Chapter 5
Woody Plant Invasions in Pampa Grasslands: A Biogeographical and Community Assembly Perspective

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5.1 Introduction

Grasslands provide a number of ecosystem services that have been essential to human well-being since pre-historical times (Gibson 2009). Yet they also represent the most endangered terrestrial biome due to conversion into agricultural systems (Sala 2001). The grassland biome covers 15 million km² (11 %) of the Earth's surface with non-woody vegetation, excluding deserts and savannas (Sala 2001). Natural grasslands encompass vast regions including the North American Great Plains, the Eurasian steppes of Russia, China and Mongolia, and the South American Pampas (Gibson 2009).

Temperate grasslands occur in areas with *c.* 250–1,200 mm of annual precipitation, being replaced by deserts and forests at lower and higher precipitation, respectively. With mean annual temperatures above *c.* 16 °C and 500–1,200 mm/year, grasslands give way to savannas and open woodlands (Whittaker 1975). Nevertheless, grasslands often occupy areas that are wet enough to support forests (Bond 2008). The existence of grassy—treeless—vegetation where climate would permit forests

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has long intrigued researchers (Christy 1892; Parodi 1942; Ellenberg 1962; Walter 1967). While climatic grassland/forest boundaries have been maintained for millennia, modern grasslands appear to be changing as a result of woody invasions (Bond 2008; Simberloff et al. 2010; Lamarque et al. 2011).

Woody plant encroachment reflects the synergistic influence of various drivers of global environmental change (Hobbs 2000). Land-use changes associated with agriculture and domestic grazing have caused the widespread loss or fragmentation of large areas of temperate grasslands (Sala 2001; Gibson 2009). These landscape-level modifications have often been followed by the introduction of exotic tree species, many of which became invasive of natural or seminatural grasslands (Richardson and Rejmánek 2011). In addition, anthropogenic changes in disturbance regimes created novel opportunities for woody species establishment within herbaceous vegetation (Hobbs and Huenneke 1992; Bond 2008). These changes may interact with altered precipitation patterns, affecting expansion rates of native or exotic tree species (Dