparse cover of shrubs/dwarf-shrubs, perennial grasses	Mitchell grasslands in Australia; desert grasslands of USA and Mexico
Subtropical Climates (C)	Temperate mid-latitude grasslands, prairies	Hot humid summers with thunderstorms, mild winters; temperate forests predominate this climate	Southern Tallgrass prairie USA; Campos and Pampas of South America
Temperate Climates (D)	Temperate mid-latitude grasslands, prairies	Temperate climate with cold winters	Northern Tallgrass prairie; northern China, Manchuria
Polar (F)	Graminoid tundra	No tree growth due to short vegetation period; low vegetation dominated by graminoids and dwarf-shrubs	East Siberia; Alaska and northern Canada; Svalbard
Highland climates (H)	Montane grasslands	No specific highland climate, depends on region; Subalpine and alpine meadows	Andes; East Africa; New Zealand
In any climate	Secondary grassland	Develops after clearing of forest vegetation	Calcareous grasslands of Europe

suspect that many biodiversity hotspots in grasslands have been overlooked due to the above mentioned misconception of the role of disturbances such as fire or herbivores.

Grasslands provide many ecological and socio-economic values. They form the basis for livestock production, as more than half of them are used as permanent pastures (Steinfeld et al. 2006), and are thus important for the global food supply, especially in the poorer regions of the world (Boval and Dixon 2012; O'Mara 2012). Beside the provision of fodder, grasslands play an important role for the global carbon cycle (Gibson 2009). Generally, forests (natural or plantation) are seen as a major opportunity for carbon sequestration, mainly due to their large amounts of aboveground biomass (e.g. Wright et al. 2000). However, mature forests show only little net growth and the rates of new accumulation of carbon in the biomass are low (Mannetje 2007). In contrast, grasslands show a constant retake of carbon, high ratios of below- to aboveground biomass (e.g. Miranda et al. 2014), and high amounts of carbon being stored in the soil (Gibson 2009). Given the extensive area they occupy, they hence contribute considerably to the global sequestration of carbon. This potential strongly depends on the management practice and can be negatively affected by overgrazing (FAO 2010). Finally, grasslands are relevant for recreation and contribute to scenic beauty in many regions of the world (Gibson 2009). All these aspects emphasize that grasslands play a fundamental role for the survival of the human population, while they suffer from many threats that come along with this role.

1.2 Threats to grasslands

In contrast to the clearing of tropical forests, the threat of grassland ecosystems, especially in the tropics, receives much less public attention (Bond and Parr 2010; Parr et al. 2014). However, grasslands are among those habitats that are most affected by past and future land-use change and loss of biodiversity (Sala et al. 2000; Newbold et al. 2015). At the same time many studies from around the world show, that grasslands are subject to the invasion of non-native species which may be the second largest threat to these systems (e.g. Seastedt and Pyšek 2011). In the following sections, the different causes for threats and their consequences will be outlined in detail.

1.2.1 Land-use change

Transformation of grassland to other land use

Due to their large extent, grasslands are suffering severely from land-use changes. Losses are not universal but show considerable regional differences. According to Hoekstra et al. (2005) 46% of temperate grasslands, savannas and shrublands, 24% of (sub-) tropical grasslands and savannas, 27% of flooded grasslands and savannas, and 13% of montane grass- and shrubland have been converted to other land uses until now. These estimates only represent a minimum estimation of loss, as the resolution of land cover data used was 1km² and only fully converted cells were considered. Thus, the total area of conversion is presumably much larger. Furthermore, loss itself needs to be differentiated to what type of land use grasslands are transformed to, as not each transformation will have the same consequences for the system (Neke and Du Plessis 2004).

a) Transformation to cropland

Ramankutty and Foley (1999) estimate that on a global scale, grasslands, savannas and steppes have suffered a net loss of 6.7mio km² between 1700 and 1992 to the conversion to cropland and the major part (4.7mio km²) was lost after 1850. According to their calculations, cropland increased globally in that period from 4% in the year 1700, to 18% in 1992. However, there are strong regional differences in the amount and means of transformations: Almost half of the grassland area of South Africa was transformed by 1995, mainly to irrigated agriculture as most areas were climatically not suitable for extensive crop production (Neke and Du Plessis 2004). In the North American prairies, less than half of the original grassland area remains, and Stephens et al. (2008) predict that the current rate (0.4%) of annual grassland conversion to cropland will further increase in the future, and that especially high quality soils will be at risk. Baldi and Paruelo (2008) found also high rates of transformation to cropland in the Rio de la Plata region in South America, with Argentina suffering larger quantities of transformation than Uruguay and Brazil. Consequences of conversion to arable fields are changes in soil physical and chemical properties due to compaction and addition of fertilizer (McLauchlan 2006), and replacement of grassland species by arable species as only few are able to persist within the new land use. Forecasts based on current and past conversion rates estimate that by 2050 the global agricultural area (cropland *and* pastureland) will have increased by another 18%, and that these changes will be concentrated in Latin America and sub-Saharan central Africa (Tilman et al. 2001).

While these studies show a continuous increase in total area of cropland, transitions are not accounted for, whether or not new areas are converted *or* 'old' areas are abandoned as well, and thus the net increase in cropland area might be much higher than calculated (Hurtt et al. 2006). Ramankutty and Foley (1999) estimate that ca. 0.6mio km² of cropland within grassland-savanna biomes have been abandoned since 1850. A comprehensive evaluation of these secondary grasslands is missing (Bond and Parr 2010), but some case studies suggest that secondary grassland is developing in these areas, although differing from the original grassland in species composition and soil properties (e.g. Redhead et al. 2014).

b) Transformation to forest plantations

Besides the conversion to cropland, afforestation of natural grassland areas, mostly with non-native tree species, is an increasing driver of grassland area loss (Veldman et al. 2015b; Veldman et al. 2015c). This threat arises mainly by the misconception that grasslands are a stage of forest degradation, policies aiming to reach forest transition (from net forest loss to forest recovery) and thus there is generally a high acceptance for afforestation of formerly treeless areas for the purpose to sequester carbon (Putz and Redford 2010). Large parts of permanent grassland have even been classified as opportunities for afforestation (Veldman et al. 2015c). The global area of plantations already comprises 3.5% of total forest area and is increasing at a rate of about 2% annually (FAO 2006). However, thorough quantitative assessments, how much of these plantations have been established on formerly open land, including grassland, is not available. Regional assessments suggest, that conversions are especially high in tropical and subtropical countries, and that grasslands are more often converted than natural forests (Nahuelhual et al. 2012). Only recently, concerns have been raised that transitions from open vegetation to plantation can have negative consequences (Farley 2007) including decreases in soil water retention (Farley and Kelly 2004), declining soil C stocks (Guo and Gifford 2002) and nutrient supplies (Berthrong et al. 2009), and lower plant species richness (Bremer and Farley 2010). Some plantation areas are not replanted after harvest but abandoned. So far, no global assessments on the magnitude of these abandoned areas are available and only few local studies indicate that secondary grassland regenerating in these areas has a vegetation composition different from the original grassland vegetation (e.g. Zaloumis and Bond 2011).

Both, the transformation to cropland and to forest plantations are accompanied by the increasing fragmentation of the remaining grasslands (e.g. Roch and Jaeger 2014). This fragmentation is intensifying the effects of transformations as it leads to dispersal limitations and isolation of populations ultimately resulting in extinction risks for species of all taxonomic orders (e.g. Soons et al. 2005; Joshi et al. 2006).

Degradation of grassland quality

Land-use change does not only encompass the obvious loss of area due to transformation but comprises qualitative features of the remaining grasslands as well. The degradation of grassland includes various aspects from structural changes over changes in species numbers and composition, to changes in abiotic properties and ecosystem functions. These changes are most often caused by alterations of grassland management practices, i.e. an increase or decrease of grazing pressure by native herbivores or introduced livestock, and changes to the fire regime. The consequences of management changes strongly depend on the climatic region and productivity of the grassland as well as its evolutionary history with grazers (Milchunas et al. 1988).

For productive grasslands with a long exposure to grazing, the often-quoted model by Milchunas et al. (1988) predicts positive effects of medium grazing intensity on species richness which has been supported by the findings of many studies (Osem et al. 2002; Bakker et al. 2006; Lezama et al. 2014; Fraser et al. 2015). Although co-evolved with grazers, heavy grazing still has severe consequences for grassland properties, including diversity loss, the exposure of bare soil or rock, and the formation and expansion of grazing lawns (e.g. Biondini et al. 1998; Archibald 2008; Cingolani et al. 2014). Olff and Ritchie (1998) point out that the severity of these effects may depend on the type of herbivore involved, i.e. whether large or small herbivores are concerned. The case that grazers are removed from grasslands with a long history of grazing is not included in the model. However, this development also has severe consequences. Exclusion experiments show increasing amounts of litter, declines in species numbers and changes in composition with dominance of a few species, e.g. tussock grasses (for exclusion of introduced livestock see Loydi et al. 2012; for removal of native herbivores Burns et al. 2009). Although burning selects for different traits in species, Bond and Keeley (2005) have shown that fire can be treated as an alternative consumer of biomass. Studies conducted in regions with fire-adapted grassland systems, hence, show changes after fire suppression similar to those observed with herbivore exclusion (e.g. Hinman and Brewer 2007; Spasojevic et al. 2010). It has been recently hypothesized that these grasslands may also possess an internal threshold after which a shift from grassland to shrubland is caused (Ratajczak et al. 2014). Therefore, both types of disturbances are necessary for the maintenance of productive grassland with a long history of grazing.

While abandonment of management seems a major threat in grasslands adapted to grazing, the opposite is true for non-adapted grassland systems. Many grassland areas that have evolved without large grazing animals are subject to grazing since European settlement. For unproductive ecosystems with a short evolutionary history with grazers, Milchunas et al. (1988) predicted declines in species richness with grazing of any intensity. Although studies from grasslands in New Zealand, Australia and Patagonia generally confirm signs of degradation by grazing (MacLeod and Moller 2006; Lunt et al. 2007; Fensham et al. 2014; Oliva et al. 2016), strong declines in species richness as predicted by the model have not been reported. A point not considered in the model is whether the removal of these herbivores will allow the grasslands to recover again or whether the transitions have reduced their resilience (Lunt et al. 2007; Whitehead et al. 2014; Oliva et al. 2016). In arid or semiarid rangelands the effects of overgrazing ultimately will lead to desertification (Milton et al. 1994), which has been identified as a process threatening large parts of the global (arid) grasslands (Spinoni et al. 2015).

While satellite images are adequate to quantify loss of grassland itself, it can only in few severe cases be assessed if the grassland is in some kind of degraded state or not (e.g. Neke and Du Plessis 2004). In order to qualify the stage of a grassland system and to determine conservation or rather degradation status, on-ground assessments are necessary.

1.2.2 Invasions by non-native species

Beside the various effects of land-use changes, the second aspect that has been identified as a threat to grasslands is the invasion of non-native plants (Firn et al. 2011; Seastedt and Pyšek 2011; Seabloom et al. 2013). There are studies compiling extensive lists of non-native species for many grasslands of the world, examining regions (e.g. South Island of New Zealand; Day and Buckley 2013), biomes (e.g. Pampa in South America; Fonseca et al. 2013) or entire countries (USA; DiTomaso 2000). Two main groups of invasions in grasslands can be distinguished: On the one hand, many species have been and still are intentionally introduced into grasslands as fodder plants and are able to further invade into surrounding natural grasslands (Low 1997; Driscoll et al. 2014). Examples include *Agropyron cristatum* in the USA (Henderson and Naeth 2005), *Andropogon gayanus* in Australia (Petty et al. 2012), and *Melinis minutiflora* in Brazil (Rossi et al. 2014). Ongoing land-use changes and disturbances may further facilitate the invasion of non-native species into these systems (e.g. Davis et al. 2000; MacDougall and Turkington 2005). Besides herbaceous species, a second group of common invaders in grassland systems are woody species, mostly pines that arrive there from adjacent plantations (e.g. Zalba and Villamil 2002; de Abreu and Durigan 2011). Given the relative novelty of many plantations, the extent of these invasions may further increase in the future (Zalba and Villamil 2002).

While there are many different non-native species in the grasslands throughout the world, these species are not equally problematic, as only some might start to exert influences on the grassland system. These impacts include reductions in native species diversity (e.g. Hejda et al. 2009) or changes to ecosystem functions like carbon storage (Koteen et al. 2011) or nutrient cycling (Vitousek 1990). The biggest challenge for the management of these species is the uncertainty of predictions, as not every species has a measureable impact, the same species might have an impact in one region but not in another and impacts might be delayed. Much effort has been made to develop tools with which species likely to invade can be predicted in advance (e.g. Pheloung et al. 1999; Andreu and Vilà 2010) or for those species that have already invaded, provide a framework to measure impact or its invasiveness (e.g. Parker et al. 1999; Randall et al. 2008). These tools, however, can only be employed if extensive and detailed information about the species is available, which is rarely the case. While increasingly precise technologies are developed to track invasions of woody species from plantations via satellite images (e.g. Visser et al. 2014), information on all other non-native species still requires data from vegetation surveys. In order to reduce the threat to grassland by non-native species, effective tools for regional conservation managers are necessary that allow detection of potentially problematic species, prioritization and reaction in sufficiently short time scales.

1.3 Restoration of grasslands

In response to the increasing threats to global biodiversity the field of ecological restoration has emerged, aiming to develop methods to assist the "recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004). Requirements for successful restoration include reliable information on the properties of the system to be restored, a thorough discussion on potential reference systems and the identification of drivers that trigger changes (Hallett et al. 2013). A challenge, restoration ecologists are increasingly facing, is the presence of non-native species in degraded areas and the questions whether and how these species affect the system and might even counteract restoration measures (Norton 2009). This challenge was partly self-made as for many years, restoration used non-native species, for example for the rehabilitation of mined sites, or generally as a means to rapidly re-vegetate bare ground (Bauman et al. 2015). In contrast to that, many recent studies tackle the question if it is possible to design invasion-resistant communities during restoration using theories of invasion ecology, e.g. limiting similarity (Bakker and Wilson 2004; Funk et al. 2008; Abella et al. 2012; Mahaney et al. 2015).

Despite these efforts to develop adequate restoration strategies, land use in many regions has modified ecosystems to such a degree and non-native species may have reached dominance in the communities, with the consequence that recovery of near-natural systems has become difficult (Le Maitre et al. 2011). Consequently, a recent debate in conservation and restoration ecology is the question how to deal with these 'novel ecosystems' (Lindenmayer et al. 2008). This term was coined by Hobbs et al. (2009) and has created much controversy, and it seems a fatalistic answer to the question whether restoration or management of non-native species can be successful at all (e.g. Murcia et al. 2014). Hobbs et al. (2009) propose that although the novelty of an ecosystem might not satisfy traditional conservation paradigms, it should in some cases nevertheless be accepted given restricted financial and practical possibilities of restoration. Decisions on the state of novel ecosystems, and subsequent restoration strategies, however, can only be made on a substantial data basis, and regional studies are necessary to adequately judge whether and to what extent an ecosystem is degraded, and whether or not non-native species could or should be accepted as part of the system.

1.4 Aims and objectives

This PhD thesis aims to develop strategies for the conservation and restoration for subtropical grasslands in Southern Brazil that are subject to degradation processes caused by different drivers. In order to do so, two aspects have to be considered: (1) The identification of the reference: which properties of the grassland are aimed for? And (2) the identification of drivers and their respective changes: Which drivers have created or are still creating changes to which properties of the grassland system? Both, land-use changes and invasions of non-native species, have previously been identified as a threat for grasslands and will therefore be considered in the subsequent chapters as the key drivers.

The three main chapters of this PhD thesis will tackle the two questions concerning both drivers on two levels, a theoretic basis and an applied level, and combine the results to develop thorough strategies (see Figure 1). Chapter 2 develops a framework that theoretically describes different forms of degradation caused by land-use changes compared to reference grassland. Based on these considerations, chapter 3 presents field data from the study region to determine attributes of the reference system, changes by land use and develops implications for restoration and conservation strategies. While both chapter 2 und 3 focus on the aspects of land-use changes, chapter 4 considers the invasion of non-native plants. It creates a decision tree that uses distribution data to derive management decisions for non-native plants. Based on the results of all three main chapters, it is possible to draw conclusions on how conservation of grassland could be achieved, where opportunities for restoration lie, and which role non-native species play for the realization of the developed strategies.

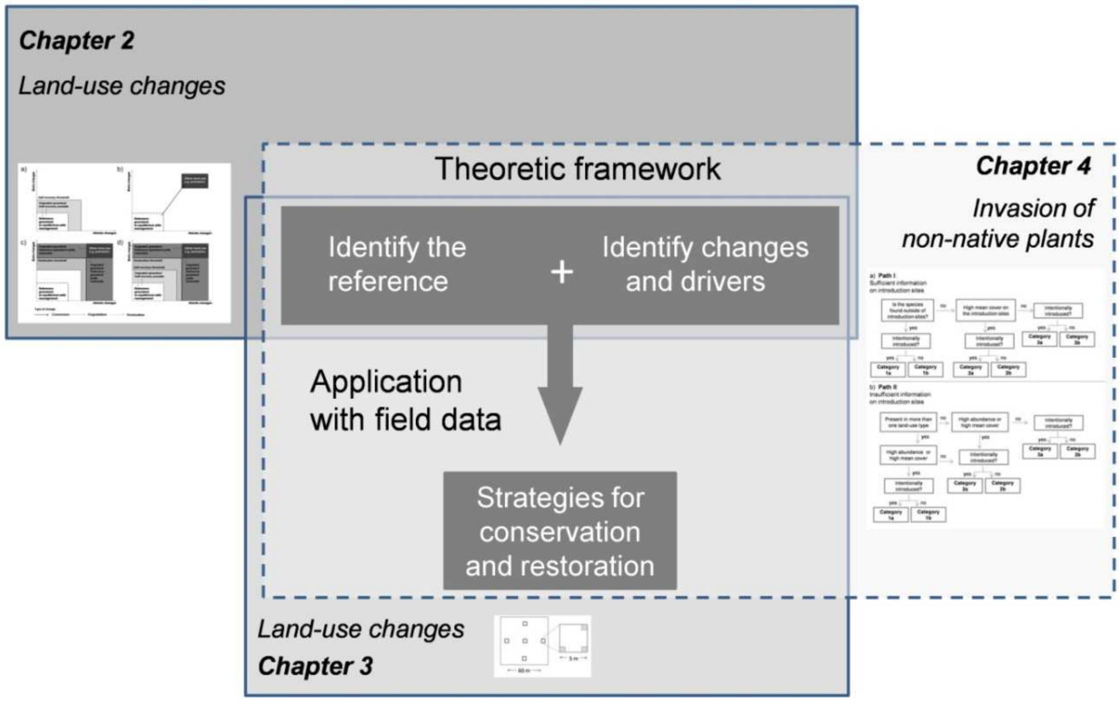


Figure 1 Conceptual diagram showing how the three main chapters of the PhD thesis combine theoretical frameworks and field date to derive strategies for conservation and restoration of grasslands in Southern Brazil under the changing land use and invasion by non-native plant species.

Outline of the main parts of the PhD thesis

Chapter 2

Grassland degradation and restoration: a conceptual framework of stages and thresholds illustrated by Southern Brazilian grasslands

In the first main chapter of the PhD thesis a conceptual model is introduced that enables to describe how different processes of degradation influence tropical and subtropical grassland systems and their restorability. The framework distinguishes degradation through modification of management intensity and degradation through conversion to other land uses. It further integrates two types of thresholds, one until which self-recovery of the system is possible and one until which restoration of the system (with additional technical measures) is feasible. The framework is illustrated by studies from grasslands in Southern Brazil.

Chapter 3

Effects of management intensity and temporary conversion to other land use on subtropical grasslands in Southern Brazil

In contrast to the previous main chapter, this one is based on a comprehensive set of field data, and shows how different land uses affect biotic and abiotic components of grasslands in the highlands of Southern Brazil. One focus lies on permanent grasslands that have experienced changes in management intensity, and it is shown how these changes lead to distinctions from reference grasslands. A second focus lies on the question whether or not secondary grasslands that develop after some other forms of land use still hold characteristics of permanent grasslands. The findings from both parts are integrated to formulate recommendations for the conservation and restoration of these grasslands.

Chapter 4

Setting priorities for monitoring and managing non-native plants: towards a practical approach

In this chapter a decision tree is introduced that allows land-managers to set priorities for the management of non-native species. The tree ranks non-native species based on their distribution data into 'spreading', 'establishing' and 'sporadic' and gives indications which species are in need for management or monitoring and which further information need to be gathered. The tree is tested with distribution data of non-native plant species in the study region and advantages and limitations to its applicability are discussed. Furthermore, the advantages of this approach over the current practice of a national list of invasive species are highlighted.

In the **general discussion** of the PhD thesis the findings from the three chapters are integrated to develop recommendations on how to improve the situation of grasslands in the study region. These findings can also give implications, which factors should be considered in other subtropical grassland regions when looking for strategies to mitigate impacts from land-use changes and invasion of non-native species.

1.5 Study system

Study region

As study system the highland grassland region of Brazil's southernmost state Rio Grande do Sul was chosen (see Figure 2). The region is located in the three municipalities of São Francisco de Paula (29°26'S, 50°34'W), Cambará do Sul(29°02'S, 50°34''W) and Jaquirana (28°53'S,50°21'W). The highland shows a slight incline towards the east, and altitudes are consequently ranging from ca. 810 to 1125 m a.s.l. Above the volcanic rhyodacite bedrock acidic cambisols and leptosols have developed as characteristic for the region (Almeida 2009). The current climate is subtropical humid (Köppen's Cfb) with annual mean temperatures of 16–22°C, occasional frost during winter, and an average annual precipitation of ca. 2250mm without marked dry periods (Nimer 1989).

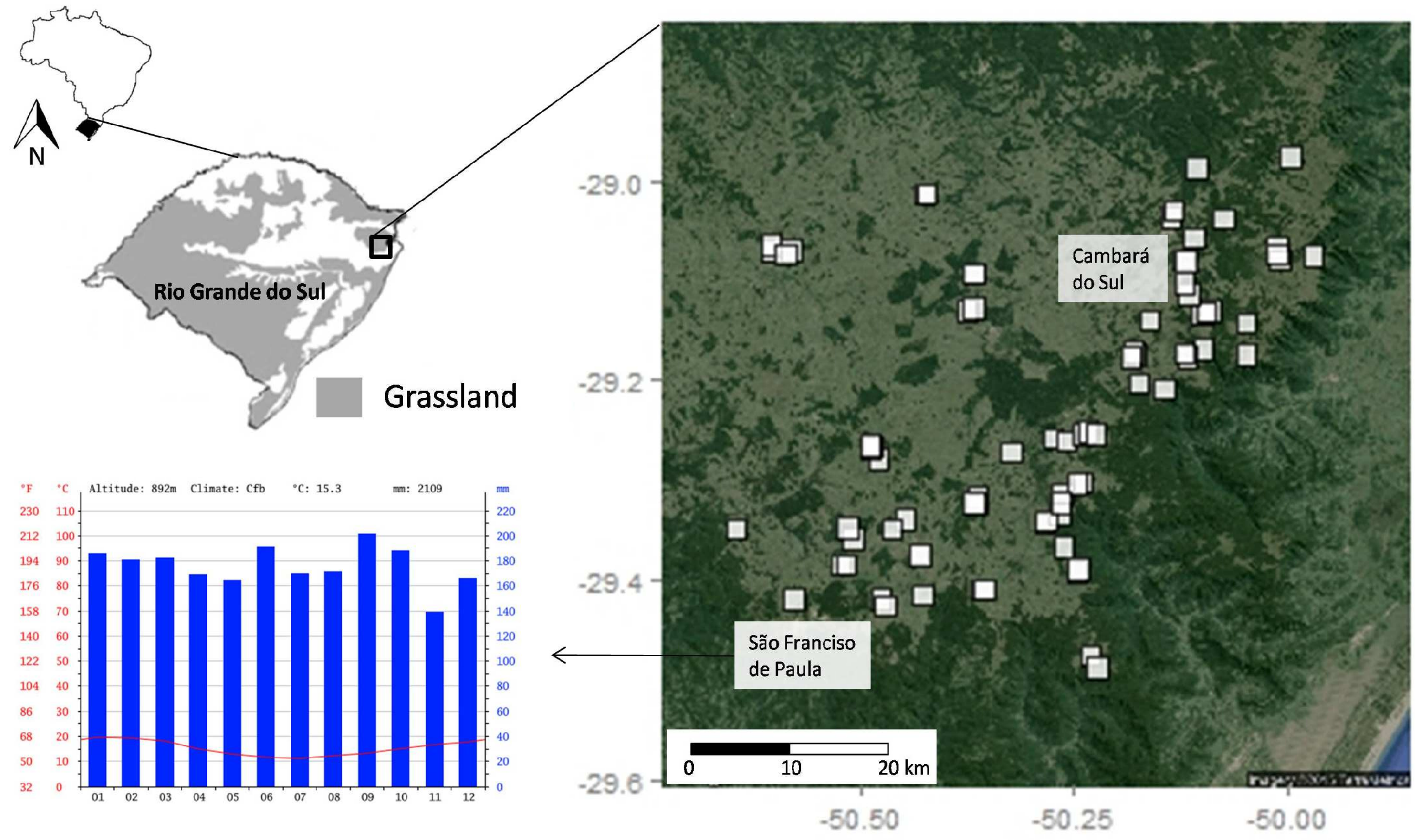


Figure 2 Study region in the highland grasslands of Rio Grande do Sul, Southern Brazil. The majority of the study sites are located in the municipalities of São Francisco de Paula and Cambará do Sul and the climate is Köppen's Cfb. Backgroundmap was derived from (Google Earth (2015), climatedate from Climate-data.org (2015).

This climate is suitable for forest vegetation, yet, the main vegetation is a mosaic of extensive grasslands with forests of *Araucaria angustifolia*, the latter predominantly found along rivers and streams. This current vegetation is a relic from a cooler and drier postglacial period (Behling et al. 2007). The grasslands were grazed by megaherbivores until colonization by Native Americans ca. 10,000 BP (Lima-Ribeiro and Diniz-Filho 2013). Besides herbivores, fire was a constant factor shaping and maintaining the system (Behling 2002; Behling et al. 2004). With the European settlement, a grassland management developed, that consists of cattle grazing throughout the year in medium stocking rates (0.5head of cattle ha^{-1}) and burning at the end of winter to remove excess dead biomass (Nabinger et al. 2000). The grasslands are very species-rich with more than 2600 known plant species (Boldrini 2009), while less than 0.5% of the total grassland area of Rio Grande do Sul is under legal protection (Overbeck et al. 2007). However, the two national parks *Aparados da Serra* and *Serra Geral* as well as the state parks *Tainhas* and *Aratinga* lie partly within the study region.

Study locations

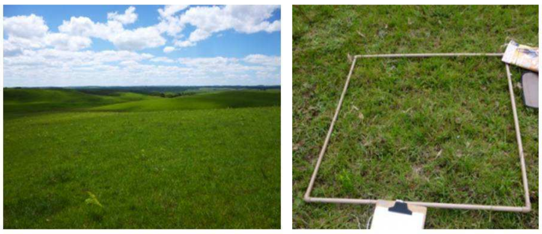
Land-use changes during the last decades have caused a decline in natural grassland area resulting from extensive pine plantations (*Pinus elliottii* and *P. taeda*) and expanding agricultural fields, mostly potato, corn and soybean. In 2002, only 38% (5424km²) of natural grassland remained in the highland region (Cordeiro and Hasenack 2009). Recent studies on landowner preferences indicate that conversion will continue in the future, as agriculture is perceived as more profitable than cattle ranching (Henderson et al. 2015). At the same time traditional grassland management undergoes changes, i.e. intensification of management to increase production (Ferreira et al. 2011; Tiecher et al. 2014), and decreasing management intensity mostly in conservation units due to restrictions for the use of livestock and fire.

Five types of land use were chosen that are representative for the different types of grassland in the study region (see Box 1). This choice includes three permanent grasslands: traditionally managed grassland with medium stocking rates and prescribed burning or mowing every 1–2 years (1a); occasionally burned grassland with reduced stocking rates, where biomass removal declined two or more years ago (1b); and unburned grassland with high stocking rates, fertilized and over-sown with non-native species (1c). Moreover, two secondary grasslands were included in the study that are subdivided based on their land-use history: Secondary grassland recovering from conversion to arable land, with grazing at variable stocking rates (1d); and secondary grassland recovering after logging of pine plantations, currently grazed with low stocking rates (1e). Agricultural areas that are still actively cultivated and plantations themselves were not included in the sampling.

Although land use is changing rapidly, no concise studies are available that identify possible areas where restoration is necessary or possible and which grassland properties would be suitable as a reference for restoration. Furthermore, the extent of non-native species invasions is unknown and management is thus also lacking a decision basis of which species should be prioritized for monitoring and management.

Box 1 Overview over five land-use types in the study region

Permanent grasslands



a) Permanent grassland with management of medium intensity: Usually burned every 1-2 years at the end of winter to remove excess biomass; structure is thus variable throughout the year; medium stocking rates; single *Araucaria* individuals on rocky outcrops possible

b) Permanent grassland with management of low intensity: regular burning has become infrequent, i.e. minimum 2 years maximum 20 years since regular burning ceased; dominance of tussock grasses and encroachment of shrubs (*Baccharis uncinella*); reduced grazing intensity; mostly in conservation units

c) Permanent grassland with management of high intensity: grassland is not burnt anymore; it has been oversown with mixtures of non-native forage species (mostly *Trifolium repens, T. pratense, Holcus lanatus* and *Lolium multiflorum*); fertilization and liming but no tillage; grazing with higher stocking rates; only on private intensive production systems

Secondary grasslands

d) Secondary grassland recovering after abandonment of *agricultural fields* on areas that were originally grassland; crops include potato, corn, and various vegetables; during agricultural use, regular use of fertilizer and deep soil tillage; after agricultural use most often over-sown with non-native forage species; varying stocking rates; time since abandonment ranges from 1 to 8 years

e) *Secondary grassland* regenerating in *logged pine plantations* that were originally grassland; after logging generally low grazing pressure; no fertilization, seeding or tillage during or after abandonment; areas most often in conservation units, where re-planting is restricted; time since abandonment ranges from 1 to 11 years

Chapter 2

Grassland degradation and restoration: a conceptual framework of stages and thresholds illustrated by Southern Brazilian grasslands

This chapter is the identical reproduction of the following publication:

Andrade B.A.[1], **Koch C**.[1], Boldrini I.I., Vélez-Martin E., Hasenack H., Hermann J.-M., Kollmann J., Pillar V.D., Overbeck G.E. (2015): Grassland degradation and restoration: a conceptual framework of stages and thresholds illustrated by Southern Brazilian grasslands. Natureza & Conservação 13(2): 95-104. DOI: 10.1016/j.ncon.2015.08.002

Author contributions: [1]These authors contributed equally to this article. All authors discussed the initial idea for this paper at a DFG-sponsored workshop in Freising (June 2012); BOA and **CK** wrote the paper together with GEO; EVM and HH provided the GIS data and performed the spatial analysis including the creation of the respective maps; the chapter was improved and edited by JK and JMH, and all authors contributed to the final version of this manuscript.

Abstract

Land degradation is a complex concept that integrates different aspects, including changes in soil conditions, biodiversity, productivity and socio-economic implications, compared to a reference state. We propose a new conceptual framework to analyze degradation stages and restoration thresholds in species-rich natural grasslands. The framework integrates different degradation stages with their respective thresholds and describes key processes of land-use change that lead to certain stages and thresholds. Specifically, we discuss two scenarios of grassland degradation, i.e. unsuitable grassland management and complete change of land use, sometimes followed by spontaneous recovery. We illustrate the framework with the case of south Brazilian grasslands, which are rich in biodiversity, but suffer from a series of degradation processes and are poorly considered from a conservation perspective. The conceptual framework can be applied by studies on degradation and restorability of tropical and subtropical grasslands after changes in management or transition to other land use; it will facilitate decisions on alternative management and conservation.

2.1 Introduction

Land-use change and degradation of natural ecosystems are principal causes for losses of biodiversity and ecosystem functions (Sala et al. 2000). Concrete numbers on land degradation are often only available for the complete loss of natural ecosystems, for example after conversion to more productive systems such as arable fields or tree plantations (for Brazil, e.g. IBGE 2012). However, degradation also includes less marked changes in structure, composition or ecological processes within the ecosystem. Therefore, degradation needs to be analyzed at different spatial scales, from a local focus on specific degradation processes to landscape and regional scales, and using diverse methods including remote sensing, plot-based measurements, experiments, expert knowledge and assessment of stakeholder experience (Reed et al. 2011). To provide a better understanding of the dynamics of degraded ecosystems and to facilitate mitigation of degradation processes and restoration, the concept of thresholds between alternative stages has been developed. While the framework suggested by Briske et al. (2006) focuses on definition and description of thresholds, Hobbs et al. (2009) described 'historical', 'hybrid' and 'novel' stages and identified 'restoration thresholds' when ecological, cultural or technical obstacles prevent a system to return to its original state. However, a synthesis of these approaches is missing so far.

Grasslands are among the ecosystems with highest species richness in the world (Wilson et al. 2012), and they provide a wide range of ecosystem services. Grasslands play an important role within the global carbon cycle, as 90% of their biomass is belowground, accumulation rates are high, and decomposition of organic material slow (Gibson 2009). As main forage resource for livestock, grasslands are important for human well-being in many regions. They facilitate infiltration of water into the soil and thus support the maintenance of hydrological cycles. Finally, grasslands contribute to the landscape beauty of many regions. Thus, they are multi-functional systems but at the same time subjected to unsustainable use and conflicting interests.

Conceptual frameworks of grassland degradation have been developed specifically for rangelands, i.e. grazed systems, where stocking rates often are inadequate (e.g. Bestelmeyer 2006). At the same time, large areas of grasslands are endangered due to land-use changes or have already been lost (Sala et al. 2000), especially in tropical and subtropical regions (Bond and Parr 2010). Elsewhere, cropland on sites that originally had been grassland is abandoned for economic reasons, and grassland re-assembles spontaneously under re-introduction of moderate grazing management (Hölzel et al. 2002; Öster et al. 2009). This latter scenario, to our knowledge, has not yet been integrated in grassland or rangeland degradation models.

In this paper, we present a conceptual framework of grassland degradation that for the first time integrates different degradation stages and two types of recovery thresholds, including the most important processes related to land-use history causing stage transitions. We illustrate the framework with studies from grasslands in Rio Grande do Sul (hereafter: RS), Southern Brazil, where biodiversity is well studied, but where conservation of grassland has been neglected, and degradation processes are poorly studied (Overbeck et al. 2007; Overbeck et al. 2013). Finally, we point out how current limitations regarding knowledge on degradation processes and conservation state of grasslands should guide future research.

2.2 Conceptual framework of grassland degradation and restoration

The starting point of our framework is the use of traditionally managed grasslands as reference systems. This reference stage is comprised by grasslands composed of native species, with a specific and high biodiversity and considerable conservation value, usually due to extensive grazing and associated management practices (e.g. fire, mowing). The importance of management for maintenance of these systems and their diversity has been shown before (e.g. Overbeck et al. 2007; Pillar and Velez 2010 for Southern Brazil).

As in Hobbs et al. (2009), changes of ecosystem properties can be displayed as biotic and abiotic changes at the local scale along two axes (Figure 3). As biotic changes we consider deviation in species composition, vegetation structure (vertical and horizontal structural variables), basic ecological processes (e.g. pollination, seed dispersal), resulting from altered management, species introduction or conversion of land use. This includes alien species invasion. As abiotic changes we understand alteration in soil chemical and physical properties, as caused by fertilization or soil cultivation. The applicability of the framework is directly related to the quantification of these factors in case studies and the establishment of the thresholds according to changes in biotic and abiotic conditions in grasslands. It allows us to identify the stage of degradation of a given area and its potential for restoration. Changes in grassland management will cause properties of the system to change gradually, resulting in a decrease in resilience, but with resumption of the historical management the original properties might be reached again in many cases, i.e. a self-recovery threshold is not crossed (Figure 3a, Scenario 1). If the grassland is converted to other land use, this will lead to an almost entire change of the original properties, e.g. complete loss of the aboveground plant community (Figure 3b, Scenario 2), while abandonment of these land uses initiates re-colonization from the regional species pool (Figure 3c). This process is of particular importance in regions of the world where grassland restoration techniques have not been developed. In this context, it needs to be recognized that spontaneous recovery may often mean colonization of non-typical or alien species, i.e. trajectories of community development that not necessarily lead to the desired state.

In the framework, the distinction between two types of thresholds is important: (1) a self-recovery threshold that describes until which point a recovery without additional technical measures is possible, and (2) a restoration threshold that identifies until which point an area can be restored with technical assistance (e.g. modification of soil features, control of undesired species and introduction of desired species).

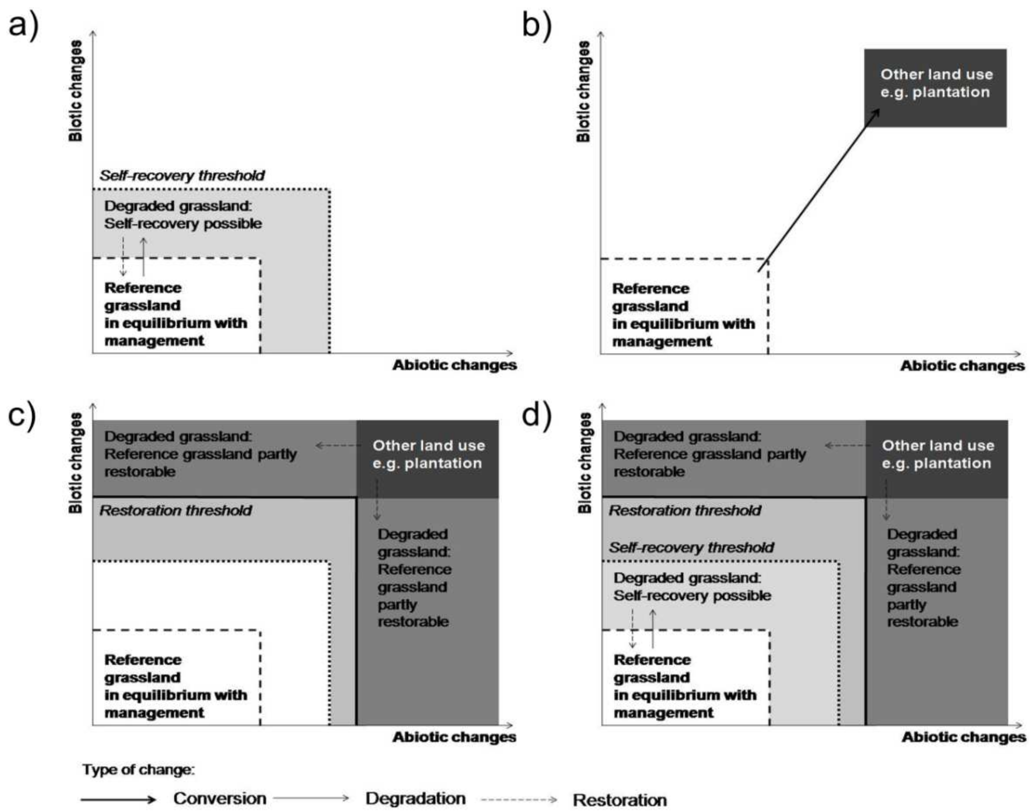


Figure 3 Conceptual framework on degradation and restoration of species-rich natural grasslands: (a) properties of the reference grassland are moderately altered if grassland management is changed, but modification is reversible; (b) after conversion to other land uses, the properties of the reference grassland are radically changed and ecosystem resilience is lost; (c) after abandonment some properties might recover (‘self-recovery threshold’) or be restorable (‘restoration threshold’); and (d) integration of the various scenarios.

2.3 South Brazilian native grasslands: origin and development

In RS, grasslands occur in the highlands in the north of the state, where they form mosaics with *Araucaria* forest, and in its southern half, in the Pampa biome, where they dominate the landscape (Overbeck et al. 2007), continuing in Uruguay and Argentina (Figure 4). South Brazilian grasslands are particularly rich in plant species, with about 2200 grassland plant taxa known only for RS (Boldrini 2009).

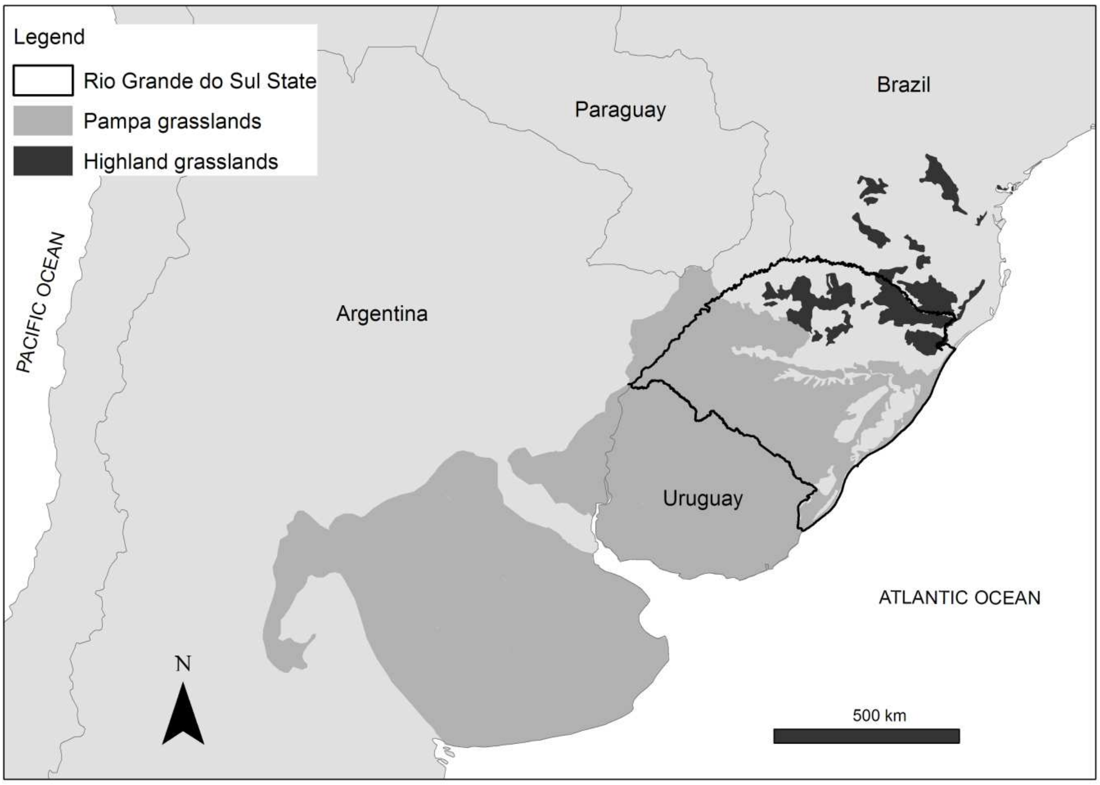


Figure 4 Location of the region used as an example for the proposed degradation framework, grasslands in Rio Grande do Sul, Southern Brazil. Shown is the original distribution of natural grasslands in southeastern South America.

Grasslands in the region are primary. They are relicts from cooler and drier periods, and were affected by forest expansion since approximately 5000 years BP, favoured by warmer and more humid climate, with increasing rates since 1500 years BP (Behling 2002). After the extinction of large herbivores (Lima-Ribeiro and Diniz-Filho 2013), these grasslands had been maintained by anthropogenic fires and by grazing of small mammals (Cione et al. 2003; Behling and Pillar 2007), and since the 17th century by introduced livestock. Today, beef production is an important economic activity in the region, with native plant species constituting most grassland vegetation. Available data indicate that plant diversity and forage production are highest under intermediate levels of grazing and intermediate fire frequency (Overbeck et al. 2005; Nabinger et al. 2009). Management thus can be considered essential for preservation of grassland biodiversity, as observed in many 'old-growth grasslands' (Veldman et al. 2015a). However, transformation rates are high: between 1986 and 2002, grassland areas suffered losses of 16%, which corresponds to a loss rate of 1000 km^2 per year (Cordeiro and Hasenack 2009).

2.4 Land-use change in the grassland region according to remote sensing

Evaluation of LANDSAT data shows that ca. 60% (104,553 km^2) of former grassland area in Southern Brazil had been destroyed by 2002 (Figure 5), mostly due to the conversion to arable fields or alien tree plantations. Losses of native grassland have not been uniform in space, but reflect soil properties and topographic constraints. In the Central Western Plateau region, native grasslands were nearly completely transformed into cropland, mostly for soybean. The coastal region has seen high rates of transformation, principally to rice and pine plantations. In the Northeastern Plateau, where soils are shallower, tree plantations and arable fields are the main causes of grassland losses. Here, land-use change has increased considerably within the past decade.

In the different regions of the state, 5–17% of the grassland area is classified as 'degraded', i.e. remote sensing data indicate former agricultural activity (e.g. tillage lines). Returning these areas to high nature conservation status might compensate for some of the ongoing losses through grassland conversion. However, compositional characteristics of vegetation itself (e.g. presence of alien species) cannot be observed by remote sensing data at this scale. In the Central Depression and in the Southwestern Grasslands of RS, for instance, a considerable proportion of the remaining grasslands mapped as 'conserved' actually have been degraded by alien forage species, which were deliberately seeded in some areas and colonized others, or by other processes. On-site ground studies are indispensable to verify the level of degradation and existence of self-recovery and restoration thresholds; remote sensing data alone can only give a limited picture of grassland degradation.

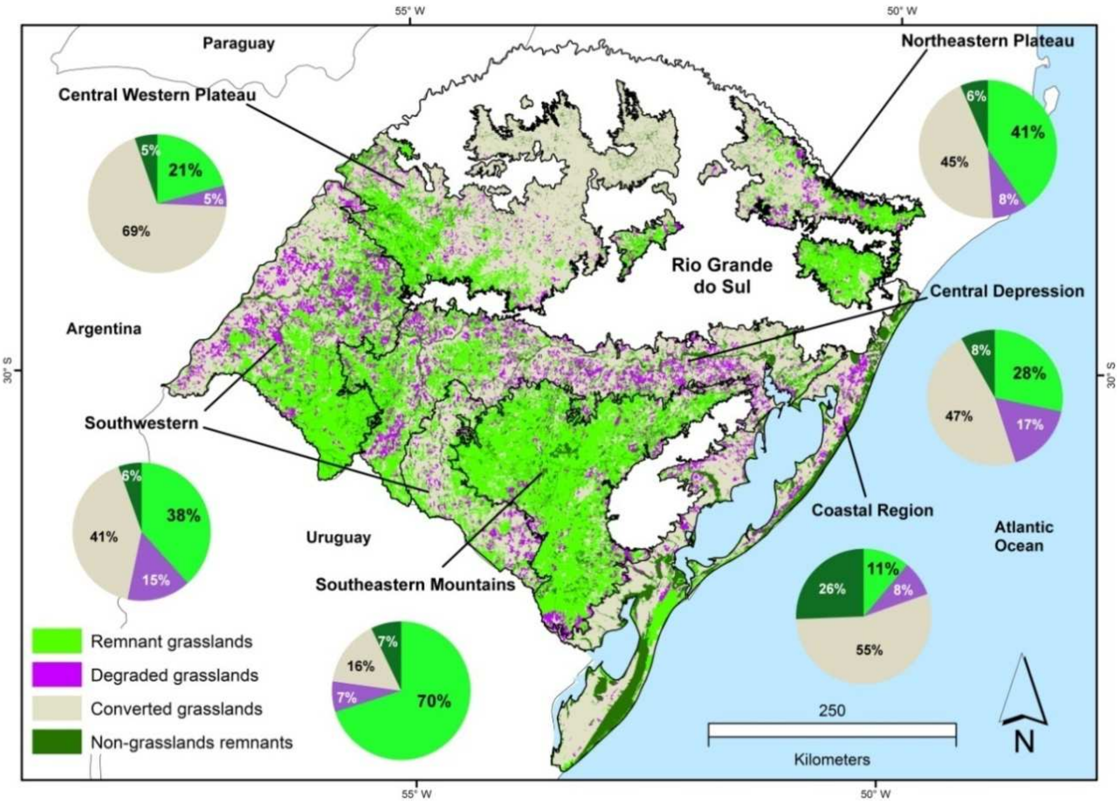


Figure 5 Distribution of grassland remnants and degraded grassland in RS State. The map is based on Landsat ETM+ images (spatial resolution: 30 m). Grassland areas with clearly visible signs of former land-use change (e.g. use as agricultural field) are considered as degraded, i.e. reflect past land-use change. Original grassland areas that have been completely transformed to other uses and not recovered to grassland comprise the category 'converted'. Regions in white are those where natural vegetation cover is forest.

2.5 Scenario 1: Degradation of grasslands after changes in management, and potential for self-recovery

Grazing

Most studies evaluating effects of different grazing intensities in RS focus on effects on forage or beef production (e.g. Maraschin and Corrêa 1994; Moojen and Maraschin

2002; Pinto et al. 2008), and only few analyze effects on species composition (Boldrini and Eggers 1997; Soares et al. 2011) or soil properties (Bertol et al. 1998). Usually, grazed grasslands with moderate grazing intensity are formed by mosaics of intensively grazed patches dominated by prostrate grasses (e.g. *Axonopus affinis* Chase, *Paspalum notatum* Flüggé), and less grazed patches dominated by tussock grasses, small shrubs or other species less attractive for grazing animals (Boldrini and Eggers 1997; Díaz et al. 2007). This heterogeneity of the vegetation leads to structural complexity and diversity.

If grazing is excluded – until now, a common practice in conservation units of Rio Grande do Sul – grassland structure quickly changes: tall tussock grasses, e.g. *Andropogon* and *Sorghastrum* spp. (Boldrini and Eggers 1997), become dominant, litter accumulates and microclimate at soil surface changes (Pallarés et al. 2005), drastically reducing plant species richness (Overbeck et al. 2005). In northeastern RS, the encroachment of shrubs of the genus *Baccharis* (principally, *B. uncinella* DC) and a slow invasion of forest pioneer species have been observed after abandonment (Oliveira and Pillar 2004) despite the accumulation of grass biomass that may hinder fast recruitment of woody pioneers.

Overgrazing, on the other hand, can lead to the replacement of productive forage plants by species with lower forage quality, resulting in increasing cover of ruderal species and bare soil, while the contribution of highly nutritional C3 grasses decreases (Pallarés et al. 2005). Ecosystem functions like water infiltration can be negatively affected as soil bulk density increases (Bertol et al. 1998). Either situation, when grazing is excluded or when the grassland is overgrazed, may be considered degraded due to changes in biotic and abiotic characteristics and the reduction of ecosystem resilience.

Introduction of alien C 3 and C 4 species and fertilization

Overseeding of natural grasslands with introduced alien species, often combined with fertilization and liming, aims to increase forage quality and quantity especially in winter (Nabinger et al. 2000). Although many native species have high productivity and nutritive potential, they are not available on the seed market, and introduced species are used instead; common species are *Lolium multiflorum* Lam., along with some European Fabaceae, e.g. *Trifolium repens* L. It has been shown that forage yield increases linearly with nitrogen addition (Brambilla et al. 2012) and promotes the increase of animal live weight gain per area, but also leads to marked changes in the floristic composition (Pallarés et al. 2005; Brambilla et al. 2012).

Introduced alien grassland species may become a serious problem when they spread to natural ecosystems. Large-scale invasion of these European-origin species that are used as forage, however, has not been reported yet, in contrast to some other species from temperate climates (e.g. *Ulex europaeus* L.) and, principally, some C 4 grass species of African origin. For example, *Eragrostis plana* Nees had invaded up to 20% of Rio Grande do Sul's grassland area by the year 2008, causing severe reduction in forage quality and native plant diversity (Medeiros et al. 2004). Medeiros and Ferreira (2011) succeeded in at least partial suppression of populations of the invasive species by a combination of soil cultivation and seeding of both native and non-native forage species.

Fire

Fire has shaped the Southern Brazilian grasslands during the past millennia (Behling and Pillar 2007). The use of burns as management tools for livestock production, traditionally applied in the highland grasslands, is controversial due to concerns regarding possible negative impacts, and thus fire had been prohibited by state legislation until recently. Regular fires select for different species groups compared to grazing (tussock vs. prostrated grasses, respectively), and selectively affect some species groups (e.g. C 3 grasses when burns occur in winter), but do not seem to cause reductions in grassland diversity (Overbeck et al. 2005). Fidelis et al. (2012) showed higher species richness in frequently burned grassland plots in comparison to sites where burning and grazing had been excluded for some years. In fact, a large part of the grassland species is adapted to fire and can resprout from underground storage organs (Fidelis et al. 2014). Invertebrate communities and processes determined by their activity, e.g. decomposition, return to pre-fire values after relatively short periods, at least under patchy fire at fine scale (Podgaiski et al. 2013; Podgaiski et al. 2014). Exclusion of fire in ungrazed areas, a common practice in conservation units, leads to the accumulation of dead biomass and the risk of high-intensity fires increases.

Potential for self-recovery and restoration after management-induced degradation

Potential for self-recovery should be high if the species present are members of the characteristic species pool of the region and changes in composition and structure were provoked mainly by changes in management. When soil conditions were changed, e.g. by liming or fertilization, self-recovery may be more difficult or even impossible, because introduced, sometimes invasive, species with high competitive abilities may be able to maintain high cover. Current research suggests that prescribed fire could be a conservation tool in areas where grazing is not feasible (Overbeck et al. 2005; Fidelis and Blanco 2014), e.g. in conservation units. Thus, intensity and frequency of management are key factors for grassland recovery after any kind of degradation (Winter et al. 2012).

2.6 Scenario 2: Degradation and potential for self-recovery after grassland conversion

For Southern Brazil, some studies on ecosystem properties and ecological processes under different types of land use in former grassland areas are available. Table 2 synthesizes the available data, considering variables of importance for regeneration or restoration after the end of intensive land use (e.g. seed bank) or that may persist in a changed condition over long periods of time.

Arable land use and its effects

Studies on the seed bank of arable fields on former grasslands in Southern Brazil show that the number of grassland species decreases with management intensity, giving place to native or alien ruderal species (Favreto et al. 2007), thus reducing recovery potential of grassland. These results are in line with studies from other grassland ecosystems around the world that show higher abundance of weed species in the seed bank after agricultural use (Hutchings and Booth 1996; Kiehl and Pfadenhauer 2007).

Table 2 Review of studies on the effect of land-use change on ecosystem processes in grasslands of Southern Brazil (RS, Santa Catarina, Paraná). All trends in comparison to reference grasslands (– , no studies available).

	Conversion to arable land	Conversion to forest plantation
Aboveground vegetation	No-tillage systems: more alien plant species[1] After abandonment: lower floristic diversity, dominance of ruderal species[2] or alien species	Usually no understory[3]
Seed bank	Lower abundance and diversity of native plant species; higher abundance of ruderals and alien plant species[4,5]	–
Litter thickness and quality	–	–
C-stock and cycling	C stock better preserved under no-tillage[7,13] C stock reduced under conventional tillage by 22%[15]	C stock lower than in pasture,[7] or unchanged[9] Rio de la Plata grasslands (further to the South): tree plantations under high precipitation (level of RS) have reduced carbon stocks in soil when compared to grassland[12]
Soil pH and nutrient status	Increased nutrient load in topsoil[11]; pH raised[14] or lowered[11]	Pine: pH lower[7,8] or unchanged[9]; N_{tot} falling[7]; P lower or higher; K^+ lower; Al^{+3} higher or unchanged[9] Eucalyptus: pH lower, K^+, Ca^{2+}, Mg^{2+} lower, increase in Na^+ and Al^{3+} [10]
Soil physical properties	Aggregate stability better preserved under no-tillage[6]	*Pinus* spp.: soil density changed

[1]Favreto et al. (2007); [2]Boldrini and Eggers (1997); [3]Souza et al. (2013); [4]Favreto and Medeiros (2006); [5]Maia et al. (2008); [6]Bertol et al. (2004); [7]Wiesmeier et al. (2009); [8]Schumacher et al. (2008); [9]Mafra et al. (2008); [10]Céspedes-Payret et al. (2012); [11]Rheinheimer et al. (1998); [12]Berthrong et al. (2012); [13]Pillar et al. (2012); [14]Almeida et al. (2005); and [15]Diekow et al. (2005).

As vegetative recovery is the principal regeneration strategy of South Brazilian grasslands after disturbance (Fidelis et al. 2009), seed input from external sources as well as abiotic conditions should be limiting for recovery of the former grassland community: the bud bank likely does not persist through periods of intensive agricultural use.

Grassland conversion also results in changes of soil properties. Arable land use increases nutrient levels of the soil (Rheinheimer et al. 1998; Perin et al. 2003), leading to different trajectories of vegetation recovery. It is well known that large quantities of carbon stored in grasslands may be rapidly transferred to the atmosphere and lost when the grassland is plowed and converted to arable fields (Sala and Paruelo 1997; Pillar et al. 2012). In a worldwide meta-analysis of carbon changes due to land-use changes, Guo and Gifford (2002) showed that a conversion of grasslands to crop rotation leads to a loss of 60% of belowground carbon. For Southern Brazil, a decrease in C-stock in soils under conventional-tilling has been shown, with magnitude depending on management intensity; no-tillage systems result in much lower losses of C in soils (Bertol et al. 2004; Diekow et al. 2005).

Tree plantations

By 2009, 6000 km^2 (10%) of grasslands in RS were converted to plantations of pines, eucalypts or acacias (Gautreau and Velez 2011). Native grassland vegetation composition is drastically affected under tree plantations, even with reduced soil disturbance for tree planting (Pillar et al. 2002). Goncalves et al. (2008) found relatively low species richness and dominance of a few ruderals and some alien species like the grass *Melinis minutiflora* P. Beauv. in the soil seed bank under tree plantations in the Central Brazilian Cerrado. Likewise, and in analogy to former agricultural fields, we can expect a low contribution of the seed bank in vegetation recovery.

Studies on effects of tree plantations on grassland soils give variable results (Table 2). Guo and Gifford (2002) stated that the conversion to plantations leads to a significant reduction of soil C stocks when coniferous species were used, while the effect with broadleaf species like eucalypts was not significant. For RS, Wiesmeier et al. (2009) found lower C-stocks under pine plantations, while Mafra et al. (2008) could not show any changes. A growing number of literature examining potential for carbon sequestration in plantations is available, with changes based on the shift from belowground biomass dominance (grassland) to aboveground biomass with litter accumulation (plantation) (Guo et al. 2008). It has been shown that this potential strongly depends on soil types (Zinn et al. 2002), and might not be true for regions with high precipitation like RS, for which a decrease in soil carbon was observed (Guo and Gifford 2002; Berthrong et al. 2012).

Potential for self-recovery and recovery thresholds after land-use change

Observational data indicate that the type of vegetation that develops after logging and abandonment differs considerably from that of reference grassland, and that species introduction likely is important if the objective is to restore grasslands. Zaloumis and Bond (2011) showed that species composition of grasslands established after logging of *Pinus elliottii* plantations in South Africa was markedly changed in comparison to reference grasslands. To what extent spontaneous regeneration will allow for return to pre-disturbance conditions is currently unknown and likely will depend on the time period of other land use (and with this, to what extent seeds or underground organs of target species remain in the ground), intensity of modifications of the site conditions (e.g. fertilization), and the landscape context (i.e. propagule sources). Both biotic and abiotic thresholds for recovery may exist, making active restoration necessary. As grasslands depend on management, intensity and/or frequency of grazing or fire will probably be crucial for the restoration process.

2.7 Discussion and conclusions

Land degradation studied on a regional scale often only considers conversion or complete losses of natural ecosystems, with limits to detect e.g. compositional changes, while at the local scale, finer effects of land management have to be considered. Both perspectives are necessary for an improved assessment of degradation and potential restoration, and differences between the two types of degradation likely imply different perceptions regarding degradation, conservation or restoration.

For our study system, conclusive evidence is available that management is necessary for maintenance of diverse and productive grasslands in this region

(Overbeck et al. 2007), and biodiversity conservation and livestock production can be considered as complementary management goals, allowing for sustainable use (e.g. Nabinger et al. 2009). Fire and grazing are selective forces that cause changes in grassland composition and structure, but their effects depend on frequency and intensity – both can contribute to conservation of biodiversity and productivity, but they can also be detrimental when frequency or intensity are too high or too low. A systematic and large-scale quantification of effects of different management types (especially intensification, Scenario 1) on different properties of the grasslands in the region is still missing, making it difficult to define degradation more precisely. Furthermore, the necessity of an integrated perspective of biodiversity conservation and sustainable use still is not widely recognized in the debate on conservation strategies (Overbeck et al. 2007; Pillar and Velez 2010).

Even though a considerable proportion of natural grasslands in Southern Brazil has been converted to other land use (Scenario 2), concerns on potential restoration of these areas have been raised only recently (Overbeck et al. 2013), and are affecting the agenda of conservation authorities. Once supported by additional empirical data, our conceptual framework can support decision making and priority setting in nature conservation by identifying whether costly restoration measures will be necessary or adaptation in management could be sufficient for self-recovery. In this, it is important to recognize that not only biotic and abiotic characteristics are covered by the framework, but that these can also be interpreted in terms of ecosystem functions and services (e.g. carbon sequestration, forage production).

Bestelmeyer (2006) points out problems and risks associated with threshold models: for instance, no single predictive thresholds – which would greatly facilitate management decisions – should be expected to exist, and parameters may reflect measurability, and not long-term degradation processes. Threshold models may become ‘insidious’ (Bestelmeyer 2006), if they lead to the belief that certain areas are not restorable anymore, because some original features of the system cannot be recovered. This, however, is not a consequence of the model per se, but of a failure of recognizing the full range of features, processes and services of any type of ecosystem.

The current debate on novel ecosystems (Hobbs et al. 2013) is centering exactly on the question of how to deal with systems that cannot be brought back to their original state. A conceptual framework of degradation and restoration based on a variety of biotic and abiotic variables (and their interactions, e.g. soil–plant feedbacks, e.g. Suding et al. 2013) has the potential to include different functions and services, and can contribute to a broader understanding of landscapes as multifunctional systems.

Young (2000) suggested that ecological restoration is the future of biological conservation. This means that degraded systems need to become a research focus, even in megadiverse countries where knowledge on biodiversity and functioning of natural ecosystems still has priorities. Conceptual frameworks such as the one presented here can support the study of degradation, conservation and restoration, in Southern Brazil and elsewhere. In order to assess conservation or degradation state and restoration potential of degraded systems and to define the recovery and restoration thresholds, it is necessary to collect data on the full gradient from conserved to degraded systems, on a regional scale. For this, we need to develop rapid assessment methods of different parameters of the system, including abiotic and biotic variables as well as measures for ecosystem functions, as proposed by Meyer et al. (2015).

Chapter 3

Effects of management intensity and temporary conversion to other land use on subtropical grasslands in Southern Brazil

This chapter is the identical reproduction of a manuscript that has been submitted to *Applied Vegetation Science:*

Koch C.,Conradi T., Gossner M.M., Hermann J.-M., Leidinger J., Meyer S.T., Overbeck G.E., Weisser W.W., Kollmann J.: Effects of management intensity and temporary conversion to other land use on subtropical grasslands in Southern Brazil.

Author contributions: This manuscript is part of a large DFG-sponsored project on grassland degradation in Southern Brazil, of which JK, WWW, MMG, JMH, STM and GEO conceived the initial ideas. The design of data collection was also discussed and decided upon with these authors. **CK** organized the field campaign with help of JMH and GEO and collected the data in the field; JL helped with the data collection in field season two; **CK** identified the plant species with help from GEO; TC performed parts of the statistical analysis and wrote sections of the statistical methods part; **CK** performed the other statistics, and wrote the main text that further was improved and edited by JK and GEO; all authors edited the final version of the manuscript.

Abstract

Question: We investigated the effects of grassland management intensity and of temporary conversion to other land uses on biotic and abiotic components of subtropical grasslands. Using species-rich permanent grasslands of medium management intensity (PG-M) as a reference we asked: (1) Does low (PG-L) and high (PG-H) intensity management of permanent grassland support plant diversity comparable to reference grasslands? (2) Do secondary grasslands regenerate after conversion to arable fields (SG-A) or pine plantations (SG-P) to a condition similar to permanent grasslands? (3) Can biotic changes be attributed to changes in vegetation structure or soil conditions?

Location: Highland grasslands of the Campos de Cima da Serra, Rio Grande do Sul, Brazil.

Methods: We analyzed plant species composition using NMDS and plant species diversity of 80 grassland sites, including three permanent grasslands and two secondary grasslands. We performed indicator species analysis to identify characteristic species for the different land-use types. We compared vegetation structure and used linear discriminant analysis (LDA) to investigate differences in soil conditions among land-use types.

Results: Both PG-L and PG-H differed from PG-M regarding vegetation composition. While PG-L shared many typical grassland species with PG-M, the communities of this land-use type were generally less diverse. PG-H, on the other hand, had not only fewer species but also deviated from PG-M in terms of species composition. Secondary grasslands both on former arable fields and plantations differed from PG-M in composition and showed lower diversity. Soil conditions of PG-L and SG-P were similar to PG-M, but distinct from PG-H and SG-A.

Conclusions: The decrease in number of species in PG-L might be reversed by resuming management, but strong compositional changes in SG-P might require re-introduction of grassland species to raise conservation value. This is also true for PG-H and SG-A: both showed similarly strong deviations from reference grasslands regarding not only

biotic but in addition also abiotic components. Overall, restoration of strongly altered land-use types to high conservation value seems feasible, and development of suitable techniques must be encouraged.

3.1 Introduction

Land use is changing rapidly around the world with a variety of forms and intensities (Ellis et al. 2010). Natural habitats are transformed into agricultural or silvicultural systems, intense land use is replacing traditional management, and marginal and degraded land is abandoned. These land-use changes are predicted to be the main reason for current and future biodiversity loss (Sala et al. 2000; Millenium Ecosystem Assessment 2005). Grasslands cover 40% of the terrestrial surface of the earth and have considerable ecological value due to their high biodiversity, groundwater production and carbon sequestration (Gibson 2009). At the same time they can have a high economic value as they are used for livestock grazing and contribute to vast amounts of food production (O'Mara 2012). Nevertheless, they have been transformed to arable fields or forest plantations at large scale (White et al. 2000; Steinfeld et al. 2006). A challenge for nature conservation and land managers is to maintain the ecological value of grasslands under productive conditions in landscapes that are rapidly changing.

In the state of Rio Grande do Sul in Southern Brazil grasslands originally covered ca. 60% and more than 15% were transformed in the years 1976–2002, mostly to arable areas (Cordeiro and Hasenack 2009). In the highland region Campos de Cima da Serra, 38% (5424km^2) of natural grassland remained in 2002. Since then, this region has experienced rapid land-use changes including grassland conversion and alterations of management but also regeneration after abandonment of intense land use. The primary vegetation are ‘old-growth grasslands’ (sensu Veldman et al. 2015a), which are extremely species-rich (>2600 plant species; Boldrini et al. 2009), and traditionally managed with medium intensity grazing (ca. 0.5 head of cattle ha^{-1}) and additional use of fire. This management was given up in parts of the region as the use of fire underlies legal restrictions, and both grazing and burning are usually excluded in conservation units. On the other hand, large parts of these grasslands are fertilized and over-sown with non-native forage species in order to increase livestock production (Ferreira et al. 2011). An average of 1000km² is annually converted into arable fields and pine plantations (Cordeiro and Hasenack 2009). In designated conservation units, converted areas, especially logged pine plantations, are abandoned but then left for succession without further restorative action. While research so far has concentrated on the description of well-preserved grassland areas (Overbeck et al. 2007), the present study focuses on the effect of management changes on grassland communities, the value of different land-use types for biodiversity conservation and potential for restoration after land-use change.

For this, we evaluated grassland plant species diversity, composition, structure and abiotic factors in five land-use types: three permanent grassland types with different management intensities (high, medium, low), and two secondary grasslands on former arable fields and abandoned pine plantations. The main aim of our research was to explore if changes in management intensity of grassland, or temporary conversion to other land uses, leads to major differences in grassland properties. Specifically, we asked the following questions:

(1) Does low (PG-L) and high (PG-H) intensity management of permanent grassland support plant diversity comparable to reference grasslands?
(2) Do secondary grasslands regenerate after conversion to arable fields (SG-A) or pine plantations (SG-P) to a condition similar to permanent grasslands?
(3) Can biotic changes be attributed to changes in vegetation structure or soil conditions?

Finally, we discuss which actions may restore degraded grassland to high nature conservation value.

3.2 Methods

Study region

The study region is located in the highlands of Rio Grande do Sul (RS) state, south Brazil (Figure 6a), extending over an area of about 4800km² within the municipalities of São Francisco de Paula (29°26’S, 50°34’W), Cambará do Sul (29°02’S, 50°34’’W) and Jaquirana (28°53’S, 50°21’W). This part of the highlands has an altitude of ca. 810–1125 m a.s.l., and is characterized by volcanic Rhyodacite bedrock with acidic Cambisols and Leptosols (Almeida 2009). The climate is subtropical humid (Köppen’s Cfb) with annual mean temperatures of 16–22°C, occasional frost during winter, and an average annual precipitation of ca. 2250mm without marked dry periods (Nimer 1989). Although this climate would be suitable to support forest vegetation, the natural vegetation of the region consists of a mosaic of mesic grasslands and *Araucaria* forests that has been shaped by natural fire and herbivores. The traditional grassland management in the region continued this disturbance regime. However, the region has been subject to diverse land-use changes during the past decades with conversion to either tree plantations of pine or eucalypt, or to arable fields, mostly corn or potato (Overbeck et al. 2013).

Site selection

We distinguished five grassland types with contrasting land-use history and current management intensity (for their detailed description see Appendix A1): (1) Permanent grassland, subdivided based on current management practices and intensities into (1a) traditionally managed grassland with medium stocking rates and prescribed burning or mowing every 1–2 years (PG-M); (1b) occasionally burned grassland with reduced stocking rates, where biomass removal declined two or more years ago (PG-L); and (1c) unburned grassland with high stocking rates, fertilized and over-seeded with non-native species (PG-H); (2) secondary grasslands, subdivided based on land-use history into (2a) secondary grassland recovering from conversion to arable land, with grazing at variable stocking rates (SG-A); and (2b) secondary grassland recovering after logging of pine plantations, currently grazed with low stocking rates (SG-P).

In total, 80 sites, with a minimum size of 1ha each, from these five land-use types were selected across the whole study region by a stratified random design (Figure 6b). Information on current and historic grassland management was obtained from interviews with landowners and conservation authorities. We accounted for possible influences by geographic location and different ages. A Mantel test revealed no correlation between compositional differences and spatial distance (r=0.008, *p*=0.41), visual inspection of correlation-plots (Appendix A2) revealed no trend of species numbers with different ages of secondary grasslands.

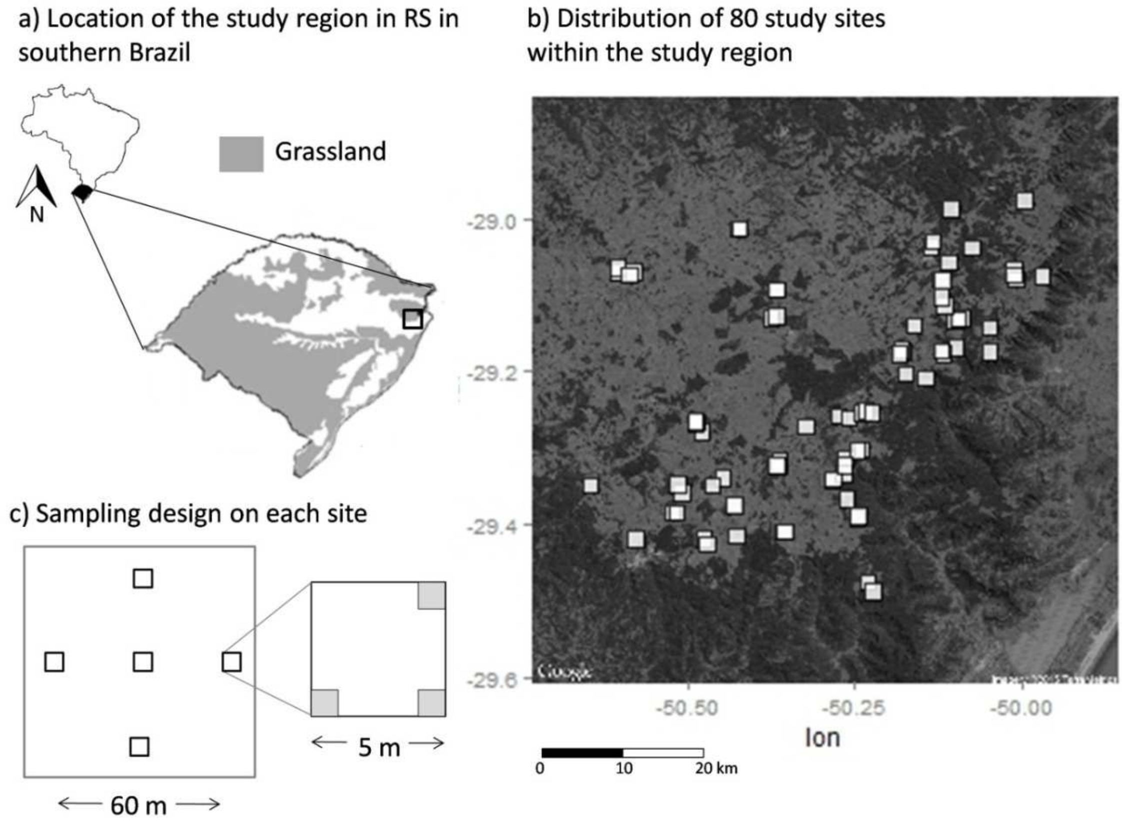


Figure 6 a) Location of the study region in the grasslands of Rio Grande do Sul, Southern Brazil, **b)** distribution of 80 study sites throughout the study region (background map ©Google Earth 2015) and **c)** sampling design on each of the 80 study sites containing five 5 m x 5m plots and a total of 15 1 m x 1m subplots.

Vegetation sampling

Fieldwork was conducted during two growing periods Nov 2013 till Feb 2014, and Nov 2014 till Jan 2015, respectively. To avoid any seasonal bias, all land-use types were sampled randomly throughout growing seasons and years. At each site, we established five 5m × 5m plots and fifteen 1m × 1m subplots in a systematic pattern (Figure 6c) to avoid subjective choice of plot location. Interspersed wetlands, rocky outcrops and steep slopes of more than 20% were avoided.

At each site, vascular plant species composition was recorded in the 15 subplots and the cover of each species was visually estimated using the Londo scale (Londo 1976). If species could not be identified they were given unique codes and remained in the dataset for all further analysis. Nomenclature of species follows the Missouri Botanical Garden database (www.tropicos.org), and a full list of species can be found in Appendix A3. In each of the five plots, the structural parameters cover of vegetation, litter, standing dead biomass, bare soil, stones, dung, pine trunks and pine litter were visually estimated using the Londo scale. Stones and dung were present with <1% in all types and were not further considered in analyses. Pine litter encompassed needles and loose branches remaining on the ground after harvest. Vegetation cover was further subdivided into that of shrubs (all woody species), graminoids (Cyperaceae, Juncaceae, Poaceae) and forbs. For graminoid species, the cover of tussocks was also recorded. Mean vegetation height was assessed calculating the mean out of five randomly placed measurements per subplot.

Sampling of environmental variables

Composite soil samples were obtained from each of the 80 sites by pooling 45 samples taken randomly at a depth of 0–10cm with a 1.6-cm diameter corer within the vegetation plots. The soil samples were analyzed by the Laboratório de Análises de Solo, Universidade Federal do Rio Grande do Sul, Porto Alegre, determining the following parameters: soil pH_{H_2O}, clay fraction, organic matter, available phosphorus and potassium extracted using Mehlich-1, KCl-extractable aluminium, calcium and magnesium, potential cation exchange capacity at pH 7.0, potential Al- and base-saturation, potential acidity, and total nitrogen extracted using Kjeldahl’s method.

Statistical analyses

To visualize patterns of compositional variation within and among land-use types, we used Nonmetric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities, which were calculated from square-root transformed and then Wisconsin double-standardized species abundances to reduce the influence of large abundance values on ordination results. As species composition was sampled in multiple plots per site, we calculated species abundance at a site as its relative frequency across the respective sampling plots. To quantify the magnitude to which contrasting land-use types have led to divergent species compositions relative to the reference grasslands (PG-M), we computed a Principal Coordinates Analysis based on Bray-Curtis dissimilarities, calculated the distance of each site to the centroid of the reference sites in principal coordinates space (Giarrizzo et al., in press), and then tested for significant pairwise differences among land-use types in this distance.

Species indicator analysis (Dufrêne and Legendre 1997) with 9999 permutations was used to determine characteristic species of each land-use type. As the analysis returned 133 species with significant Indicator values (IV), further criteria were applied to reduce number of indicators. All species with an IV ≤ 20 were not considered. A species could only be indicator for a maximum of two land-use types and a minimum difference of 1% in mean cover to the next land-use was required. Species with IV>20 for two land-use types were considered a shared indicator species, others were considered exclusive indicators.

To explore whether land-use types differed in alpha diversity we quantified the effective number of species (D) of each site as

$$D = \left(\sum_{i=1}^{S} p_i{}^{q}\right)^{1/(1-q)} \quad (1)$$

where S is the number of species recorded at this site, p_i is the relative abundance of species i, and q is a parameter that gives, with increasing values, more weight to abundant species (Hill 1973; Jost 2006). We set the values of q to 0, 1, 2, and 8, corresponding to species richness, and the numbers equivalents of Shannon entropy, the Gini-Simpson index, and the Berger-Parker index, respectively (Leinster and Cobbold 2012). Note that for q = 1, where Equation 1 is undefined, we calculated the exponential of the Shannon entropy instead, which equals the mathematical limit of Eq. 1 at q = 1 (Jost 2006). To determine whether land-use types differed in true diversity at the specified values of q, permutation t-tests using 9999 randomizations and correction of *p*-values for multiple comparisons were performed (Benjamini and Hochberg 1995).

As we were also interested in compositional variation among sites (beta-diversity) within each land-use type, we calculated the multivariate dispersion of sites for each land-use type based on distance-to-centroid values (Anderson 2006) using again Bray-Curtis dissimilarities. Additionally, we examined differences among land-use types in within-site compositional heterogeneity using the same statistical approach, but here, Bray-Curtis dissimilarities were based on the percentage cover values of the species in the sampling plots. Significant differences ($p \leq 0.05$) among land-use types in divergence from reference grasslands, as well as in within-type and within-site beta-diversity were evaluated as well with permutation t-tests using 9999 randomizations, and correction of *p*-values for multiple comparisons.

Finally, we examined whether the land-use types differed in vegetation structure and soil parameters using Kruskal-Wallis tests. Linear discriminant analysis (LDA) was used to identify those soil parameters characterizing and differentiating the different land-use types. When necessary, variables were transformed to improve homogeneity of within-group covariance. The parameters pH, K, P, base saturation and N were included in the LDA. Other parameters that were (auto-)correlated with one of them were not included. Although pH was correlated with base-saturation, LDA lost predictive power when pH was excluded, and thus this explanatory variable was kept. All statistical analyses were done using packages labdsv, MASS and vegan in the R software program (version 2.15.2, R Core Team 2012).

3.3 Results

In total, 467 species were found and only four species (0.9%) could not be identified to any family. Of these, 90.4% were native and 7.9% non-native species (Schneider 2007), whereas the origin of eight (1.7%) species could not be determined.

Effect of management intensity on species composition and diversity of permanent grasslands

The NMDS ordination of species composition indicated floristic similarity of some sites of PG-L to the reference PG-M, whereas all intensively managed sites were separated from the other two (Figure 7a). However, distance to the PG-M group centroid was significantly different for both (Figure 7b). PG-H contained on average 20% of non-native species, whereas their percentage on PG-M and PG-L was <1%. These findings were supported by the results of the indicator species analysis (see Appendix A4 for a full list of indicator species). PG-M had three (*Stenachaenium adenanthum*, *Galactia gracillima* and *Trichocline catharinensis*) and PG-L one (*Grazielia nummularia*) exclusive native indicator species, and shared three native indicator species, i.e. *Schizachyrium tenerum*, *Axonopus siccus* and *Lucilia linearifolia*. PG-H shared no indicators with PG-M or PG-L, and had, besides two native grasses, two non-native species *Prunella vulgaris* and *Avena sativa* as exclusive indicators.

Diversity profiles and pairwise comparisons showed that PG-M was significantly more diverse than PG-H and PG-L (Figure 8, Appendix A5). Although PG-L consistently had a slightly lower diversity than PG-H, this difference was not significant. Beta-diversity within the land-use types was smaller in PG-H and PG-M than in PG-L (Figure 9a) whereas PG-H showed higher within site beta-diversity than the other two (Figure 9b).

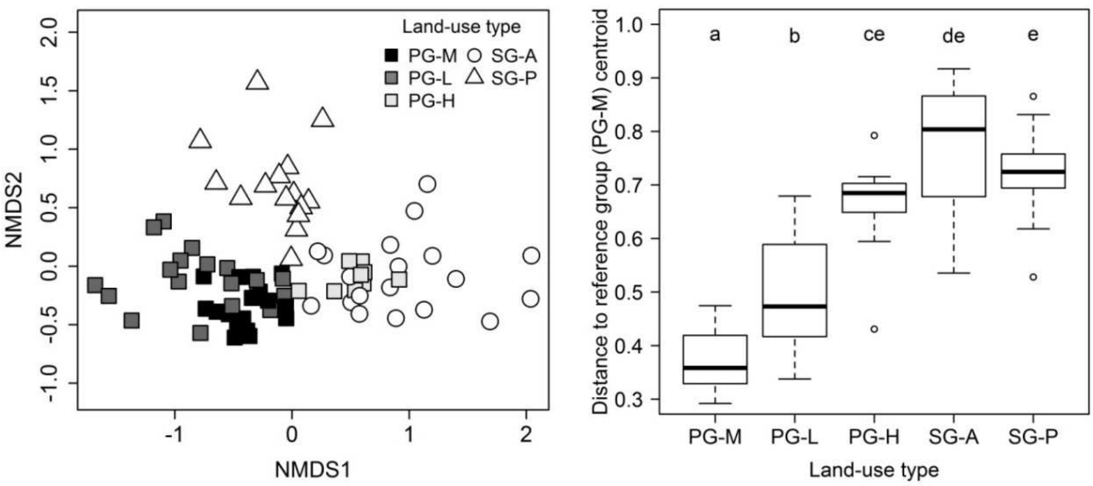


Figure 7a) NMDS ordination of species composition of 80 sites representing five contrasting land-use types in south Brazilian grasslands (stress based on two dimension = 0.15). **b)** Divergence of plant species composition from traditionally managed grasslands (PG-M). The magnitude of divergence was measured as the distance of each grassland site to the centroid of PG-M in principal coordinates space. Different letters indicate significant differences ($p \leq 0.05$) among land-use types based on permutation t-tests and correction of *p*-values for multiple comparisons. Note that there is also some natural variation among sites of the reference type. Permanent grassland (PG) of medium (-M), low (-L) and high (-H) intensity management, secondary grassland (SG) after arable use (-A) and after plantation (-P).

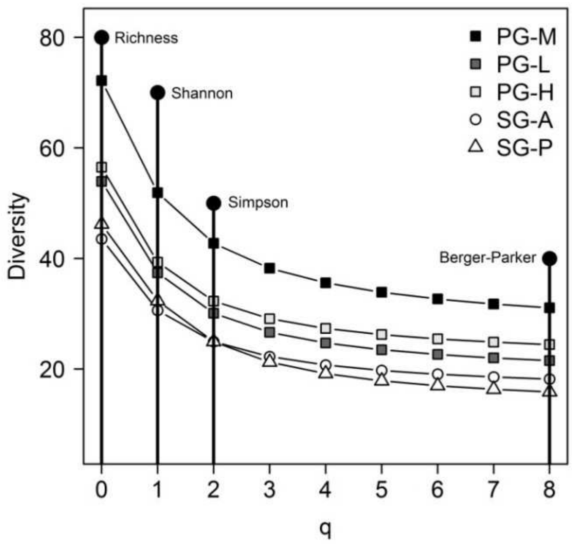


Figure 8 Diversity profiles showing differences in the effective number of species among five land-use types at increasing orders of diversity (*q*).Values for q are equal to the following measures of diversity: *q*=0: species richness, *q* =1: exponential Shannon index, *q*=2: inverse Simpson index, *q*-> ∞: Berger-Parker dominance index. Permanent grassland (PG) of medium (-M), low (-L) and high (-H) intensity management, secondary grassland (SG) after arable use (-A) and after plantation (-P).

Effect of former land use on species composition and diversity of secondary grasslands

Species composition of SG-A and SG-P was equally distinct from PG-M (Figure 7b). However, NMDS and results from indicator species analysis show that SG-A had some similarity with PG-H, sharing five indicator species, all of which were non-natives (Appendix A4). In addition, SG-A had three exclusive indicator species, i.e. *Raphanus raphanistrum* and *Rumex obtusifolius* (both non-native) and *Soliva sessilis* (native). SG-P had the shrub *Baccharis uncinella* and the grass *Dichanthelium sabulorum* as exclusive indicator species and shared only the shrub *Senecio brasiliensis* with SG-A. While SG-A contained up to 25% of non-native species, the percentage was <1% on SG-P.

SG-A and SG-P exhibited the lowest diversity of all grasslands, but were not significantly different from each other (Figure 8, Appendix A5). At q=2 the lines of these land-use types cross, indicating that although SG-A is slightly less species rich than SG-P, the communities of this land-use type are more even. Species turnover was higher for these two secondary grasslands in comparison to PG-M both for the land-use type and site specifically (Figure 9a, b).

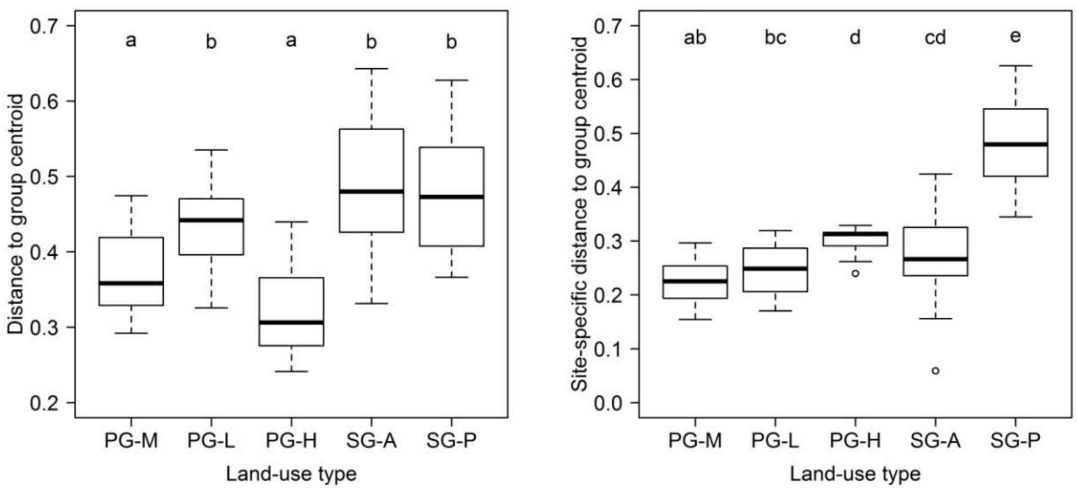


Figure 9 Beta-diversity (species turnover) between **(a)** and within sites **(b)** of respective land-use types in south Brazilian grasslands. Different letters indicate significant differences ($p \leq 0.05$) among land-use types based on permutation *t*-tests and correction of *P*-values for multiple comparisons. Permanent grassland (PG) of medium (-M), low (-L) and high (-H) intensity management, secondary grassland (SG) after arable use (-A) and after plantation (-P).

Effect of land use on vegetation structure

The vegetation structure of PG-H was similar to that of PG-M, whereas many structural characteristics were changed under PG-L (Appendix A6). While total cover of vegetation and bare soil showed no significant difference between the three grassland types, PG-L had significantly more litter (p<0.01) and dead biomass accumulated (p<0.001) than both other grasslands, and canopy height was also significantly higher (p<0.001). Although all three grasslands had a similar cover of graminoids, the proportion of tussocks was higher in PG-L. PG-H had a significantly higher cover of forbs (p<0.001) than the other two, and PG-L contained a significantly higher cover of shrubs than both PG-M and PG-H.

The structure of secondary grasslands on former arable fields and on former plantations differed strongly from permanent grasslands (Appendix A6). While SG-A showed similar total cover of vegetation to permanent grasslands, this was reduced significantly in SG-P due to pine stumps and about 25% pine litter. However, the vegetation on SG-P was taller (p<0.001), and the proportion of shrubs was comparable to grassland under low intensity management. Both secondary grasslands contained less cover of graminoids (p<0.001), and especially the typical tussock grasses were missing.

Effect of land use on abiotic factors

Linear discriminant analysis revealed that base saturation was able to explain 92% of between land-use type variance (Figure 10). Land-use types SG-A and PG-H differed clearly from PG-M, PG-L and SG-P along this discriminant, while the latter three were only slightly separated. The second discriminant (LD2) explained a further 5% of between type variance, and N was strongest associated with this. The remaining discriminants LD3 and LD4 (not shown) explained 2% and 1%, respectively, and were strongest associated with N and pH. The Huberty Index I showed with a value of 0.76 that predictive power of the model was high. Most misclassifications occurred between the cluster PG-M, PG-L and SG-P and within the cluster PG-H and SG-A, indicating strong similarity in soil parameters within these two groups. Detailed results from Kruskal-Wallis tests in Appendix A6 support these findings.

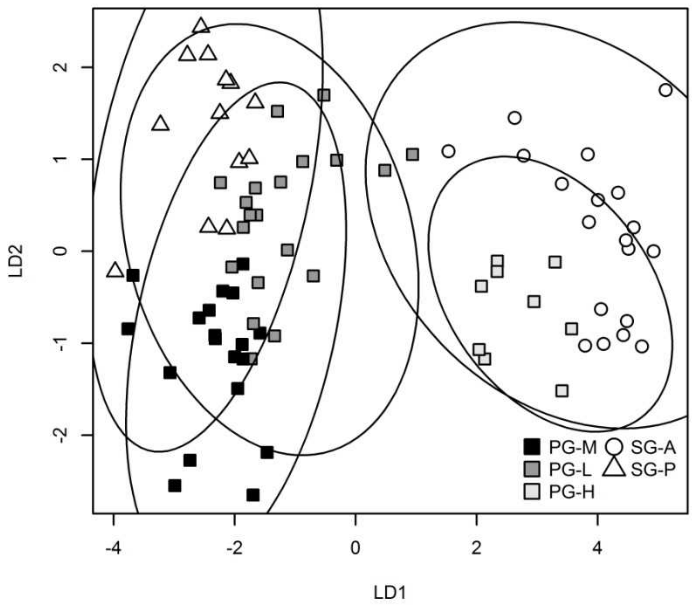


Figure 10 Classification of five land-use types based on soil parameters using linear discriminant analysis. LD1 explained 92% of variance with base saturation most strongly associated to this discriminant, LD2 explained 5% with N associated. LD3 and LD4 (not shown) explained 2 and 1%, respectively, with N and pH associated. Huberty Index I of 0.76 showed high predictive power of the model. Permanent grassland (PG) of medium (-M), low (-L) and high (-H) intensity management, secondary grassland (SG) after arable use (-A) and after plantation (-P).

3.4 Discussion

Do grasslands under low and high intensity management support plant diversity comparable to the reference?

A low intensity management (PG-L) resulted in some differences to grassland managed with medium intensity. Although typical grassland species, especially tussock grasses and tall forbs, were able to persist in PG-L, significant changes in species composition could be detected and the number of species was reduced. These results are in line with studies from other grassland systems that show a decline in species numbers when fire or grazing is excluded (Hinman and Brewer 2007; Klimeš et al. 2013) or marked changes in species composition (Uys et al. 2004; Loydi et al. 2012). These changes are usually attributed to structural changes resulting from low intensity management or abandonment rather than changes of abiotic conditions. The accumulation of litter observed in PG-L of our study and in other regions (Pucheta et al. 1998; Enyedi et al. 2008) can inhibit the germination of some species (e.g. Morgan and Lunt 1999) or trap seeds (Ruprecht and Szabó 2012). At the same time, abandonment can also lead to an increased competition by species, i.e. shrub and tree species (e.g. Briggs et al. 2002) or tussock grasses (Feldman and Lewis 2005; Overbeck et al. 2005), that otherwise would be reduced by management.

Under low intensity management, permanent grassland still contributes to biodiversity conservation. However, an issue that cannot be addressed with the data presented here is whether diversity can be recovered when management of medium intensity is re-introduced. Some studies in other grassland systems already examined this question and showed that the increased shrub cover was not reduced by the re-introduction of fire (Heisler et al. 2003), and recovery of the community was never complete (Klimeš et al. 2013), pointing out the need to assess if grasslands under low intensity management might reach a temporal threshold after which recovery is not possible.

Grasslands under high intensity management (PG-H), with fertilization, over-seeding and high stocking rates, showed large differences to traditionally managed grasslands as also observed in other studies (Lanta et al. 2009; Tiecher et al. 2014). They shared no indicator species with PG-M, and NMDS showed a clear distinction of species composition between the two, which was also due to the high proportion of non-native species in PG-H. Contribution of these areas to biodiversity conservation is thus much lower compared with PG-L. While PG-H had a similar vegetation structure to PG-M, chemical soil properties showed marked changes due to the application of fertilizer. Despite the loss of many native species in this form of management, PG-H has advantages over another widely applied form of intensive grassland management, the cultivated pasture. In contrast to this form of pasture management, where deep soil cultivation measures are usually applied and pasture species are sown in high densities (e.g. Swanepoel et al. 2015), the soil surface is kept intact under PG-H, and some native species are able to persist inspite of the high intensity management. The question if recovery to communities similar to PG-M is possible in these areas when traditional management is re-introduced has not been addressed so far.

Do grasslands regenerate after some form of arable field use or pine plantations?

Species composition and species numbers of secondary grasslands after use as pine plantations (SG-P) were very distinct from all other land-use types. Studies from other regions indicate that these differences remain even after longer time intervals (Piqueray et al. 2011; Zaloumis and Bond 2011). Findings from our soil analysis suggest that soil properties of former pine plantations are unlikely to be the limiting factor for species regeneration. Rather, dispersal limitation and regeneration from seed bank are more important for the recovery of these sites, as both are a ubiquitous feature of many types of grassland (Pinto et al. 2014; Vieira et al. in press). The high beta-diversity among SG-P grasslands (Figure 9a) supports the view that divergent successional trajectories are largely driven by stochastic dispersal events (Cadotte 2006). An aspect not systematically tested in this study is the management after abandonment. Experiments are necessary to answer the question if follow-up management like physical removal or burning of pine litter, could lead to an increase of typical species from PG-M grassland. Conservation managers might need to consider the active re-introduction of propagules of typical grassland species in order to re-establish typical grassland communities.

Species composition and species numbers in secondary grasslands forming after arable use (SG-A) differed from that of traditionally managed grasslands. They shared no indicator species with PG-M and contained high percentages of non-native species. Many examples show that without active restoration species composition and numbers of former arable sites remain quite distinct from typical grassland communities even after long time intervals (e.g. Snow et al. 1997; Redhead et al. 2014). In addition to the already mentioned short longevity of grassland soil seed banks, arable management with for example deep tillage has further negative effects on the seed bank (Bekker et al. 1997), and seed banks may contain arable weeds that dominate after abandonment (Donath et al. 2007). In our study region the common practice after abandonment of arable fields is to sow non-native species, and it can thus be expected that these species also contribute to differences in the seed bank, although studies examining this are missing so far. In contrast to secondary grasslands after pine plantations, former arable fields display the additional alteration of abiotic factors resulting from years of intense uses of fertilizer (McLauchlan 2006) and the absence of typical tussock grasses. These changes pose a challenge for restoration and application of active restoration measures will be necessary to establish communities of similar composition and richness to PG-M on former arable fields.

Techniques to restore grassland on former arable fields are well developed in Europe (Török et al. 2011). Many successful efforts applied a combination of measures aiming to improve abiotic and biotic conditions (e.g. topsoil removal, hay transfer or direct seeding; Muller et al. 2014). First applications in tropical regions, however, show that establishment of seedlings was very poor (Le Stradic et al. 2014) indicating the need for further pilot studies.

3.5 Conclusions

The increasing demand for production of livestock, crops and wood negatively affects remnant permanent grasslands. If the latter are used at medium intensity, they are most species-rich and contribute to biodiversity conservation. Our results show that grasslands are able to maintain typical plant species under reduced or abandoned management. However, this option has in the long term negative outcomes for conservation and would not be sensible for conservation units (Pillar and Velez 2010). Although grasslands of high intensity management lost most of their species richness, they present an option for intensified land use that is still less destructive than arable fields.

Secondary grasslands recovering after other land use most often lose their value for biodiversity. However, as former pine plantations showed at least abiotic similarity with reference grasslands, restoration efforts should be focused here. Former arable fields, on the other hand, differ strongly from the reference grassland in both biotic and abiotic aspects. Thus, it should be considered to use these sites to create intensive pastures since soil conditions are already suitable for this type of land use. This might help avoiding new conversions of intact permanent grassland and thus contribute to their protection.

Chapter 4

Setting priorities for monitoring and managing non-native plants: towards a practical approach

This chapter is the identical reproduction of a manuscript that has been submitted to *Environmental Management:*

Koch C., Jeschke J.M., Overbeck G.E., Kollmann J: Setting priorities for monitoring and managing non-native plants: towards a practical approach**.**

Author contributions: **CK** and JK created the initial idea of the framework which was improved with help from JMJ; **CK** collected the data in the field and identified the plants with help from GEO; **CK** wrote the chapter which was improved and edited by JK, JMJ and GEO.

Abstract

Land managers face the challenge to set priorities in monitoring and managing non-native plant species, as resources are limited and not all non-natives become invasive. Existing frameworks that have been proposed to rank non-native species require extensive information on their distribution, abundance and impact. This information is difficult to obtain and often not available for many species and regions. National watch or priority lists are helpful, but it is questionable whether they provide sufficient information for environmental management on a regional scale. We therefore propose a decision tree that ranks species based on more simple albeit robust information, but still provides reliable management recommendations. To test the decision tree, we collected and evaluated distribution data from non-native plants in highland grasslands of Southern Brazil. We compared the results with lists from the national Invasive Species Database for the state RS to discuss advantages and disadvantages of the different approaches on a regional scale. Out of 38 non-native species found, only four were also present on the national list. If management would solely rely on this list, many species that were identified as spreading based on the decision tree would go unnoticed. With the suggested scheme, it is possible to assign species to active management, to monitoring or further evaluation. While national lists are certainly important, management on a regional scale should employ additional tools that adequately consider the actual risk of non-natives to become invasive.

4.1 Introduction

The invasion of non-native organisms is one of the main threats for global biodiversity (Sala et al. 2000). However, not every species that is introduced to a new range will establish, spread or have an impact (Blackburn et al. 2011). Furthermore, impact can be defined in various ways (Jeschke et al. 2014), for example as species loss due to invaders (Hejda et al. 2009), changes in ecosystem functions (Ehrenfeld 2010; Gutiérrez et al. 2014), or economic costs for eradication of non-natives (Pimentel et al. 2000). In order to identify potentially harmful species, researchers as well as practitioners have made great efforts to disentangle mechanisms of invasion

(Rejmanek and Richardson 1996; Lockwood et al. 2013), predict invasions (Kolar and Lodge 2001; Van Kleunen et al. 2010) and assess their potential impacts (Magee et al. 2010; Dana et al. 2014).

There are several approaches for the evaluation of non-native species, either focusing on pre-border or post-border assessment. The most commonly used pre-border approach is the Australian Weed Risk Assessment (A-WRA) in which species are screened for their potential to become invasive in a given region before they are intentionally imported (Kumschick and Richardson 2013). This assessment is based on a scoring system of 49 questions concerning the biogeography (e.g. climatic match), invasion history elsewhere and biological characteristics (e.g. undesirable traits) of a particular species (Pheloung et al. 1999). Although originally designed for Australia and tested for New Zealand, the A-WRA has been adapted and applied in many regions e.g. in Hawaii and other Pacific islands (Daehler et al. 2004), Florida (Gordon et al. 2008), as well as in the Czech Republic (Křivánek and Pyšek 2006). A shortcoming of this type of assessment is the inconsistent understanding of what the ‘invasiveness’ or ‘weediness’ of a species is constituted of, i.e. what damage has been measured elsewhere to call a species invasive (Kumschick and Richardson 2013). At the same time, species that are introduced for the first time or have only been recently introduced elsewhere cannot be correctly evaluated with this approach (Hulme 2012; McGregor et al. 2012). While matching climatic factors are certainly important, other factors such as propagule pressure or land-use changes can likewise be crucial for the success of an invasion (Thomas and Moloney 2015), but these factors are not included in these assessments. Despite all shortcomings, pre-border assessments have so far prevented the intentional introduction of a large number of potentially harmful species (e.g. 609 plants on Australian prohibition list, status 2011; Roberts et al. 2011). Moreover, prevention has been shown to be less costly than management after introduction, and thus is highly desirable both from the economic and conservation point of view (e.g. Keller et al. 2007). However, a large number of non-native species is already present around the world, and thus post-border assessments have been developed, mostly to assess the various impacts of these species in the invaded range. Pre-border risk assessments rely to some extent on results of these post-border impact studies, as they use the invasion history elsewhere as a central criterion for their scoring.

While first frameworks ranked non-native species in post-border assessments according to their range and a rather unspecific measure, i.e. the individual effect (Parker et al. 1999), more recent frameworks integrate large amounts of parameters for the classification of an invader (e.g. Thiele et al. 2010; Leung et al. 2012; Blackburn et al. 2014). These parameters can be very laborious to measure (Sandvik et al. 2013). This means that in practice thorough information is often available for only a small number of species, particularly in countries where resources for research are limited (McGeoch et al. 2010). Managers in a regional context ask for reliable, easy to apply and economically sound tools to prioritize species and to derive management decisions (Roura-Pascual et al. 2009). One simple approach to support management is to create so-called watch lists as often developed for pre-border assessments (Faulkner et al. 2014), with a focus on those species already present in a region (Essl et al. 2011). A potential problem with these lists lies in the misperception that they are comprehensive and already include all possible invaders (Daehler et al. 2004), and that economic interests associated with a species may create biases in expert judgements (Pheloung et al. 1999). McGeoch et al. (2012), however, identified a lack of knowledge as the main error occurring during listings of invasive alien species leading to vast underestimations of numbers of these species.

An example of a country where a national list has been established is Brazil. Since 2003, several institutions have been working together to compile a database that contains species already present in Brazil and that are considered invasive (i.e. creating an impact on biodiversity and ecosystems), either in Brazil or elsewhere (I3N Brazil Invasive Alien Species Database 2015). In December 2015, this database contained a total of 189 plant species, which is relatively low given the size and biodiversity of the country. The database is yet far from complete, and although it is possible to derive lists for each individual state, there are large knowledge gaps, for example on the actual distributions of some species (Zenni and Ziller 2011; Dias et al. 2013). National lists such as this one certainly contain valuable information, but considering these knowledge gaps might in many cases be insufficient for making comprehensive decisions about monitoring and managing non-native species on a regional level. Given this situation, we propose a simple decision tree that can be used on a regional scale and allows land managers to rank non-native species based on their spatial distribution that can be recorded in relatively fast and cost-efficient sampling procedures.

We applied and tested the decision tree in a grassland region of Rio Grande do Sul (RS), Southern Brazil, where a lack of data for sufficient risk assessment has been identified recently (Rolim et al. 2015). In this region, we collected data on non-native plant species and compared them to the subset for RS of Brazil's above-mentioned national Invasive Alien Species Database to evaluate differences in assessment outcomes. We discuss the advantages and shortcomings of the proposed decision tree for prioritizing non-native species for management on a regional scale. Finally, we suggest management implications based on the ranking results.

4.2 Methods

Decision tree for classifying and managing non-native species

We call a species *non-native* if its presence in an area is the result of intentional or unintentional introduction by human activity (Richardson et al. 2000). The decision tree is based on mapping of non-native species in different land-use types. It takes into account that the quality of information concerning introduction sites might differ among species and provides two alternative decision paths (Figure 11). *Path I* is chosen when sufficient information on introduction sites is available, i.e. if it is known that the species has been introduced to a number of sites and that it was definitely not introduced to others (Figure 11a). If reliable information on where introduction took place is not available, *path II* of the decision tree has to be chosen (Figure 11b). This is most often the case for accidentally introduced species but can also be true for some intentional introductions. Two parameters appear in both paths of the decision tree: the mean cover of a species and its frequency (proportion of plots within an area where the species is present). The cut-off values for these two parameters need to be defined in accordance with the ecosystem of application, to appropriately reflect the characteristics of the system of interest. The decision tree results in three broad categories with two sub-categories each that are indicative of certain characteristics of the species' distribution, which furthermore have implications for management (see Table 3).

The first question in *path I* addresses whether the species is present in areas that have not been identified as introduction areas. If this is the case, the species is classified as '*spreading'*, either in *category 1a* (intentional introduction) or *1b* (unintentional). For those species not present outside introduction areas, cover on the introduction sites is evaluated in the next step. If the mean cover of the species is higher than the pre-defined cut-off value, the species is classified as '*establishing'*, either in *category 2a* (intentional introduction) or *2b* (unintentional). A species that has a mean cover below the cut-off value on the introduction sites is classified as *'sporadic',* either in *category 3a* if it was intentionally introduced, or *category 3b* if not intentionally introduced.

The first question in *path II* (insufficient information on introduction sites) asks whether a species is present in more than one land-use type. If this is not the case, the next question is, if the species has either a high mean cover or a high frequency. If this is also not the case, the species is classified in *category 3b* or *3a*, respective of intentional introduction. Both cases, a species present in only one land-use type but rather common (high frequency or high mean cover) or present in more than one land-use type but generally rare, will lead to its categorization into *category 2a* if it is intentionally introduced, or *category 2b* if not. Only if the species is present in more than one land-use type and appears there in high frequency or cover, it is classified either in *category 1a* (intentional introduction) or *1b* (unintentional).

The resulting categories are not only indicative of certain characteristics of the species' distribution but will have implications for their management (see Table 3). Species in *category 1* are able to spread from introduction sites or to colonize more than one land-use type. Eradication measures for these species should only be pursued if introduction pathways are identified and further introduction is prevented. The collected vegetation data may give indications where introductions took place and which factors may have caused the introduction. If introduction of the non-native species cannot be stopped, e.g. because it is of great economic interest, management should focus on priority areas, for example by preventing future introduction close to conservation units and establish monitoring of existing populations nearby.

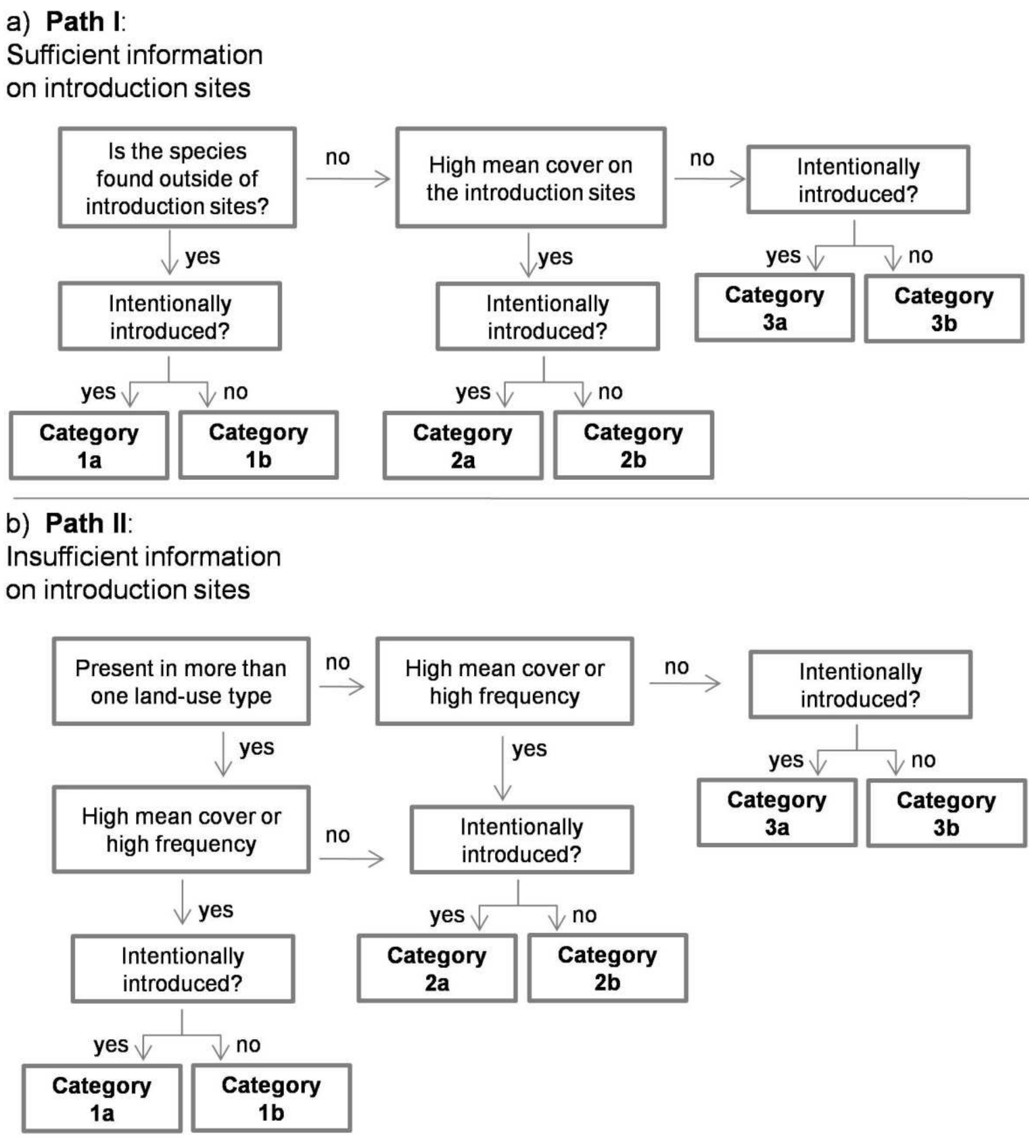


Figure 11 Decision tree for non-native species displaying (a) sufficient information on the introduction sites (path I), and (b) only scarce or no information on where the species was introduced (path II). The tree results in six categories that are indicative for management options or, alternatively, need of further information on the respective species.

Species in *category 2* are not yet spreading but well established on the sites of introduction, or either appear in areas with different land use or reach high cover in one land use. The important question for managers concerning these species is whether the introduction has been too recent to result in a spread, or whether these species are unlikely to spread at all. Information from introduction elsewhere might help to answer this question but in the meantime these species should receive a thorough monitoring.

For species ranked into *category 3* the management decision highly depends on invasion history elsewhere. If there is no record, species can be assigned for monitoring in low frequency to ensure that their status remains. If information on invasion history elsewhere is available, the species should be targeted for eradication as this measure may still be feasible at this stage of low distribution.

Table 3 Ranking categories resulting from the decision tree on non-native plant species, and corresponding species characteristics and management implications. Categories are based on the distribution of a species that can be either 'spreading' (= expanding its range), 'establishing' (= not spreading but present in high frequency or cover) or 'sporadic' (= neither spreading nor establishing). They further take into account whether a species is intentionally or unintentionally introduced.

Category		**Characteristics**	**Implications for management**
1a	Spreading, intentionally introduced	Species is spreading beyond the area it has been introduced to, this includes areas of other land use; species often has a socio-economic use, e.g. forage value	Introduction of these species within and in proximity of conservation units should be prevented. If that is not possible because introduction is realized on private land, monitoring for this species should be enforced surrounding the areas of introduction to prevent spread
1b	Spreading, unintentionally introduced	A species able to colonize different types of land use and showing high frequencies in these areas	Identification of introduction pathways is necessary to regulate these; active management should only be pursued if active introduction is terminated; experience on management options can be obtained from other regions
2a	Establishing, intentionally introduced	Species is not spreading from introduction areas but is establishing where it is introduced	Establish monitoring to determine if introduction was too recent for the species to develop spread or whether it is unlikely to spread; information about invasion history elsewhere can be helpful
2b	Establishing, unintentionally introduced	A species able to colonize different types of land use but still in low frequencies	
3a	Sporadic, intentionally introduced	The species is neither spreading from introduction sites nor establishing in high frequency	Clarify if species is known to be invasive elsewhere; if that is the case, eradication measures should be pursued at this early stage of invasion; intentional introduction should be terminated
3b	Sporadic, unintentionally introduced	Only sporadically appearing species; could be either due to short time since introduction or because the species will be unsuccessful	If species is not invasive elsewhere: sporadic monitoring, whether or not the species appears after 2 years in additionalareas

Testing the decision tree

The study region chosen for testing the decision tree are the highland grasslands in RS, Southern Brazil, around the municipalities of São Francisco de Paula (29°26'44.282''S, 50°34'49.152''W) and Cambará do Sul (29°2'52.508''S, 50°34'49.152''W). The highlands have an altitude of 800–1150 m a.s.l. The climate of the region is Koeppen's Cfb with an average annual precipitation of over 2250mm without marked dry periods, and an annual mean temperature of 14.5°C with occasional frost in winter (Nimer 1989). The characteristic vegetation is a mosaic of *Araucaria* forests and extensive natural grasslands. Recently, large parts of the grasslands have been converted to pine plantations (*Pinus elliottii* or *P. taeda*) or agricultural fields, mostly planted with corn, potato or soybean (Overbeck et al. 2007). The remaining grasslands are managed in a range of intensities. The five land-use types used for testing the decision tree on potentially invasive non-native plant species are: (1) permanent grassland that is traditionally managed with grazing and burning under medium intensity (PG-M); (2) permanent grassland where grazing pressure is reduced and burning has not been conducted since at least 2 years (PG-L); (3) permanent grassland that is fertilized, over-sown with forage species and intensively grazed (PG-H); (4) secondary grassland that is regenerating in areas formerly under arable land use, which have often been over-sown with non-native forage species (SG-A); and (5) secondary grassland that is regenerating in areas of logged pine plantations (SG-P). A total of 80 sites were sampled, distributed throughout the whole region and representing all five land-use types, with a minimum of 10 and a maximum of 19 sites per category (Figure 12a). All landowners of these 80 sites were interviewed to obtain detailed information about the introduction history of the non-native species, and thus it was possible to identify which species were intentionally introduced and on which of the 80 sites their introduction took place.

Over two years (November 2013 to February 2014, and November 2014 to January 2015), cover data of non-native species were obtained. The long time period was due to a comprehensive vegetation survey done within another project, while collecting distribution data on non-native plants was only a minor component that

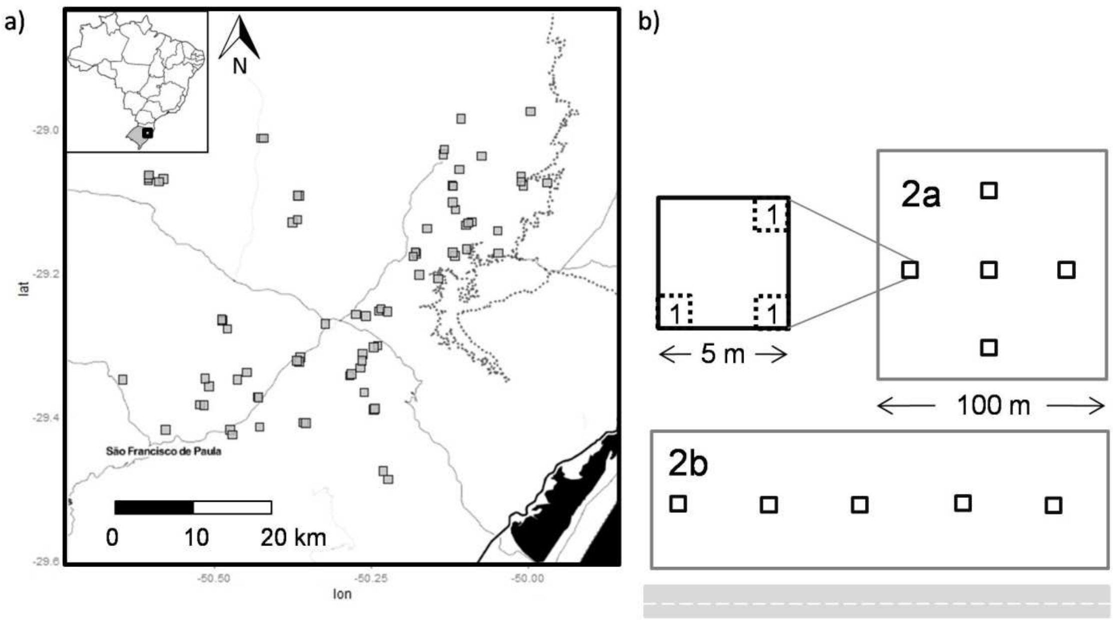


Figure 12a) Location of the sites for testing the decision tree on non-native plant species in the grassland region of Rio Grande do Sul (Brazil). Dotted line indicates border to neighbor state Santa Catarina. **b)** Sampling design. Cover of all herbaceous non-native species was recorded on fifteen 1x1-m^2 plots (labelled '1'), and individuals >50cm of woody non-native species were recorded within 1ha at the centre ('2a') and 1ha at the edge of each site parallel to the nearest road or track ('2b').

could have been realized within 3 hours per site. Each site had a minimum of 1ha, and sampling was conducted at two scales (Figure 12b) to account for differences among species (Barney et al. 2015).

On fifteen 1x1-m^2 plots on each site, cover of herbaceous non-native species was recorded using a decimal scale (Londo 1976); for each species, the mean cover and its frequency per site were calculated. Non-native woody species were recorded separately; for these, all individuals with heights>50cm were counted within 1ha at the centre of the site, and within a 1-ha transect along the site edge towards nearby roads or tracks, or in cases of absence of roads towards the next area with different land use. The data were used to classify the species according to the decision tree described above. As stated above the cut-off values for high frequency and cover of a non-native species have to be defined according to the characteristics of the study system. In the natural grasslands of the study region, vegetation cover is mostly dominated by 1–2 grass species, and the majority of species is present in very low covers of <2% (C. Koch, unpubl. data). We therefore consider a mean cover of 5% and frequency of >30% of the plots as high for a non-native species. In order to avoid overestimation of rare species, the minimum percentage of sites for a species to be included was defined as 5% of the 80 study sites. A full list of non-native species observed in the study region can be found in Appendix A7. Nomenclature of all species follows the Missouri Botanical Garden database (www.tropicos.org). The results were compared with lists of invasive species for the state of RS derived from the I3N Brazil Invasive Alien Species Database (2015).

4.3 Results

A total of 38 non-native species was found in the highland grasslands of RS; 21 of these species met the selection criterion of presence in 5% of the sites, and thus were evaluated based on the decision tree. The I3N Brazil Invasive Alien Species Database (2015) lists 68 non-native plant species in total for the state of RS. Only four species, namely *Cirsium vulgare*, *Pinus elliottii* and *P. taeda* (hereafter referred to as *Pinus* spp.) and *Ulex europaeus*, occurred in both lists.

Path I– classifying species when introduction areas are known

For six non-native species, the areas of introduction could be identified and these species were thus classified according to path I. Four of these species were herbaceous. They were intentionally introduced within the land-use types SG-A and PG-H as forage plants, most commonly *Lolium multiflorum* and *Trifolium repens*, followed by *Holcus lanatus* and *Trifolium pratense*. Except for *Lolium multiflorum*, these species were present on sites where they had not been introduced, and were thus classified in *category 1a* as '*spreading*'. While *Trifolium pratense* only spread to other former arable fields and traditionally managed grasslands, both *Holcus lanatus and Trifolium repens* spread to areas of all land-use types except low-intensity managed grassland and logged plantations, respectively. *Lolium multiflorum* had not spread to areas beyond the introduction sites, showed a mean cover <5% on the introduction sites, and was thus classified in *category 3a*.

In contrast to the intentionally introduced herbaceous species, the woody non-native *Pinus* spp. had been planted on the former plantations, and these areas were thus considered as 'introduction sites' and all areas with other land use as potential 'spread sites'. As pines were present on these other land-use types, they were classified in *category 1a*. The distribution of these species showed a clear spatial pattern. While on logged plantations three times more pines were found towards the edges than in the centre, individuals of *Pinus* spp. were found on 11% of PG-M and 15% of PG-L, but all within the sites and not along the borders. Both PG-H and SG-A did not contain any pine plant.

Path II– classifying species when introduction areas are unknown

Of the 15 non-native plants classified with path II, 14 species were herbaceous. Only *Prunella vulgaris* and *Raphanus raphanistrum* were present in a single land-use type (i.e. PG-H and SG-A, respectively) and had low cover and low frequencies, and could thus be classified in *categories 3b* and *3a*, respectively. None of the other 12 species, which were present on more than one land-use type, showed high cover or frequency, and all were thus classified in *category 2b* (unintentionally) or *2a* (intentionally introduced), i.e. *Avena sativa* and *Lotus corniculatus* in the latter case. None of the species was able to colonize all five land-use types, but *Hypochaeris radicata*, *Rumex acetosella* and *Veronica arvensis* were present in four types. Three highly problematic grasses, *Cynodon dactylon*, *Eragrostis plana* and *Melinis repens,* which have been reported by Rolim et al. (2015) to receive much attention in invasion studies in other parts of the state of RS, were not present in any of the study sites.

Besides pines, the only other non-native woody species found in the study area was the shrub *Ulex europaeus.* The introduction history of this species is not clear, although it was initially introduced for planting hedges, it has long been considered undesirable due to its unpalatability. However, information on introduction sites is scarce and the species was thus classified using path II. Counting individuals on a 1-ha scale revealed that this species was present in more than one land-use type, albeit in low frequency, resulting in *category 2a*. Most plants of *Ulex europaeus* could be found in PG-L, fewer in logged plantations, PG-M and PG-H; only one former arable field contained *Ulex europaeus*. The species showed a distribution inverse to that of the pines: only 7% of all plants were found at the centre of the sites, whereas 93% were found at the margins towards roads or other land uses. A summary of the classification of the 21 non-native plants found in the highland grasslands of RS is given in Table 4.

Table 4 Classifications of non-native plants in the highland grasslands of NE Rio Grande do Sul, using the decision tree shown in Figure 11.

Cat	Species		Cat.	Species	
1a	*Holcus lanatus*	*Trifolium pratense*	1b	---	
	Pinus spp.*	*Trifolium repens*			
2a	*Avena sativa*		2b	*Cirsium vulgare**	*Rumex acetosella*
	Lotus corniculatus			*Crepis capillaris*	*Rumex obtusifolius*
	*Ulex europaeus**			*Hypochaeris radicata*	*Silene gallica*
				Plantago lanceolata	*Taraxacum officinale*
				Poa annua	*Veronica arvensis*
3a	*Lolium multiflorum*		3b	*Prunella vulgaris*	
	Raphanus raphanistrum				

*Listed in I3N Brazil Invasive Alien Species Database for Rio Grande do Sul

4.4 Discussion

Suitability of the decision tree to identify potentially invasive non-native species

The grassland surveys identified 38 species as non-native in the study region in the highlands of RS in Southern Brazil, and while only few species were intentionally introduced as forage plants or for cellulose production, the majority was considered accidentally introduced. This number corresponds to only 14% of the 270 herbaceous species that are non-native in RS according to Schneider (2007). Only four of these species were also listed among the 68 invasive plant species for RS according to the I3N Brazil Invasive Alien Species Database (2015), i.e. *Cirsium vulgare*, *Pinus* spp. and

Ulex europaeus. At the same time, the three grasses cited by Rolim et al. (2015), *Cynodon dactylon*, *Eragrostis plana* and *Melinis minutiflora*, as most invasive for the state of RS and also listed in the database for the state of RS, were not found in the highland study region, although they are common in other parts of the state. The comparably low number of non-native species and absence of many known invaders may be attributed to three factors: (1) the rather recent acceleration in land-use change, (2) the remoteness of the highland region, and (3) the climatic characteristics of the region that may lead to reduced invasion success especially of the tropical grasses. The region still contains vast areas of natural vegetation, and aside from the main roads, many tracks have not been paved yet. Roadsides themselves have not been sampled as done by Schneider and Irgang (2005), and given the evidence from other studies, that roadsides can be important habitats for non-native species and facilitate their movement (e.g. Pauchard and Alaback 2004; Christen and Matlack 2009; Fuentes et al. 2010; Joly et al. 2011), it can be expected that an inclusion of this habitat type would probably result in a higher total number of non-native species. Frost events can occur during winter in the highland region which may impede the persistence of some African grasses like *Melinis minutiflora*. However, if the main reason for the low number of non-native species is that land-use changes accelerated only recently, future assessments will not only find more non-native species, but more of them will also be widespread.

National databases for invasive species are an important source of information, but they take time to be generated and to become comprehensive. For example, after more than 10 years of data gathering, Brazil's list still contains fewer than 200 plant species. If management solely focuses on official species lists, it may in some cases come too late for effective control actions. In the case of our study region, only four species, namely *Cirsium vulgare, Pinus* spp. and *Ulex europaeus,* would be considered invasive, and management would be focussing solely on these species. Management of non-natives should thus not *only* rely on lists that have been produced by experts on invasion probability, but should also and perhaps more importantly rely on field data for a more realistic impression on the actual magnitude and spatial distribution of a species (Fuentes et al. 2010).

Management recommendations derived from the classification

On the basis of the distribution data, 21 of the 38 non-native species in the region have been classified and can now be assigned to suitable monitoring and management actions (see column 'Implications for Management', Table 3). Five species have been classified in *category 1*, indicating that they are spreading. All of them were intentionally introduced (*category 1a*) in high frequencies with either the purpose of fodder provision or cellulose production. From a logical point of view, attempts to eradicate these species should only be pursued under the condition that their intentional future introduction is avoided. Otherwise, spending money for their management seems ill advised. However, this decision is not taken easily as cases where economically useful species become invasive are not uncommon and generally create conflicts between different stakeholders (Caplat and Coutts 2011; Van Wilgen and Richardson 2014). Another aspect in eradication planning concerns the feasibility of such measures, i.e. if eradication is still possible or whether the species is already so widely distributed that any management attempts seem futile. At least for invasive woody species assessments show, that local eradication is possible if their distribution is still limited, but that in most cases follow up treatments or several clearings in the same area have to be conducted (Marais et al. 2004).

No unintentionally introduced species was classified in *category 1b*. However, a large number of species was classified in *category 2*, indicating that the group of species classified in *category 1* could increase in the future. To improve predictability, an important follow-up question for managers is whether a species was introduced too recently to have spread or whether it lacks the ability to spread in the given context. A frequent monitoring of the observed populations and information about invasion history in other regions can help addressing this question. As the species *Cirsium vulgare* and *Ulex europaeus* are also listed on the national database of invasive species, they should receive specific monitoring, and management should be coordinated with attempts in other states. The classification of *Ulex europaeus* shows that the proposed cut-off values in the decision tree may not be adequate for woody species with unknown introduction sites. We used a large sampling scale of 1ha to count individuals of woody species. It would be advisable to adjust the cut-off values from initially 30% cover to 0.5% which would still correspond to around 50 individuals of the woody species (assuming a diameter of 1m per shrub). Otherwise, woody species with unknown introduction areas would only be classified in *category 1* if they already build massive stands of >1000 individuals.

Three species were classified in *category 3* and two of them were intentionally introduced. The distribution data indicate that the species are sporadic, and thus management could now be implemented with low effort. The most important question concerning these species is whether they are known to be invasive somewhere else. Studies from other regions show that all of these species have been considered invasive elsewhere (*Lolium multiflorum,* Collinge et al. 2011; *Prunella vulgaris*, Godoy et al. 2011; *Raphanus raphanistrum,* Warwick and Francis 2005), and management should thus be initiated. For the intentionally introduced species, socio-economic benefits and costs will be decisive for the pursuit of eradication measures. For the unintentionally introduced *Prunella vulgaris*, management needs to encompass the identification of the introduction pathways. Given that the species has only been found in land-use type PG-H, where other species have been seeded, it is likely that it has reached these areas as contaminants with seed material.

Of the 38 non-native species, 17 had fewer than five areas of presence and were considered too rare to be adequately assessed. These species should, however, be placed on a watch list that aims to determine if their observed rarity was due to lack of data, short time period since introduction or their actual inability to spread in the region.

Applicability of the decision tree

We collected a large amount of species distribution data to apply and test the decision tree proposed above. This necessity for rather detailed data collection in the field could be perceived as a drawback of the proposed method. However, any management of non-native species, whether it is based on governmental priority lists or decision trees, requires species distribution data in order to know where the populations of a given species can be found and management actions can be coordinated. Additionally, it is important to note that our approach does not require complete sampling of the plant community, but only cover assessment of exotic species. The data should ideally be collected in different habitat types and under different anthropogenic pressures, so that a realistic picture of the species distribution can be achieved. Having identified which types of areas are more prone to contain non-native species, spatial predictions about future invasion risks accompanying ongoing land-use changes are possible (cf. Chytrý et al. 2012). In our case, we limited sampling to grasslands or former grasslands, which constitute an important vegetation type in the region. As stated above the inclusion of roadsides could be a valuable extension for future sampling.

A shortage of information makes any assessment more difficult and susceptible for misinterpretation. In their modification of the A-WRA, Fuentes et al. (2010) have suggested not only using species distribution data but also time of residency as factors to set management priorities. While the latter may be available for intentionally introduced species, those arriving unintentionally may go unnoticed for some time thus underestimating their residence time. In our decision tree, path II overcomes the challenge of not having sufficient information on introduction sites, making the classification of species possible even when information on introduction sites is scarce. Hulme (2012) pointed out, that risk assessments cannot rank species adequately if their introduction in another region has been too recent. A short time period since introduction has been identified to be a source of inaccuracy for our ranking as well (*category 2*), requiring further monitoring and observations of the species in question. McGregor et al. (2012) indicate that ranking species based on A-WRA is difficult when these are closely related and share many traits. As ranking in the proposed decision tree is solely based on distribution characteristics, such a bias caused by similarity due to relatedness is avoided.

The decision tree focuses on distribution and ranking of non-native species according to their frequency, cover and observed spread. It is not a direct assessment of impact. Prioritization would of course be optimized if species imposing a high impact on the native ecosystem could be identified. This, however, is laborious as impact can have numerous dimensions, whereas managers need a quick decision tool. While Ricciardi and Cohen (2007) pointed out that spread is not a good predictor for impact, we need to keep in mind that the likelihood of a species creating an impact increases with the extent of its area (Parker et al. 1999), thus making distribution data a key component for any assessment.

One important point to emphasize is that this classification is corresponding to a defined point in time. Just because a species has been classified in this evaluation as sporadic does not mean this species cannot be spreading in the future, as dynamics of invasions over time are highly variable and unknown (Strayer et al. 2006), lag phases have been observed in many cases (Crooks 2005) and continuous changes in land use could further promote invasions (Strum et al. 2015). The same restriction holds true for other assessments. Another factor that has to be remembered not only for our decision tree but also in any other risk assessment or evaluation framework is that none of these will produce results that are 100% correct and we should always be aware of possible shortcomings in our methods and sources of uncertainty (Daehler et al. 2004).

4.5 Conclusions

It is essential that predictive tools that have already been developed and tested are widely applied to further reduce the risk of intentionally introducing harmful species. For those non-native species already present in an area, thorough strategies need to be applied that also account for specifics of the invaded regions (e.g. Roura-Pascual et al. 2009). The application of the decision tree in the case study in Southern Brazil showed that evaluation based on regional distribution data can lead to concrete recommendations for the management of non-native species. In our case, the difference in outcome compared to the national invasive species database emphasized that although the latter is important, management decisions can better be made in a regional context and could otherwise be misleading. We should thus not *only* rely on lists that have been produced by expert judgments on invasion probability but base decisions in a regional context on field data.

There is one big obstacle that remains to make management more feasible: the question how management can treat those species continuously introduced for economic reasons that start to become invasive. Studies around the world have pointed out the huge risks associated with introduced plantation trees (Dodet and Collet 2012) or herbaceous forage species (Driscoll et al. 2014), but introductions of these groups have continued on a broad scale due to economic interests, not only in Brazil. Similar to pre-border assessments for species proposed for introduction, it would be desirable to establish tools that allow the effective withdrawal of permissions for introduction if the species turns out to be invasive after all.

Chapter 5
General discussion

The increasing threats for grassland on a global scale make thorough strategies for their conservation and restoration on regional and local scales necessary. As funds, manpower and time is often very limited for land managers, these strategies need to be designed as efficient as possible. In the general introduction I pointed out, that the process to derive sound restoration strategies comprises two main steps with the respective questions: (1) The identification of the reference: Which properties of the grassland are aimed for? And (2) the identification of drivers and their respective changes: which drivers have created or are still creating changes to which properties of the grassland system? – The final chapter of the PhD thesis synthesizes the main findings of the previous three chapters to answer these two questions, and to develop a balanced strategy for the restoration and conservation of subtropical grasslands in Southern Brazil.

5.1 Identification of reference grasslands

A basic prerequisite for any successful restoration is the definition of targets or goals, on which monitoring can be based and hence success of the restoration can be measured (e.g. Bakker et al. 2000; Hallett et al. 2013). In chapter 2, permanent grassland of medium intensity management (PG-M), classified based on the current management intensity, was predefined as a reference to describe degradation. It was further used in chapter 3 as a reference to measure deviations of several properties caused by other land uses. However, it has not been debated so far, whether this choice of reference is adequate for restoration and conservation of grasslands in the study region.

Many projects state that conditions of pre-European settlement are the reference for restoration actions, although these conditions are in most cases unknown (e.g. in North America; Thorpe and Stanley 2011). However, in the study region, records confirm that the mosaic of grassland and *Araucaria* forest seen today has been present in this region for several thousand years, and that fire played an important role during this whole time (Behling 2002). Although we cannot say with certainty that the grassland we find today is constituted of exactly the same species as in historic times, aiming for grasslands, that are subject to disturbances, i.e. influenced by burning and grazing, seems adequate.

While it was sufficient to use management intensity as a means to categorize different types of areas in chapters 2 to 4 of this thesis, it is not adequate to define a reference for restoration based on management intensity. Results from chapter 3 show that areas categorized as PG-M display a high variability of some properties, e.g. species numbers. At the same time some areas defined as PG-L based on current management, are hard to distinguish from PG-M. While management intensity can certainly serve as a means to reach restoration targets, it would be more preferable to define the reference based on quantifiable properties of the grassland. As the here examined grassland system is subject to disturbances, it would be furthermore inappropriate to take a static view of these reference properties, but it would be more adequate to define an envelope of ranges of conditions (Kirkman et al. 2013).

Goals in restoration and conservation can generally be focusing on different levels of organization, i.e. taking single species, communities, ecosystems or specific services of the system as goals (Ehrenfeld 2000), and debates about which would be the appropriate level have been long. Focusing on individual species like in re-introduction projects, includes the risk that although one focal species can be re-established, habitat quality may not meet expectations (Bakker et al. 2000). Considering the high species number and low frequencies of species in the study region, it would be unrealistic to find a single target species for restoration. Instead of focusing on single species, Martin et al. (2005) propose different measures of diversity to measure restoration success. Aiming at a mere number of species for restoration seems likewise inadequate, as this number could be composed of whichever species, also including non-native species, ruderal species or even forest species. Bakker et al. (2000) suggested that instead of using biodiversity itself as a target, defining a target community would be more adequate. For the here examined grasslands, I suggest to combine these two approaches and define a minimum diversity and a set of target species, which can be derived, e.g. from indicator species lists (see chapter 3 and Appendix A4). Based on the results from chapter 3, measurable goals for restoration would thus be a high mean native species richness as well on a small scale (min. 20 species per $1m^2$) as accumulated per site (min. 60 species on $15m^2$) and the presence of species identified during indicator analysis. In addition to goals referring to target species, structural characteristics of the grassland can be defined as goals for restoration. This could in our case be a mean shrub cover that does not exceed 5% and a mean cover of tussocks between 10 and 50%. Abiotic factors do not need to be defined as goals for restoration as it is generally assumed, that vegetation composition will encompass these factors automatically (e.g. Bakker et al. 2000; Fagan et al. 2008).

A more and more adopted strategy in defining restoration goals is to also include socio-economic features, i.e. accounting for services the reference system could provide (e.g. Bullock et al. 2011; Wortley et al. 2013). These services might be closely linked to requirements of the local population and can therefore also increase acceptance of restoration measures (Miller and Hobbs 2007). In our study region the use of grasslands for meat production has long been an important socio-economic factor and the whole gaucho culture is closely linked to the herding of cattle in productive grasslands (Overbeck et al. 2013). To account for this, sufficient productivity of the grassland can be defined as an additional goal for restoration. Sufficient productivity is composed of the two measureable aspects forage quantity and quality. Forage quantity corresponds to net primary productivity (NPP), where several protocols have been established for its measurement (e.g. Ni 2004; Meyer et al. 2015). These measurements generally imply harvest at peak biomass and an exclusion of grazing animals to not distort the results. As aboveground biomass in this project was sampled throughout the vegetation season, not accounting for peak biomass, the obtained values are not suitable to define an adequate goal of forage quantity (for detailed description and results of phytomass sampling see Appendix A8). Forage quality consists of the two main components neutral detergent fiber (NDF) and crude protein (CP) (Ball et al. 2001). These components are also highly variable through the year and their determination is very laborious (also see Appendix A8). In order to have an easier to measure, but still valid indicator for sufficient productivity of a site, the estimation of the proportion of dead biomass in the aboveground biomass and litter could be an alternative measure. It can be assumed that a large proportion of standing dead biomass decreases the palatability of the grassland. Based on mean values obtained in chapter 3, a measurable target for restoration would be a maximum percentage of standing dead biomass and litter of 10%.

In summary, the measureable goals for grassland restoration and conservation in the study region are: high mean native species richness as well on a small scale (min. 20 species per 1m²) as accumulated on each site(min. 60 spp. on accumulated 15m²), presence of species identified during indicator species (not all at once but some); mean shrub cover of ≤5%; tussocks cover between 10 and 50% and a proportion of standing dead biomass and litter below 10%.

Besides defining measureable properties of the reference system, with which restoration success can be determined, another set of measures serves to diagnose the damages to the system (Hobbs 2007). As described by the framework in chapter 2, degradation can be seen as any changes in properties of a system, independent if it is abiotic, biotic or also ecosystem functions. If the aim is to thoroughly describe which properties of the system have all undergone changes, all properties need to be measured. However, as a more practical solution it would be advisable to focus on those properties that are directly linked to the goals drived from the reference system. In addition to this, properties that are influencing some of these aspects should also be measured, e.g. plant community is closely linked to soil properties (Miller and Hobbs 2007). So although soil properties themselves are not part of the defined goals, they are a necessary condition for some of the defined goals and thus need to be accounted for when measuring changes.

5.2 Management strategies mitigating changes from land-use and invasions

It is not sufficient to only measure what has been changed in a system. Possibly more important is to link these changes to the drivers that have caused them. If these drivers would still be active when restoration measures are implemented, e.g. if sources of water pollution in a river are not identified and removed, the effectiveness of restoration measures would be reduced and limited resources wasted. After having identified the properties of a reference grassland and changes that would be suitable to measure, I will now discuss for each type of area examined in this study, which changes can be attributed to land-use changes, which role non-native species play for the respective changes and which the implications for the restoration are, in cases of secondary grassland areas, and for conservation, in cases of permanent grasslands.

5.2.1 Former arable fields

Secondary grasslands developing on former arable fields (SG-A) meet almost none of the reference grassland characteristics described above. The mean number of species both per m² and per site was much lower than 20 and 60, respectively. Many non-native species were present, while none of the target community species could be found. While the mean cover of shrubs did not exceed the goal, percentage of tussocks was well below the desired amount. Furthermore, abiotic conditions largely differed from reference grasslands. The parameter indicative for suitability as pasture, however, is met: standing dead biomass and litter do not exceed 10%.

The use as agricultural fields was the driver that caused changes in this area type and the legacy of this use can still be observed. While abiotic changes were caused by fertilization during agricultural use, it cannot be answered here, whether the changes in biotic composition and absence of typical grassland species can be solely attributed to either changes of soil conditions, the presence and competition with non-native species, the short longevity of the seed banks or a combination of the three. Results from chapter 4 show, that the introduced forage species were highly abundant and spreading, increasing the probability that they also create a competitive situation for native species. Most unintentionally introduced non-native species were only present in low numbers thus being very unlikely to exert competitive impacts here.

Extensive restoration measures will be necessary to reach the goals defined under section 5.1. These would initially include some measures to decrease the abiotic deviations. Studies have shown that especially the high phosphorous levels on former arable fields can be detrimental for grassland restoration success (Fagan et al. 2008). A laborious but also effective measure would be the removal of topsoil that has been suggested and applied in many grasslands in Europe (Török et al. 2011 and references therein). The creation of extensive areas of bare ground with this measure could, however, be counterproductive as many non-target species are likely to colonize these areas, e.g. wind-dispersed native Asteraceae shrubs or the invasive species *Ulex europaeus*. Many studies on restoration measures have been conducted on calcareous grasslands. While some aspects like the high soil fertility are a shared problem, acidic grasslands in addition suffer from the elevation of the pH-value (Owen et al. 1999). Owen and Marrs (2000) suggest using bracken litter or sulphur to achieve an acidification of former arable soils to re-create acid grasslands. *Pteridium esculentum* is a species frequently found on burned grasslands in the region and could be applied as a means to decrease abiotic deviations. However, experiments need to confirm transferability of the results from Owen and Marrs (2000) and to determine the amounts of litter necessary to obtain the respective pH-values.

Improving soil conditions alone will not be sufficient to re-establish species of the target community. Studies from Europe and North America show that unaided regeneration of grassland communities after arable field use is highly depending on proximity of propagule sources, may take a long time and still be less similar to target communities (e.g. Fagan et al. 2008; Blumenthal et al. 2005). Active re-introduction may thus be an alternative which is generally realized by sowing of target species or hay transfer (e.g. Kiehl et al. 2010). As seed production of native species in the region is not pursued so far, hay transfer may be more feasible. The best way to conduct this has however to be determined, as studies from other regions in Brazil showed difficulties to apply this method in a tropical context (Le Stradic et al. 2014). While native species have to be actively supported, at the same time some of the non-native species present in this type of grassland have been identified in chapter 4 as in need for management. It should be furthermore taken care that the exotic species *Trifolium repens*, *Trifolium pratense* and *Holcus lanatus* are not introduced in surrounding areas, as they might be able to establish in open spaces during restoration.

In Europe, the question how to deal with abandoned areas has been thoroughly assessed given the densely populated area and the necessity to either re-use or valuate an abandoned area for conservation purposes. In regions where still large amounts of natural vegetation are present, the necessity for restoration measures is not well pronounced and thus the active re-validation of these abandoned areas is surprisingly limited so far. Considering the ongoing conversion of grassland to agricultural areas that will also continue in the future (Henderson et al. 2015), it seems thus even more pressing to improve restoration efforts.

5.2.2 Former plantations

Secondary grasslands developing after the logging of pine plantations (SG-P) meet none of the goals defined for the restoration of grassland. The mean number of native species was much lower on both scales and all target community species were missing. The non-native plants *Pinus* ssp. and also *Ulex europaeus* were present in some areas. While the proportion of tussocks was generally very low, the mean cover of shrubs often exceeded 5% and the amount of standing dead biomass and litter exceeded 10% by far due to large amounts of pine residuals. Abiotic deviations caused by land use were however comparatively low.

The extensive time these areas have been used as pine plantations (mean time under plantation: 24 years, see Appendix A1) is the main cause that regeneration of typical grassland species from the seed bank is not possible anymore. However, the large amount of pine residuals (up to 25% of the areas covered with branches, needles and stumps) is also likely a factor that is still actively impeding the re-vegetation of the sites (e.g. Navarro-Cano et al. 2010). It should thus be considered to remove them either mechanically or by burning (e.g. Pywell et al. 2002; Szitár et al. 2014). Other than that, extensive measures for soil improvement like for arable fields are not necessary. In chapter 4, it was shown that areas of SG-P can contain large proportions of regeneration of pines, and invasions of *Ulex* were also more frequent than in other land-use types. Experience from other regions suggests that if these woody species are restricted to a certain geographic range, e.g. the area of a former plantation, eradication measures can be successful (Marais et al. 2004; Cuevas and Zalba 2010). These may, however, include several follow up measures. Great care has also to be taken when the above mentioned measures to remove pine litter are applied, as the created bare soil may provide sites for invasive species' establishment. Similarly to arable fields, former plantations also require the active re-introduction of native plant propagules to meet the goals concerning the target community.

Although SG-P are so far not meeting any of the defined goals for grassland restoration, they still have a large potential for grassland restoration. Especially within and in proximity to protected areas, extensive areas of plantations are logged and it would be desirable to improve these areas. Given that pasture use potential in their current state is very low (see Appendix A8), a restoration would also increase economic returns from these areas for land owners in the future.

5.2.3 Permanent grasslands under low intensity management

Permanent grasslands under low intensity management (PG-L) show the smallest deviations from conservation goal conditions. Although they contain generally fewer species than aimed for, they hold many species of the target community and non-native species are only sporadically encountered. Likewise, no deviation of abiotic factors could be detected. Structural parameters and productivity are the factors mostly differing from the goals: they exceed the aspired shrub and tussock cover by far and the acceptable amounts of dead biomass also do not meet the goal of pasture productivity.

The driver causing these changes is the abandonment of regular removal of biomass, leading to the accumulation of dead biomass, dominance of tussocks and increased presence of shrubs (e.g. Briggs et al. 2005; Overbeck et al. 2005). In the respective areas, this driver is still active and the majority of these sites are found within conservation units. Changes in species numbers cannot be attributed to abiotic changes or sporadic non-native species but rather to the high amounts of biomass.

A suggestion for conservation measures would simply be the re-introduction of management. Given the large amounts of excess dead biomass, it is unlikely that this could be achieved by re-introducing cattle as these would probably not find sufficient fodder. A fire would on the other hand pose the danger of being too strong and uncontrolled (e.g. Govender et al. 2006). A mowing treatment that would initially remove biomass and that is then followed by burning and re-introduction of grazing would be a better solution. There have been studies in other regions investigating if a re-introduction of management would be sufficient to create reference grassland conditions (e.g. Klimeš et al. 2013). Experiments are necessary to test if this can be achieved in the study region as well.

Tropical grassy biomes have been identified in recent years to be somewhat misunderstood and that the means for their conservation are often not adequate (Parr et al. 2014; Veldman et al. 2015a). The here examined grassland is a typical example for this. While conservation certainly had good intentions, the way it was implemented in the study region, turns out to be detrimental for the grassland (Pillar and Velez 2010). It would be desirable, that a rethinking would take place here acknowledging that conservation does not automatically mean exclusion of anthropogenic influences but that conservation can actually be achieved through the active use of the grassland.

5.2.3 Permanent grasslands under high intensity management

Permanent grasslands under high intensity management (PG-H) only reached some of the defined goals for grassland conservation. On the one hand, they met none of the goals concerning the target community: they generally displayed a reduced number of species, target grassland species were absent and a high percentage of non-native species was present instead. On the other hand, structural characteristics of the reference were met: the cover of shrubs was low, tussocks were present but not exceeding 50% and amounts of litter and standing dead biomass were very low. Abiotic changes were similar to SG-A, and very different from the reference.

The driver for the observed changes here is the intensive management with fertilization and introduction of non-native species. In contrast to former arable fields, these factors are still actively pursued on an annual or biannual basis. There are no studies available that deal with the question, if the termination of this intensive management and the return to typical management practices would ultimately lead to the re-establishment of the target grassland community. As these areas are still actively and very intensively used, they are, however, no real candidates for the conservation of reference grasslands and the current form of grassland management will thus be continued. Anyhow, some precautionary additions to the present form of land use should be considered. This concerns especially the introduction of non-native species that have been ranked in chapter 4 as spreading or establishing. It would be desirable to conduct studies examining the forage value and options of propagation of several native species to reduce and ultimately terminate the active introduction of these potentially invasive species. This would also reduce the risk that these areas serve as starting point for future invasions.

5.3 General implications for management

In summary, both abandoned land uses have with the help of more or less intense measures the potential to restore a grassland that might not meet all goals but has at least more similarity to the target than it has now. Grasslands in conservation units need the re-introduction of active management to prevent their transformation into forest systems. On the contrary, grasslands of high intensity management are an important component of current pasture use, thus the likelihood of these areas being available for grassland conservation in the future is quite low.

During the PhD project work it became clear that land-use change and its consequences are an obvious and relatively easy to determine driver of changes in grassland systems. Although the presence of non-native species was accounted for, it is generally difficult to assign direct impacts to these species. Especially in the context of anthropogenic land use, it is hard to determine whether a species is the active driver of changes or rather the passenger of other changes caused by land use (MacDougall and Turkington 2005). Figure 13 summarizes the direct drivers of land-use changes observed, their respective changes and possible responses by management. An additional column describes the indirect drivers that are acting in front of the direct drivers. These are drivers on a larger scale like legal restrictions or economic developments that create pressures or incentives in land use that in turn cause changes. It is important to acknowledge these drivers as well, as they are not static and are able to explain developments of the direct drivers.

In the study region these indirect drivers have been very important: Due to economic developments on the global cellulose market, the main cellulose factory in the region was closed down and thus large proportions of pine plantations were logged and not re-planted. Once the global price will recover, this development is likely to be reversed and instead of areas newly available for grassland restoration, large areas of intact grassland will be transformed into plantations. Thus while restoration and conservation strategies are developed on a local or regional scale, large scale pressures need to be accounted for in the successful planning and implementation of these strategies.

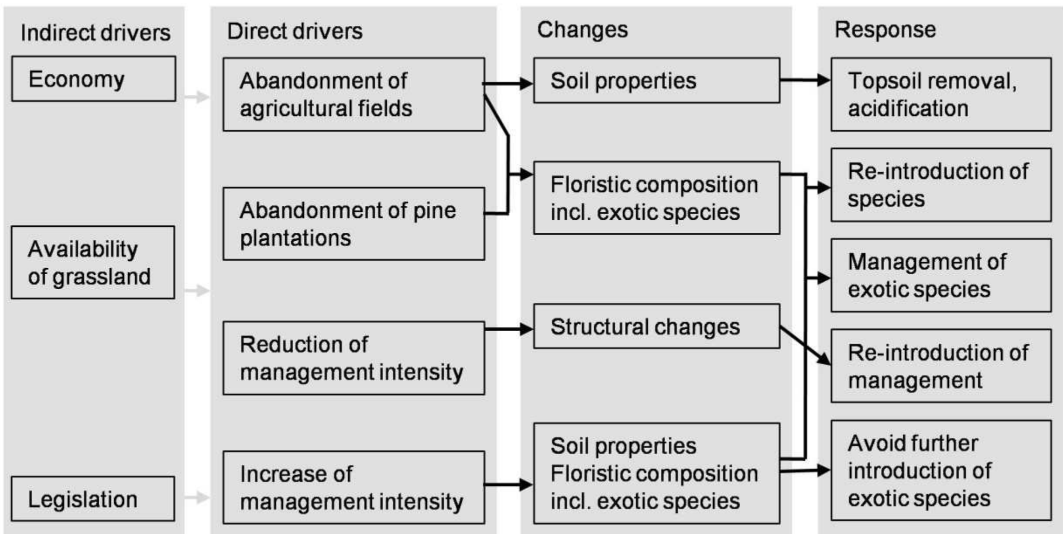


Figure 13 Overview of direct and indirect drivers, their respective changes and possible implications for management that have been identified during the PhD project for the Campos de Cima da Serra in Rio Grande do Sul, Brazil.

5.4 Concluding remarks

In the study region in Southern Brazil, a thorough strategy is missing, that accounts for conservation needs and restoration potentials in different types of areas. With the here collected data, it is possible to define goals for restoration of grasslands that have a high value for conservation and maintain at the same time a value as basis for livestock production. Based on these goals, areas with secondary grasslands that do not yet meet these goals were identified and suggestions for restoration measures were given. At the same time, grassland management practices that lead to deviations from these goals were recognized. A determination of thresholds both for restoration and self-recovery like described in chapter 2, could, however, not be achieved with the snapshot assessment conducted in this thesis. Long-term observations and also experimental studies are necessary that assess, e.g. whether and under which conditions a re-introduction of propagules on degraded secondary grasslands can be successful. Long-term studies or rather long-term monitoring is also important if restoration measures should indeed be adopted. On the one hand, the danger exists that short-term improvements will be lost after longer times and success of other measures might on the other hand take some time to unfold.

Restoration and conservation are both topics that are always explicitly or implicitly based on value systems and discussions. What is it, that we want to protect or re-establish and how can we achieve this protection. Discussions about novel ecosystems have emerged in the past years in the restoration community. These discussions suggest instead of actively interfering in all thinkable ways that some novel systems should be acceptable as they are. Truitt et al. (2015) have recently pointed out the danger to talk about novel ecosystems when it is not clear where novelty starts and how it can be quantified. Would for example an abandoned plantation already have to be considered as novel, as the here establishing community is not naturally existing anywhere? Nowadays it is probably not realistic to aim to establish pre-European conditions in all ecosystems. However, we should not dread the efforts to try to design restoration and conservation strategies as efficient as possible, before giving up and just accept novelty.

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Appendix

A1 Chapter 3

Land-use types and their management characteristics in the highlands of South Brazil

Current average grazing intensity is expressed in heads of cattle per month (HCM), per ha and year; time since change of land use indicates for SG-A and SG-P years since land use is abandoned, and for PG-H time since intense management started, i.e. first time sown with non-native forage species.

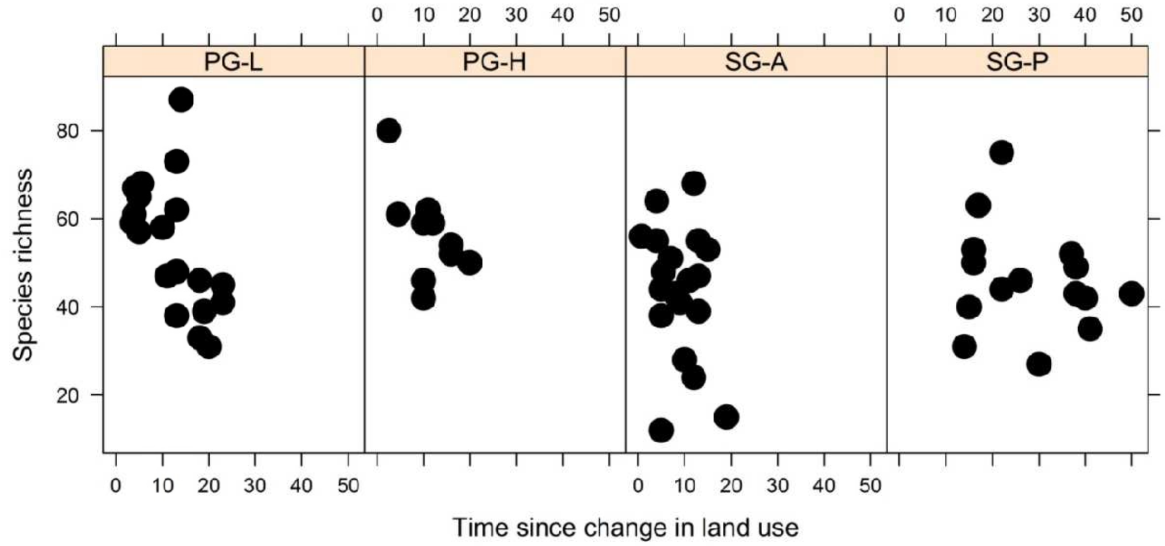
	(1a) Permanent grassland, medium intensity (PG-M)	(1b) Permanent grassland, low intensity (PG-L)	(1c) Permanent grassland, high intensity (PG-H)	(2a) Secondary grassland on ex-arable field (SG-A)	(2b) Secondary grassland after pine plantation (SG-P)
No. of sites sampled	17	19	10	19	15
Current average grazing intensity (HCM $(ha*year)^{-1}$)	6.1	5.1	15.6	13.7	2.4
Fire frequency	≥2 in 5 years	<2 in 5 years	--	--	--
Tillage	Never	Never	Never	During arable use	Never
Liming or fertilization	Never	Never	Regularly	During arable use	Never
Over-seeding with non-native species	Never	Never	Regularly	During arable use	Never
Years as non-grassland (mean ± SD)	--	--	--	6 ± 5	24 ± 11
Time since land-use change (mean ± SD)	--	--	11 ± 5	3 ± 2	4 ± 3

A2 Chapter 3

Correlationplots between the factor time of land use and species richness.

Time since change of land use and species richness were visually assessed for different land-use types and no trends could be observed. Time since change comprised different dimensions for the different land-use types. For PG-L: years since regular burning of the grassland ceased; for PG-H: years since first time over sown with non-native species; for SG-A: time since grassland was converted into agricultural field and for SG-P: time since grassland was converted into plantation of pine.

PG-L = Permanent grassland with management of low intensity, PG-H = Permanent grassland with management of high intensity, SG-A = Secondary grassland after agricultural use, SG-P = Secondary grassland after silvicultural use. PG-M is not shown as this land use did not experience any change in land use.



A3 Chapter 3

Complete list of species that could be separated on the 80 study sites in Rio Grande do Sul.

Incomplete species names indicate that species could not be identified until species level but was given a unique name to distinguish from other species during analysis. Three species could not be assigned to any genus and although included in the analyses are not listed here. Nomenclature follows the Missouri Botanical Garden database (www.tropicos.org). NA in family indicates that species could not be assigned to any family.

Species name	Growth form	Non-native	Family
Achyrocline satureioides (Lam.) DC.	herb	.	Asteraceae
Achyrocline sp.	herb	.	Asteraceae
Acicarpha tribuloides Juss.	herb	.	Calyceraceae
Acmella bellidioides (Smith) R.K.Jansen	herb	.	Asteraceae
Adesmia tristis Vogel	herb	.	Fabaceae
Adiantopsis chlorophylla (Sw.) Fée	fern	.	Pteridaceae
Aeschynomene falcata (Poir.) DC.	herb	.	Fabaceae
aff. *Gomphrena celosioides* Mart.	herb	.	Amaranthaceae
Agalinis communis (Cham. & Schltdl.) D'Arcy	herb	.	Orobanchaceae
Agarista nummularia (Cham. & Schltdl.) G. Don	herb	.	Ericaceae
Agenium villosum (Nees) Pilg.	graminoid	.	Poaceae
Agrostis montevidensis Spreng. ex Nees	graminoid	.	Poaceae
Agrostis sp.1	graminoid	.	Poaceae
Agrostis tenuis Vasey	graminoid	x	Poaceae
Alstroemeria isabellana Herb.	herb	.	Alstroemeriaceae
Amaranthus lividus L.	herb	x	Amaranthaceae
Anagallis arvensis L.	herb	x	Primulaceae
Andropogon lateralis Nees	graminoid	.	Poaceae
Andropogon macrothrix Trin.	graminoid	.	Poaceae
Andropogon ternatus (Spreng.) Nees	graminoid	.	Poaceae
Anthemis cotula L.	herb	x	Asteraceae
Anthemis mixta L.	herb	x	Asteraceae
Aphanes arvensis L.	herb	x	Rosaceae
Apiaceae 1	herb	.	Apiaceae
Araucaria angustifolia (Bertol.) Kuntze	tree	.	Araucariaceae
Aristida flaccida Trin. & Rupr.	graminoid	.	Poaceae
Aristida megapotamica Spreng.	graminoid	.	Poaceae
Asclepias mellodora A.St.-Hil.	herb	.	Apocynaceae
Aspilia montevidensis (Spreng.) Kuntze	herb	.	Asteraceae
Asteraceae 1	herb	.	Asteraceae
Asteraceae 2	herb	.	Asteraceae

Asteraceae 3	herb	.	Asteraceae
Austroeupatorium inulifolium (Kunth) R.M. King & H. Rob.	shrub	.	Asteraceae
Avena sativa L.	graminoid	x	Poaceae
Axonopus affinis Chase	graminoid	.	Poaceae
Axonopus compressus (Sw.) P. Beauv.	graminoid	.	Poaceae
Axonopus ramboi G.A. Black	graminoid	.	Poaceae
Axonopus siccus (Nees) Kuhlm.	graminoid	.	Poaceae
Axonopus suffultus (Mikan ex Trin.) Parodi	graminoid	.	Poaceae
Baccharis anomala DC.	vine	.	Asteraceae
Baccharis apicifoliosa A.A. Schneid. & Boldrini	shrub	.	Asteraceae
Baccharis articulata (Lam.) Pers.	shrub	.	Asteraceae
Baccharis crispa Spreng.	shrub	.	Asteraceae
Baccharis dracunculifolia DC.	shrub	.	Asteraceae
Baccharis erigeroides DC.	shrub	.	Asteraceae
Baccharis ochracea Spreng.	shrub	.	Asteraceae
Baccharis pentodonta Malme	shrub	.	Asteraceae
Baccharis pseudovillosa L. Teodoro & J. Vidal	shrub	.	Asteraceae
Baccharis punctulata DC.	shrub	.	Asteraceae
Baccharis retusa DC.	shrub	.	Asteraceae
Baccharis schultzii Baker	shrub	.	Asteraceae
Baccharis sp.	shrub	.	Asteraceae
Baccharis subtropicalis G. Heiden	shrub	.	Asteraceae
Baccharis tridentata Vahl	shrub	.	Asteraceae
Baccharis uncinella DC.	shrub	.	Asteraceae
Baccharis vulneraria Baker	shrub	.	Asteraceae
Blechnum australe L.	fern	.	Pteridaceae
Blechnum imperiale (Fée & Glaz.) H. Chr.	fern	.	Pteridaceae
Borreria dasycephala (Cham. & Schltdl.) Bacigalupo & E.L. Cabral	herb	.	Rubiaceae
Borreria palustris (Cham. & Schltdl.) Bacigalupo & E.L. Cabral	herb	.	Rubiaceae
Borreria tenella (Kunth) Cham. & Schltdl.	herb	.	Rubiaceae
Borreria verticillata (L.) G. Mey.	herb	.	Rubiaceae
Briza minor L.	graminoid	x	Poaceae
Bromus catharticus Vahl	graminoid	.	Poaceae
Buchnera longifolia Kunth	herb	.	Orobanchaceae
Bulbostylis aff. *capillaris*	graminoid	.	Cyperaceae
*Bulbostylis*aff. *juncoides*	graminoid	.	Cyperaceae
Bulbostylis aspera M.G. López	graminoid	.	Cyperaceae
Bulbostylis capillaris fo. *stenantha* Kük. ex Barros	graminoid	.	Cyperaceae
Bulbostylis capillaris var. *elatior* (Griseb.) Osten	graminoid	.	Cyperaceae
Bulbostylis capillaris var. *tenuifolia* (Rudge) C.B. Clarke	graminoid	.	Cyperaceae
Bulbostylis communis var. scabrida M.G. López & D.A. Simpson	graminoid	.	Cyperaceae
Bulbostylis contracta (Osten) M.G. López & D.A. Simpson	graminoid	.	Cyperaceae
Bulbostylis glaziovii (Boeckeler) C.B. Clarke	graminoid	.	Cyperaceae

Bulbostylis hirtella (Schrad. ex Schult.) Nees ex Urb.	graminoid	.	Cyperaceae
Bulbostylis sp.	graminoid	.	Cyperaceae
Bulbostylis sp. 1	graminoid	.	Cyperaceae
Bulbostylis sphaerocephala var*. brunneovaginata* (Boeckeler) C.B. Clarke	graminoid	.	Cyperaceae
Bulbostylis sphaerocephala var*. sphaerocephala* (Boeck.) C.B. Clarke	graminoid	.	Cyperaceae
Bulbostylis subtilis M.G. López	graminoid	.	Cyperaceae
Calamagrostis longearistata (Wedd.) Hack. ex Sodiro	graminoid	.	Poaceae
Calamagrostis viridiflavescens var*. viridiflavescens* (Poir.) Steud.	graminoid	.	Poaceae
Calea phyllolepis Baker	shrub	.	Asteraceae
Calibrachoa sellowiana (Sendtn.) Wijsman	herb	.	Solanaceae
Calydorea campestris Baker	herb	.	Iridaceae
Calydorea crocoides Ravenna	herb	.	Iridaceae
Campomanesia aurea O. Berg	shrub	.	Myrtaceae
Carduus nutans L.	herb	x	Asteraceae
Carex feddeana H. Pfeiff.	graminoid	.	Cyperaceae
Carex fuscula subsp*. catharinensis* (Boeck.) Luceño & Alves	graminoid	.	Cyperaceae
Carex longii subsp*. meridionalis* (Kük.) Luceño & Alves	graminoid	.	Cyperaceae
Carex phalaroides subsp*. phalaroides* Kunth	graminoid	.	Cyperaceae
Carex sororia Kunth	graminoid	.	Cyperaceae
Carex sp. 1	graminoid	.	Cyperaceae
Centella asiatica Urb.	herb	.	Apiaceae
Cerastium commersonianum DC.	herb	.	Caryophyllaceae
Cerastium dicrotrichum Fenzl ex Rohrb.	herb	.	Caryophyllaceae
Cerastium rivulare Cambess.	herb	.	Caryophyllaceae
Chaptalia exscapa (Pers.) Baker	herb	.	Asteraceae
Chaptalia graminifolia (Dusén ex Malme) Cabrera	herb	.	Asteraceae
Chaptalia mandonii (Schultz-Bip.) Burkart	herb	.	Asteraceae
Chaptalia nutans (L.) Polak	herb	.	Asteraceae
Chaptalia runcinata Kunth	herb	.	Asteraceae
Chascolytrum lamarckianum (Nees) Matthei	graminoid	.	Poaceae
Chascolytrum poomorphum (J. Presl.) Essi, Longhi-Wagner & Souza-Chies	graminoid	.	Poaceae
Chascolytrum rufum J. Presl	graminoid	.	Poaceae
Chascolytrum sp.	graminoid	.	Poaceae
Chascolytrum subaristatum (Lam.) Desv.	graminoid	.	Poaceae
Chascolytrum uniolae (Nees) Essi, Longhi-Wagner & Souza-Chies	graminoid	.	Poaceae
Chenopodium haumanii Ulbr.	herb	.	Amaranthaceae
Chevreulia acuminata Less.	herb	.	Asteraceae
Chevreulia revoluta A.A. Schneid. & Trevis.	herb	.	Asteraceae
Chevreulia sarmentosa (Pers.) Blake	herb	.	Asteraceae
Chromolaena ascendens (Sch. Bip. ex Baker) R.M. King & H. Rob.	herb	.	Asteraceae

Chromolaena squarrulosa (Hook. & Arn.) R.M. King & H. Rob.	shrub	.	Asteraceae
Chrysolaena cognata (Less.) Dematt.	herb	.	Asteraceae
Chrysolaena flexuosa (Sims) H.Rob.	herb	.	Asteraceae
Chrysolaena lithospermifolia (Hieron.) H. Rob.	herb	.	Asteraceae
Cirsium vulgare (Savi) Ten.	herb	x	Asteraceae
Clethra sp.	tree	.	Clethraceae
Coccocypselum cordifolium Nees & Mart.	herb	.	Rubiaceae
Coleostephus myconis (L.) Cass.	herb	.	Asteraceae
Convolvulus crenatifolius Ruiz & Pav.	herb	.	Convolvulaceae
Conyza blakei (Cabrera) Cabrera	herb	.	Asteraceae
Conyza bonariensis (L.) Cronquist	herb	.	Asteraceae
Conyza floribunda Kunth	herb	.	Asteraceae
*Conyza primulifoli*a (Lam.) Cuatrec. & Lourteig	herb	.	Asteraceae
Conyza sp. 1	herb	.	Asteraceae
Conyza sp. 2	herb	.	Asteraceae
Crepis capillaris (L.) Wallr.	herb	x	Asteraceae
Criscia stricta (Spreng.) Katinas	herb	.	Asteraceae
Crotalaria hilariana Benth.	herb	.	Fabaceae
Cunila galioides Benth.	herb	.	Lamiaceae
Cuphea carthagenensis J.F. Macbr.	herb	.	Lythraceae
Cuphea glutinosa Cham. & Schltdl.	herb	.	Lythraceae
Cuphea lindmaniana Koehne ex Bacigalupi	herb	.	Lythraceae
Cuphea sp.	herb	.	Lythraceae
Cyclopogon sp. 1	herb	.	Orchidaceae
Cyclospermum leptophyllum (Pers.) Sprague ex Britton & P. Wilson	herb	.	Apiaceae
Cypella cf. fucata Ravenna	herb	.	Iridaceae
Cyperaceae 1	graminoid	.	Cyperaceae
Cyperus aggregatus (Willd) Endl.	graminoid	.	Cyperaceae
Cyperus esculentus L.	graminoid	x	Cyperaceae
Cyperus hermaphroditus (Jacq.) Standl.	graminoid	.	Cyperaceae
Cyperus reflexus Vahl	graminoid	.	Cyperaceae
Cyperus rigens J. Presl & C. Presl	graminoid	.	Cyperaceae
Cyperus sp. 1	graminoid	.	Cyperaceae
Cyperus sp. 2	graminoid	.	Cyperaceae
Cyperus sp. 3	graminoid	.	Cyperaceae
Danthonia cirrata Hack. & Arechav.	graminoid	.	Poaceae
Danthonia montana Döll	graminoid	.	Poaceae
Danthonia montevidensis Hack. & Arechav.	graminoid	.	Poaceae
Danthonia secundiflora subsp. secundiflora J. Presl	graminoid	.	Poaceae
Danthonia sp.	graminoid	.	Poaceae
Deparia petersenii (Kunze) M. Kato	fern	.	Athyriaceae
Desmanthus tatuyensis Hoehne	herb	.	Fabaceae
Desmodium adscendens (Sw.) DC.	herb	.	Fabaceae

Desmodium affine Schltdl.	herb	.	Fabaceae
Desmodium incanum DC.	herb	.	Fabaceae
Desmodium triarticulatum Malme	herb	.	Fabaceae
Desmodium uncinatum (Jacq.) DC.	herb	.	Fabaceae
Dichanthelium sabulorum (Lam.) Gould & C.A. Clark	graminoid	.	Poaceae
Dichondra macrocalyx Meisn.	herb	.	Convolvulaceae
Dichondra sericea Swartz	herb	.	Convolvulaceae
Digitaria ciliaris (Retz.) Koeler	graminoid	x	Poaceae
Digitaria eriostachya Mez	graminoid	.	Poaceae
Drosera brevifolia Pursh	herb	.	Droseraceae
Eleocharis squamigera Svenson	graminoid	.	Cyperaceae
Eleocharis viridans Kük.	graminoid	.	Cyperaceae
Elephantopus mollis Kunth	herb	.	Asteraceae
Eleusine tristachya (Lam.) Lam.	graminoid	.	Poaceae
Eragrostis airoides Nees	graminoid	.	Poaceae
Eragrostis cataclasta Nicora	graminoid	.	Poaceae
Eragrostis lugens Nees	graminoid	.	Poaceae
Eragrostis neesii Trin.	graminoid	.	Poaceae
Eragrostis polytricha Nees	graminoid	.	Poaceae
Eragrostis sp. 1	graminoid	.	Poaceae
Erechtites hieraciifolius (L.) Raf. ex DC.	herb	.	Asteraceae
Erechtites valerianifolius (Link ex Spreng.) DC.	herb	.	Asteraceae
Eriochrysis villosa Swallen	graminoid	.	Poaceae
Eriosema campestre Benth.	herb	.	Fabaceae
Eriosema campestre var. macrophyllum (Grear) Fortunato	herb	.	Fabaceae
Eriosorus myriophyllus (Sw.) Copel.	fern	.	Pteridaceae
Eryngium ciliatum Cham. & Schlcht.	herb	.	Apiaceae
Eryngium ebracteatum Lam.	herb	.	Apiaceae
Eryngium horridum Malme	herb	.	Apiaceae
Eryngium sanguisorba Cham. & Schltdl.	herb	.	Apiaceae
Eupatorium betonicaeforme (DC.) Baker	herb	.	Asteraceae
Eupatorium serrulatum DC.	herb	.	Asteraceae
Euphorbia hirtella Boiss.	herb	.	Euphorbiaceae
Euphorbia peperomioides Boiss.	herb	.	Euphorbiaceae
Euphorbia stenophylla (Klotzsch & Garcke) Boiss.	herb	.	Euphorbiaceae
Eustachys uliginosa (Hack.) Herter	graminoid	.	Poaceae
Evolvulus sericeus Swartz	herb	.	Convolvulaceae
Facelis retusa (Lam.) Schultz-Bip.	herb	.	Asteraceae
Festuca ulochaeta Nees ex Steud.	graminoid	.	Poaceae
Galactia gracillima Benth.	herb	.	Fabaceae
Galactia marginalis Benth.	herb	.	Fabaceae
Galactia neesii DC.	herb	.	Fabaceae
Galinsoga quadriradiata Ruíz & Pav.	herb	.	Asteraceae
Galium humile Cham. & Schltdl.	herb	.	Rubiaceae

Galium hypocarpium (L.) Endl. ex Griseb.	herb	.	Rubiaceae
Galium noxium (A. St.-Hil.) Dempster	herb	.	Rubiaceae
Galium uruguayense Bacigalupo	herb	.	Rubiaceae
Gamochaeta americana (Mill.) Weddell	herb	.	Asteraceae
Gamochaeta coarctata (Willd.) Kerguélen	herb	.	Asteraceae
Gamochaeta falcata (Lam.) Cabrera	herb	.	Asteraceae
Gamochaeta sp.	herb	.	Asteraceae
Gamochaeta subfalcata (Cabrera) Cabrera	herb	.	Asteraceae
Gaylussacia angustifolia Cham.	shrub	.	Ericaceae
Geranium albicans A. St.-Hil.	herb	.	Geraniaceae
Geranium sp.	herb	.	Geraniaceae
Glandularia catharinae (Moldenke) N. O'Leary & P. Peralta	herb	.	Verbenaceae
Glandularia jordanensis (Moldenke) N. O'Leary & P. Peralta	herb	.	Verbenaceae
Glandularia lobata (Vell.) P. Peralta & Thode	herb	.	Verbenaceae
Glandularia marrubioides (Cham.) Tronc.	herb	.	Verbenaceae
Glandularia peruviana (L.) Small	herb	.	Verbenaceae
Glandularia sp.	herb	.	Verbenaceae
Glandularia thymoides (Cham.) N. O'Leary	herb	.	Verbenaceae
Glechon ciliata Benth.	herb	.	Lamiaceae
Grazielia gaudichaudeana (DC.) R.M. King & H. Rob.	herb	.	Asteraceae
Grazielia nummularia (Hook. & Arn.) R.M. King & H. Rob.	shrub	.	Asteraceae
Gymnopogon burchellii (Munro ex Döll) Ekman	graminoid	.	Poaceae
Gymnopogon grandiflorus Roseng., B.R. Arrill. & Izag.	graminoid	.	Poaceae
Habenaria parviflora Lindl.	herb	.	Orchidaceae
Habenaria repens Nutt.	herb	.	Orchidaceae
Halimium brasiliense (Lam.) Grosser	herb	.	Cistaceae
Herbertia lahue (Molina) Goldblatt	herb	.	Iridaceae
Herbertia sp.	herb	.	Iridaceae
Holcus lanatus L.	graminoid	x	Poaceae
Holocheilus brasiliensis (L.) Cabrera	herb	.	Asteraceae
Hybanthus parviflorus (Mutis ex L. f.) Baill.	herb	.	Violaceae
Hydrocotyle exigua Malme	herb	.	Araliaceae
Hypericum carinatum Griseb.	herb	.	Hypericaceae
Hypericum cordatum (Vell. Conc.) *subsp. cordatum*	herb	.	Hypericaceae
Hypericum cordatum (Vell.) N. Robson	herb	.	Hypericaceae
Hypochaeris chilensis (Kunth) Britton	herb	.	Asteraceae
Hypochaeris lutea (Vell.) Britton	herb	.	Asteraceae
Hypochaeris megapotamica Cabrera	herb	.	Asteraceae
Hypochaeris radicata L.	herb	x	Asteraceae
Hypochaeris sp.	herb	.	Asteraceae
Hypochaeris tropicalis Cabrera	herb	.	Asteraceae
Hypoxis decumbens L.	herb	.	Hypoxidaceae
Hyptis sp.	herb	.	Lamiaceae

Hyptis stricta Benth.	herb	.	Lamiaceae
Iridaceae 1	herb	.	Iridaceae
Jaegeria hirta (Lag.) Less.	herb	.	Asteraceae
Juncus capillaceus Lam.	graminoid	.	Juncaceae
Juncus sp.	graminoid	.	Juncaceae
Juncus tenuis Willd.	graminoid	.	Juncaceae
Krapovickasia macrodon (DC.) Fryxell	herb	.	Malvaceae
Kyllinga brevifolia Rottb.	graminoid	.	Cyperaceae
Kyllinga odorata Vahl	graminoid	.	Cyperaceae
Kyllinga pumila Michx.	graminoid	.	Cyperaceae
Kyllinga sp.	graminoid	.	Cyperaceae
Kyllinga vaginata Lam.	graminoid	.	Cyperaceae
Lepidium aletes J. F. Macbr.	herb	.	Brassicaceae
Lessingianthus hypochaeris (DC.) H. Rob.	herb	.	Asteraceae
Lessingianthus sellowii (Less.) H. Rob.	herb	.	Asteraceae
Linum erigeroides A. St.-Hil.	herb	.	Linaceae
Lobelia camporum Pohl	herb	.	Campanulaceae
Lobelia hederacea Cham.	herb	.	Campanulaceae
Lolium multiflorum Lam.	graminoid	x	Poaceae
Lotus corniculatus L.	herb	x	Fabaceae
Lucilia linearifolia Baker	herb	.	Asteraceae
Lucilia nitens Less.	herb	.	Asteraceae
Lupinus gibertianus C.P.Sm.	herb	.	Fabaceae
Luzula ulei Buchenau	graminoid	.	Juncaceae
Lycopodium clavatum L.	fern	.	Lycopodiaceae
Lysimachia parvula	herb	.	Primulaceae
Macroptilium prostratum (Benth.) Urb.	herb	.	Fabaceae
Mecardonia procumbens (Mill.) Small	herb	.	Plantaginaceae
Mecardonia procumbens var. tenella (Cham. & Schltdl.) V.C. Souza	herb	.	Plantaginaceae
Melastomataceae 1	herb	.	Melastomataceae
*Miconia hyemalis*A. St.-Hil. & Naudin	shrub	.	Melastomataceae
Mikania decumbens Malme	shrub	.	Asteraceae
Mimosa dutrae var. dutrae Malme	herb	.	Fabaceae
Mimosa myriophylla Bong. ex Benth.	herb	.	Fabaceae
Mnesithea selloana (Hack.) de Koning & Sosef	graminoid	.	Poaceae
Moritzia dasyantha Frenzen.	herb	.	Boraginaceae
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	tree	.	Primulaceae
Myrsine sp.	tree	.	Primulaceae
Myrtaceae 1	shrub	.	Myrtaceae
Nassella juergensii (Hack.) Barkworth	graminoid	.	Poaceae
Nassella megapotamia (Spreng. ex Trin.) Barkworth	graminoid	.	Poaceae
Nassella mucronata (Kunth) R.W. Pohl	graminoid	.	Poaceae
Nassella planaltina (A. Zanin & Longhi-Wagner) Peñail.	graminoid	.	Poaceae
Nassella sp.	graminoid	.	Poaceae

Nassella tenuiculmis (Hack.) Peñail.	graminoid	.	Poaceae
Nassella vallsii (A. Zanin & Longhi-Wagner) Peñail.	graminoid	.	Poaceae
Nierembergia sp. 1	herb	.	Solanaceae
Nothoscordum bonariense (Pers.) Beauverd	herb	.	Amaryllidaceae
Nothoscordum gracile (Aiton) Stearn	herb	.	Amaryllidaceae
Nothoscordum montevidense Beauverd	herb	.	Amaryllidaceae
Noticastrum decumbens (Baker) Cuatrec.	herb	.	Asteraceae
Ophioglossum sp.	herb	.	Ophioglossaceae
Orchidaceae 1	herb	.	Orchidaceae
Orchidaceae 2	herb	.	Orchidaceae
Orthopappus angustifolius (Sw.) Gleason	herb	.	Asteraceae
Oxalis bipartita A. St.-Hil.	herb	.	Oxalidaceae
Oxalis brasiliensis Lodd.	herb	.	Oxalidaceae
Oxalis conorrhiza Jacq.	herb	.	Oxalidaceae
Oxalis eriocarpa DC.	herb	.	Oxalidaceae
Oxalis lasiopetala Zucc.	herb	.	Oxalidaceae
Oxalis sp.	herb	.	Oxalidaceae
Oxalis tenerrima Kunth	herb	.	Oxalidaceae
Pamphalea sp.	herb	.	Asteraceae
Panicum superatum Hack.	graminoid	.	Poaceae
Paronychia camphorosmoides Cambess.	herb	.	Caryophyllaceae
Paronychia chilensis DC.	herb	.	Caryophyllaceae
Paspalum compressifolium Swallen	graminoid	.	Poaceae
Paspalum dilatatum Poir.	graminoid	.	Poaceae
Paspalum maculosum Trin.	graminoid	.	Poaceae
Paspalum notatum Flüggé	graminoid	.	Poaceae
Paspalum pauciciliatum (Parodi) Herter	graminoid	.	Poaceae
Paspalum plicatulum Michx.	graminoid	.	Poaceae
Paspalum polyphyllum Nees ex Trin.	graminoid	.	Poaceae
Paspalum pumilum Nees	graminoid	.	Poaceae
Paspalum sp. 1	graminoid	.	Poaceae
Paspalum umbrosum Trin.	graminoid	.	Poaceae
Passiflora caerulea L.	vine	.	Passifloraceae
Perezia squarrosa (Vahl) Less.	herb	.	Asteraceae
Petunia altiplana T. Ando & Hashim.	herb	.	Solanaceae
Pfaffia tuberosa (Sprengel) Hicken	herb	.	Amaranthaceae
Phytolacca thyrsiflora Fenzl ex J.A. Schmidt	herb	.	Phytolaccaceae
Pinus sp.	tree	x	Pinaceae
Piptochaetium alpinum L.B. Sm.	graminoid	.	Poaceae
Piptochaetium montevidense (Spreng.) Parodi	graminoid	.	Poaceae
Piptochaetium sp. 1	graminoid	.	Poaceae
Plantago australis subsp. australis Lam.	herb	.	Plantaginaceae
Plantago australis subsp. hirtella (Kunth) Rahn	herb	.	Plantaginaceae
Plantago lanceolata L.	herb	x	Plantaginaceae

Plantago major L.	herb	x	Plantaginaceae
Plantago sp.	herb	.	Plantaginaceae
Plantago tomentosa Lam.	herb	.	Plantaginaceae
Plantago turficola Rahn	herb	.	Plantaginaceae
Pleurostachys stricta Kunth	graminoid	.	Cyperaceae
Poa annua L.	graminoid	x	Poaceae
Poaceae 1	graminoid	.	Poaceae
Polygala altomontana Lüdtke, Boldrini & Miotto	herb	.	Polygalaceae
Polygala brasiliensis L.	herb	.	Polygalaceae
Polygala extraaxillaris Chodat	herb	.	Polygalaceae
Polygala linoides Poir.	herb	.	Polygalaceae
Polygala pulchella A. St.-Hil & Moq.	herb	.	Polygalaceae
Polygala pumila Norlind	herb	.	Polygalaceae
Polygala sabulosa A.W. Benn.	herb	.	Polygalaceae
Polygala subverticillata Chodat	herb	.	Polygalaceae
Polygonum hydropiperoides Michx.	herb	.	Polygonaceae
Polygonum punctatum Elliott	herb	.	Polygonaceae
Portulaca oleracea L.	herb	x	Portulacaceae
Praxelis pauciflora(Kunth) R.M. King & H. Rob.	herb	.	Asteraceae
Prunella vulgaris L.	herb	x	Lamiaceae
Pseudognaphalium cheiranthifolium (Lam.) Hill	herb	.	Asteraceae
Pteridium esculentum (G.Forst.) Cockayne	fern	.	Dennstaedtiaceae
Pterocaulon sp.	herb	.	Asteraceae
Raphanus raphanistrum L.	herb	x	Brassicaceae
Relbunium valantioides (Cham. & Schltdl.) K. Schum.	herb	.	Rubiaceae
Rhynchanthera brachyrhyncha Cham.	herb	.	Melastomataceae
Rhynchosia corylifolia Mart. ex Benth.	herb	.	Fabaceae
Rhynchospora barrosiana Guagl.	graminoid	.	Cyperaceae
Rhynchospora crinigera Boeck.	graminoid	.	Cyperaceae
Rhynchospora flexuosa C.B. Clarke	graminoid	.	Cyperaceae
Rhynchospora gollmeri Boeck.	graminoid	.	Cyperaceae
Rhynchospora setigera Griseb.	graminoid	.	Cyperaceae
Richardia humistrata (Cham. & Schltdl.) Steud.	herb	.	Rubiaceae
Rubiaceae 1	herb	.	Rubiaceae
Ruellia sp.	herb	.	Acanthaceae
Rumex acetosella L.	herb	x	Polygonaceae
Rumex obtusifolius L.	herb	x	Polygonaceae
Rumohra adiantiformis (G. Forst.) Ching	fern	.	Dryopteridaceae
Salvia brevipes Benth.	herb	.	Lamiaceae
Salvia procurrens Benth.	herb	.	Lamiaceae
Schizachyrium sp.	graminoid	.	Poaceae
Schizachyrium tenerum Nees	graminoid	.	Poaceae
Scleria ciliata Michx.	graminoid	.	Cyperaceae
Scleria distans Poir.	graminoid	.	Cyperaceae

Scleria sellowiana Kunth	graminoid	.	Cyperaceae
Selaginella tenuissima Fée	fern	.	Selaginellaceae
Senecio brasiliensis (Spreng) Less. *var. brasiliensis*	shrub	.	Asteraceae
Senecio conyzifolius Baker	herb	.	Asteraceae
Senecio sp.	herb	.	Asteraceae
Setaria parviflora (Poir.) Kerguélen	graminoid	.	Poaceae
Setaria vaginata Spreng.	graminoid	.	Poaceae
Sida rhombifolia L.	herb	.	Malvaceae
Sida sp. 1	herb	.	Malvaceae
Silene gallica L.	herb	x	Caryophyllaceae
Sisyrinchium megapotamicum Malme	herb	.	Iridaceae
Sisyrinchium micranthum Cav.	herb	.	Iridaceae
Sisyrinchium palmifolium L.	herb	.	Iridaceae
Sisyrinchium sellowianum Klatt	herb	.	Iridaceae
Sisyrinchium sp.	herb	.	Iridaceae
Sisyrinchium vaginatum Spreng.	herb	.	Iridaceae
Skeptrostachys cf. *balanophorostachya* (Rchb. f. ex Warm.) Garay	herb	.	Orchidaceae
Solanaceae 1	herb	.	Solanaceae
Solanum aculeatissimum Jacq.	herb	.	Solanaceae
Solanum nigrescens M. Martens & Galeotti	herb	.	Solanaceae
Solanum pseudoquina A. St.-Hil.	tree	.	Solanaceae
Solanum sp.	herb	.	Solanaceae
Solanum variabile Mart.	tree	.	Solanaceae
Solidago chilensis Meyen	herb	.	Asteraceae
Soliva sessilis Ruiz & Pav.	herb	.	Asteraceae
Sonchus oleraceus L.	herb	x	Asteraceae
Sorghastrum pellitum (Hack.) Parodi	graminoid	.	Poaceae
Sorghastrum sp. 1	graminoid	.	Poaceae
Spergula arvensis L.	herb	x	Caryophyllaceae
Spergularia grandis (Pers.) Cambess.	herb	.	Caryophyllaceae
Spermacoce sp. 1	herb	.	Rubiaceae
Sporobolus camporum Swallen	graminoid	.	Poaceae
Sporobolus indicus (L.) R. Br.	graminoid	.	Poaceae
Stachys arvensis L.	herb	x	Lamiaceae
Steinchisma decipiens (Nees ex Trin.) W.V. Br.	graminoid	.	Poaceae
Steinchisma hians (Elliott) Nash	graminoid	.	Poaceae
Stenachaenium adenanthum Krasch.	herb	.	Asteraceae
Stenachaenium megapotamicum (Spreng.) Baker	herb	.	Asteraceae
Stenocephalum megapotamicum (Spreng.) Sch. Bip.	herb	.	Asteraceae
Stevia involucrata Sch. Bip. ex Baker	herb	.	Asteraceae
Stevia lundiana DC.	herb	.	Asteraceae
Stylosanthes leiocarpa Vogel	herb	.	Fabaceae
Stylosanthes montevidensis Vogel	herb	.	Fabaceae
Symphyotrichum squamatum (Spreng.) G.L. Nesom	herb	.	Asteraceae

Taraxacum officinale Weber ex F.H. Wigg.	herb	x	Asteraceae
Tephrosia adunca Benth.	herb	.	Fabaceae
Thelypteris interrupta (Willd.) K. Iwats.	fern	.	Thelypteridaceae
Tibouchina clinopodifolia Cogn.	herb	.	Melastomataceae
Tibouchina debilis Cogn.	herb	.	Melastomataceae
Tibouchina gracilis Cogn.	herb	.	Melastomataceae
Tibouchina rupestris Cogn.	herb	.	Melastomataceae
Tibouchina sp.	herb	.	Melastomataceae
Trachypogon montufarii (Knuth) Nees	graminoid	.	Poaceae
Trachypogon spicatus (L. f.) Kuntze	graminoid	.	Poaceae
Tradescantia sp. 1	herb	.	Commelinaceae
Tradescantia sp. 2	herb	.	Commelinaceae
Trichocline catharinensis Cabrera	herb	.	Asteraceae
Trifolium campestre Schreb.	herb	x	Fabaceae
Trifolium pratense L.	herb	x	Fabaceae
Trifolium repens L.	herb	x	Fabaceae
Trifolium riograndense Burkart	herb	.	Fabaceae
Trifolium sp.	herb	.	Fabaceae
Ulex europaeus L.	shrub	x	Fabaceae
Verbena bonariensis L.	herb	.	Verbenaceae
Verbena filicaulis Schauer	herb	.	Verbenaceae
Verbena hirta Spreng.	herb	.	Verbenaceae
Verbena montevidensis Spreng.	shrub	.	Verbenaceae
Vernonia hypochlora Malme	herb	.	Asteraceae
Veronica arvensis L.	herb	x	Scrophulariaceae
Veronica persica Poir.	herb	x	Scrophulariaceae
Vicia angustifolia L. ex Reichard	herb	x	Fabaceae
Vigna peduncularis (Kunth) Fawc. & Rendle	herb	.	Fabaceae
Viguiera immarginata (DC.) Herter	shrub	.	Asteraceae
Vittetia orbiculata (DC.) R.M. King & H. Rob.	shrub	.	Asteraceae
Vulpia australis (Steud.) Blom	graminoid	.	Poaceae
Vulpia bromoides (L.) Gray	graminoid	.	Poaceae
Vulpia myuros (L.) C.C. Gmel.	graminoid	.	Poaceae
Vulpia sp.	graminoid	.	Poaceae
Vulpia sp. 1	graminoid	.	Poaceae
Vulpia sp. 2	graminoid	.	Poaceae
Wahlenbergia linarioides (Lam.) A.DC.	herb	.	Campanulaceae
Zephyranthes sp.	herb	.	Amaryllidaceae
Zornia cryptantha Arechav.	herb	.	Fabaceae
Zornia pardina Mohlenbr.	herb	.	Fabaceae
Zornia ramboiana Mohlenbr.	herb	.	Fabaceae
Zornia sp.	herb	.	Fabaceae
Zornia sp. 1	herb	.	Fabaceae
Zygostigma australe Griseb.	herb	.	Gentianaceae

A4 Chapter 3

List of indicator species for five different land-use types.

Indicator species analysis resulted in a total of 133 species with significant indicator values (IV) of which only those with IV>20 were considered. A species could be indicator for maximal two land-use types. If a species was present in more than two land-use types, a minimum difference of 1% in mean cover to the next land use was required. Species that had IVs >20 for two land-use types were considered a shared indicator species, others were considered exclusive indicators; * indicates non-native origin. PG-M = Permanent grassland with management of medium intensity, PG-L = Permanent grassland with management of low intensity, PG-H = Permanent grassland with management of high intensity, SG-A = Secondary grassland after agricultural use, SG-P = Secondary grassland after silvicultural use.

	Land-use type 1	IV 1	Land-use type 2	IV 2	Mean cover				
					PG-M	PG-L	PG-H	SG-A	SG-P
Exclusive indicators									
Stenachaenium adenanthum	PG-M	35.3			0.04	0.00	0.00	0.00	0.00
Grazielia nummularia	PG-L	30.3			0.00	1.22	0.00	0.00	0.05
*Avena sativa**	PG-H	21.3			0.00	0.00	0.07	0.03	0.00
Paspalum dilatatum	PG-H	78.8			0.03	0.00	9.27	2.46	0.00
*Prunella vulgaris**	PG-H	40.0			0.00	0.00	0.12	0.00	0.00
Sporobolus indicus	PG-H	85.4			0.00	0.02	1.69	0.07	0.00
*Raphanus raphanistrum**	SG-A	31.6			0.00	0.00	0.00	0.12	0.00
*Rumex obtusifolius**	SG-A	23.9			0.00	0.00	0.06	0.18	0.00
Soliva sessilis	SG-A	45.8			0.01	0.00	0.05	1.64	0.00
Baccharis uncinella	SG-P	59.8			0.00	0.78	0.00	0.00	6.84
Dichanthelium sabulorum	SG-P	73.9			0.50	0.68	0.31	0.31	6.83
Shared indicators									
Galactia gracillima	PG-M	37.7	PG-L	8	0.06	0.03	0.00	0.00	0.00
Schizachyrium tenerum	PG-M	56.0	PG-L	43	9.27	8.10	0.15	0.01	0.00
Trichocline catharinensis	PG-M	54.0	PG-L	14	0.27	0.14	0.00	0.00	0.00
Axonopus siccus	PG-L	59.0	PG-M	25	1.50	4.43	0.01	0.00	0.00
Lucilia linearifolia	PG-L	34.0	PG-M	22	0.06	0.11	0.00	0.00	0.00
*Crepis capillaris**	PG-H	53.0	SG-A	23	0.00	0.00	1.20	0.61	0.00
*Holcus lanatus**	PG-H	37.7	SG-A	30	0.03	0.01	4.83	6.52	0.13
*Lolium multiflorum**	PG-H	53.0	SG-A	30	0.00	0.00	4.04	2.82	0.00
*Trifolium pratense**	PG-H	30.3	SG-A	30	0.02	0.00	1.98	2.56	0.00
*Trifolium repens**	SG-A	66.2	PG-H	21	0.05	0.02	6.92	25.59	0.00
Senecio brasiliensis	SG-P	42.8	SG-A	22	0.02	0.01	0.13	1.39	1.78

A5 Chapter 3

Pairwise comparison of true diversity at the specified values of *q* for five land-use types

Pairwise comparison is based on permutation t-tests and correction of *p*-values for multiple comparisons. Values for q correspond to the following measures of diversity: q=0: Species richness, *q*=1: exponential Shannon index, *q*=2: inverse Simpson index, *q*->∞: Berger-Parker dominance index. PG-M = Permanent grassland with management of medium intensity, PG-L = Permanent grassland with management of low intensity, PG-H = Permanent grassland with management of high intensity, SG-A = Secondary grassland after agricultural use, SG-P = Secondary grassland after plantation use.

		PG-L		**PG-H**		**SG-A**		**SG-P**	
		t-value	*p*-value	t-value	*p*-value	t-value	*p*-value	t-value	*p*-value
PG-M	*q* = 0	3.99	**	3.46	**	6.20	***	5.96	***
	q = 1	4.36	**	4.24	**	6.42	***	5.95	***
	q = 2	4.61	***	4.31	***	6.54	***	6.65	***
	q = 8	4.89	***	3.58	**	6.71	***	8.38	***
PG-L	*q* = 0			-0.54	n.s.	2.15	n.s.	1.68	n.s.
	q = 1			-0.61	n.s.	1.95	n.s.	1.47	n.s.
	q = 2			-0.87	n.s.	1.84	n.s.	1.87	n.s.
	q = 8			-1.58	n.s.	1.76	n.s.	3.16	**
PG-H	*q* = 0					2.69	*	2.26	n.s.
	q = 1					2.78	*	2.25	n.s.
	q = 2					2.95	*	3.01	*
	q = 8					3.47	**	5.08	***
SG-A	*q* = 0							-0.57	n.s.
	q = 1							-0.50	n.s.
	q = 2							-0.01	n.s.
	q = 8							1.32	n.s.

A6 Chapter 3

Kruskal-Wallis tests for structural parameters and soil chemical properties.

Abbreviation for soil chemical parameters: Clay fraction (Clay), pH in water, available phosphorus (P), available potassium (K, both method Mehlich-1), organic matter (OrgMat), exchangeable aluminium (Al) , calcium (Ca) and magnesium (Mg), all three in KCl, potential acidity (Al+H), potential cation exchange capacity(CecPotat pH 7.0), potential Al(AlPot)and base(BsPot)saturation, and total nitrogen (N) Kjeldahl. * indicates that soil characteristics were also used for linear discriminant analysis (LDA). All values are given as mean ± SD. Different letters indicate significant differences (p ≤ 0.05). PG-M = Permanent grassland with management of medium intensity, PG-L = Permanent grassland with management of low intensity, PG-H = Permanent grassland with management of high intensity, SG-A = Secondary grassland after agricultural use, SG-P = Secondary grassland after silvicultura luse.

	PG-M	PG-L	PG-H	SG-A	SG-P	*p*-value
Structural parameters						
Total cover of vegetation	92.4 ± 4.5 [b]	92.7 ± 7.0 [b]	95.6 ± 3.3 [b]	90.7 ± 6.4 [b]	66.4 ± 20.6 [a]	<0.001
Bare soil	1.8 ± 1.6 [ab]	1.5 ± 3.0 [b]	1.0 ± 0.9 [b]	4.4 ± 5.0 [a]	4.3 ± 4.1 [a]	<0.01
Litter	3.2 ± 2.3 [b]	7.2 ± 6.8 [a]	3.2 ± 2.8 [b]	3.1 ± 2.3 [ab]	3.3 ± 2.5 [ab]	<0.05
Dead standing biomass	5.6 ± 6.2 [b]	22.4 ± 17.6 [a]	6.6 ± 6.3 [b]	4.4 ± 3.7 [b]	8.5 ± 9.1 [b]	<0.001
Vegetation height	11.2 ± 5.0 [b]	25.8 ± 15.8 [a]	13.9 ± 4.2 [ab]	12.2 ± 8.1 [b]	18.7 ± 10.4 [a]	<0.001
Cover shrubs	1.8 ± 1.2 [c]	7.5 ± 11.9 [ab]	1.2 ± 0.8 [c]	4.6 ± 8.3 [bc]	15.1 ± 11.2 [a]	<0.001
Cover forbs	5.6 ± 4.3 [c]	4.4 ± 3.2 [c]	18.8 ± 9.8 [ab]	46.6 ± 25.0 [a]	8.4 ± 7.1 [bc]	<0.001
Cover graminoids total	86.1 ± 7.3 [a]	85.1 ± 8.7 [a]	78 ± 7.8 [a]	43.5 ± 24.0 [b]	48.7 ± 18.6 [b]	<0.001
Cover tussocks	37.5 ± 21.3 [b]	63.1 ± 18.6 [a]	31.7 ± 17.3 [bc]	5.8 ± 5.8 [d]	15.4 ± 12.6 [cd]	<0.001
Soil chemical parameters						
Clay	27.7 ± 10.7 [a]	22.7 ± 11.9 [a]	29.3 ± 10.8 [a]	31.2 ± 12.1 [a]	32.4 ± 14.1 [a]	>0.05
OrgMat	9.4 ± 1.0 [ab]	9.5 ± 1.2 [a]	9.4 ± 0.8 [ab]	8.7 ± 1.1 [b]	8.9 ± 1.2 [ab]	<0.01
pH*	4.4 ± 0.4[b]	4.3 ± 0.3 [b]	4.8 ± 0.2 [a]	4.9 ± 0.4 [a]	4.0 ± 0.2 [c]	<0.001
P*	5.3 ± 2.0 [bc]	5.1 ± 2.6 [c]	11.5 ± 7.4 [ab]	15.8 ± 12.6 [a]	5.2 ± 1.5 [bc]	<0.001
K*	137.8 ± 61.8 [a]	117.1 ± 36.3 [a]	129.9 ± 32.1 [a]	124.8 ± 71.2 [a]	92.9 ± 25.0 [a]	0.03
Al	4.9 ± 1.8 [a]	6.1 ± 2.6 [a]	0.9 ± 0.5 [b]	1.2 ± 1.2 [b]	7.5 ± 3.0 [a]	<0.001
Ca	1.6 ± 1.2 [b]	0.9 ± 0.5 [c]	9.0 ± 2.1 [a]	7.7 ± 2.7 [a]	1.1 ± 0.7 [bc]	<0.001
Mg	1.1 ± 0.9 [b]	0.7 ± 0.3 [bc]	3.4 ± 1.4 [a]	4.4 ± 2.0 [a]	0.6 ± 0.2 [c]	<0.001
Al+H	28.5 ± 4.8 [b]	30.7 ± 7.1 [b]	12.8 ± 3.6 [c]	12.7 ± 5.6 [c]	36.9 ± 6.8 [a]	<0.001
CecPot	31.7 ± 3.4 [b]	32.6 ± 7.0 [b]	25.6 ± 4.6 [c]	25.2 ± 2.3 [c]	38.8 ± 6.5 [a]	<0.001
BsPot*	10.3 ± 8.3 [b]	6.1 ± 3.4 [bc]	50.0 ± 11.2 [a]	50.4 ± 19.6 [a]	5.1 ± 2.6 [c]	<0.001
AlPot	62.3 ± 18.4 [b]	75.0 ± 77.8 [a]	7.3 ± 4.7 [c]	11.5 ± 14.4 [c]	77.9 ± 10.0 [a]	<0.001
N*	0.38 ± 0.11 [b]	0.59 ± 0.22 [a]	0.42 ± 0.10 [ab]	0.32 ± 0.06 [b]	0.42 ± 0.19 [b]	<0.01

A7 Chapter 4

Full table of non-native species in the study grasslands in the highlands of S Brazil.

Species order follows ranking categories based on an application of the suggested simple framework. Ranking category 1, spreading; 2, establishing; 3, sporadic; subcategory a indicates intentional introduction and b unintentional introduction.

Species	Family	Origin	Ranking Category
Holcus lanatus L.	Poaceae	Europe	1a
Pinus ssp. (*P. elliottii* and *P. taeda*)	Pinaceae	North America	1a
Trifolium pratense L.	Fabaceae	Europe	1a
Trifolium repens L.	Fabaceae	Europe	1a
Avena sativa L.	Poaceae	Eurasia	2a
Lotus corniculatus L.	Fabaceae	Eurasia	2a
Ulex europaeus L.	Fabaceae	Europa	2a
Cirsium vulgare (Savi) Ten.	Asteraceae	Eurasia	2b
Crepis capillaris (L.) Wallr.	Asteraceae	Europe	2b
Hypochaeris radicata L.	Asteraceae	Europe	2b
Plantago lanceolata L.	Plantaginaceae	Europe	2b
Poa annua L.	Poaceae	Europe	2b
Rumex acetosella L.	Polygonaceae	Eurasia	2b
Rumex obtusifolius L.	Polygonaceae	Europe	2b
Silene gallica L.	Caryophyllaceae	Europe	2b
Taraxacum officinale Weber ex F.H. Wigg.	Asteraceae	Eurasia	2b
Veronica arvensis L.	Plantaginaceae	Europe	2b
Lolium multiflorum Lam.	Poaceae	Europe	3a
Raphanus raphanistrum L.	Brassicacea	Europe	3a
Prunella vulgaris L.	Lamiaceae	Europe	3b
Amaranthus lividus L.	Amaranthaceae	Europe	--
Anagallis arvensis L.	Myrsinaceae	Europe	--
Anthemis cotula L.	Asteraceae	Europe	--
Anthemis mixta L.	Asteraceae	Europe	--
Aphanes arvensis L.	Rosaceae	Europe	--
Briza minor L.	Poaceae	Eurasia	--
Carduus nutans L.	Asteraceae	Europe	--
Cyperus esculentus L.	Cyperaceae	North America	--
Digitaria ciliaris (Retz.) Koeler	Poaceae	Asia	--
Plantago major L.	Plantaginaceae	Europe	--
Portulaca oleracea L.	Portulacaceae	Asia	--
Sonchus oleraceus L.	Asteraceae	Europe	--
Spergula arvensis L.	Caryophyllaceae	Europe	--
Stachys arvensis L.	Lamiaceae	Europe	--
Trifolium campestre Schreb.	Fabaceae	Eurasia	--
*Veronica persica*Poir.	Plantaginaceae	Asia	--
Vicia angustifolia L. ex Reichard	Fabaceae	Eurasia	--

A8 Chapter 5

Measurements for aboveground phytomass and forage value analysis

Aboveground phytomass was sampled to compare the productivity of the different land-use types. On each site, 5 samples of 20 x 50 cm of aboveground phytomass were cut and separated into graminoids, forbs and shrubs. Samples were oven dried for 48 hours or until dry at 70°C before weighing. The samples of graminoids and forbs were joined hereafter and mixed to get one big sample of herbaceous phytomass of each site to be analyzed in the lab for crude protein (CP) and neutral detergent fiber (NDF), the two main components of forage quality. In order to provide sufficient forage quality, the value should be higher than 8% in the case of CP and lower than 70% in case of NDF (Ball et al. 2001). These values vary depending on the type of cattle that is supposed to be grazing the area. Furthermore the values are highly depending on the timing of sampling and the composition of species in the sample. A minimum amount of 500g phytomass was needed for the analyses, which is why the samples of six (4 SG-P and 2 SG-A) areas could not be considered in the analysis and the total number of sites was thus 74. Analyses were conducted by the Laboratório de Nutrição Animal of the Faculdade de Agronomia, Universidade Federal de Rio Grande do Sul, Porto Alegre.

All statistical analyses were conducted with RStudio 0.99.441 (RStudio Team 2015). To test the effect of land-use category on aboveground phytomass and forage value, linear mixed effects models were used with phytomass, CP and NDF as the dependent variable, a categorical land-use variable as explanatory variable and random effects for the site and year during which the pertaining sample was collected. If necessary, response variables were log-transformed to improve variance homogeneity and normality of errors. After fitting the linear mixed effects model, pairwise differences among land-use categories were tested using Tukey's Post-Hoc test.

Results

The total amount of aboveground herbaceous phytomass (forbs + grasses) was highest in PG-L (532 ±76g, mean ± SE) and lowest in SG-P (134 ± 19g). While grass phytomass was the dominant component for all permanent grasslands, SG-A had the largest proportions of forb phytomass. Regarding forage quality, both PG-L and PG-M had values that were neither for CP nor for NDF within the acceptable range. Both values were acceptable for SG-A and PG-H and SG-P met one value respectively. Due to differing grazing pressures of the different sites and timing of sampling, phytomass and forage quality may be biased indicators of primary productivity.

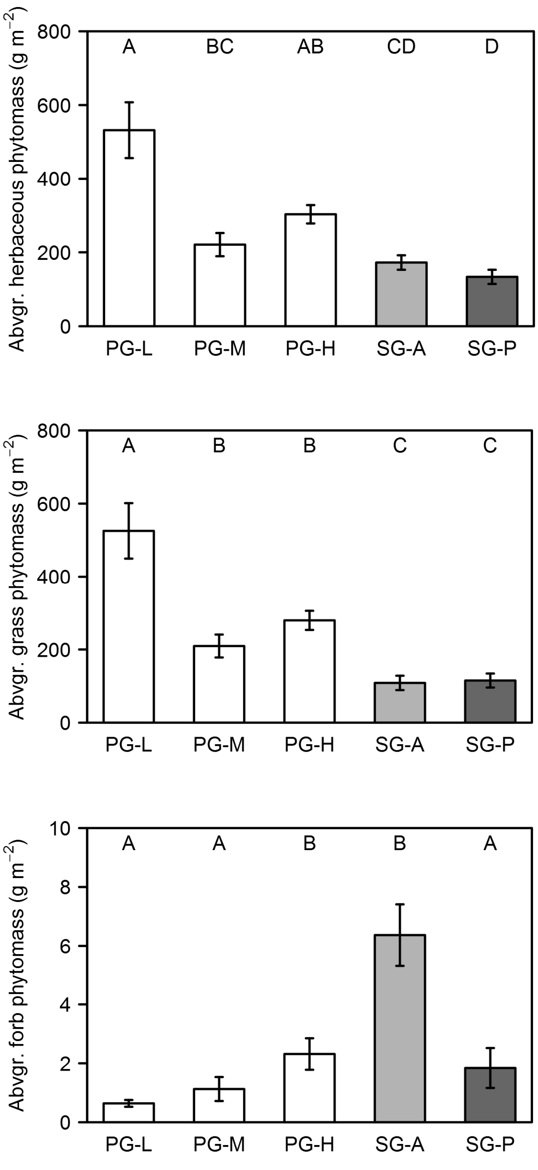


Figure A8.1 Differences in total aboveground phytomass (a), aboveground grass phytomass (b) and aboveground forb phytomass (c) in dependence of land-use types (PG-L: Permanent grassland with low-intensity management; PG-M: Permanent grassland with medium-intensity management; PG-H: Permanent grassland with high-intensity management; SG-A: Secondary grassland after agricultural use; SG-P: Secondary grassland after silvicultural use). Capital letters indicate significant differences.

Table A8.1 Linear mixed models on the effect of land-use categories (PG-L: Permanent grassland with low-intensity management; PG-M: Permanent grassland with medium-intensity management; PG-H: Permanent grassland with high-intensity management; SG-A: Secondary grassland after agricultural use; SG-P: Secondary grassland after silvicultural use) on aboveground phytomass and forage value parameters. All variables were log-transformed. Field campaign and site were treated as random effects.

	Land-use category
Aboveground grass phytomass	**$F_{4,74}$=27.40 *****
Aboveground forb phytomass	**$F_{4,74}$=20.20 *****
Aboveground herbaceous layer phytomass	**$F_{4,74}$=21.58 *****
CP	**$F_{4,68}$=29.51 *****
NDF	**$F_{4,68}$=20.58*****

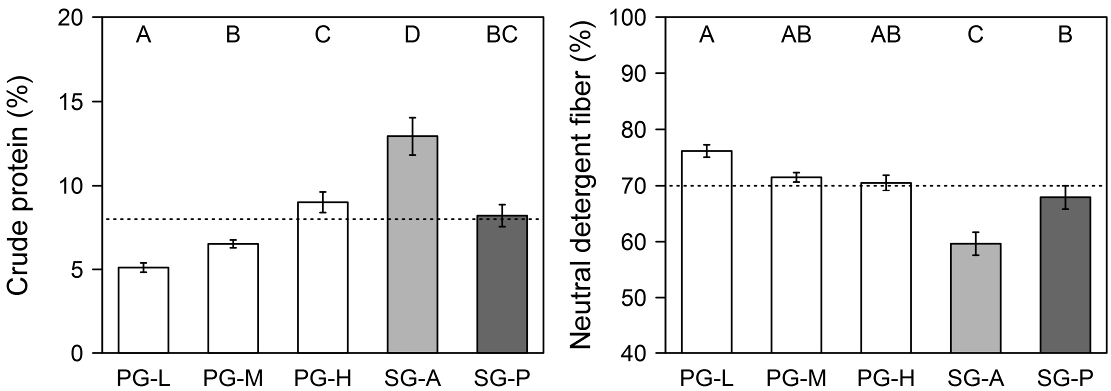


Figure A8.2 Crude protein (%) and neutral detergent fiber (%) by land-use category. Values for CP should exceed 8% and for NDF not exceed 70% to provide sufficient forage quality. Capital letters indicate significant differences.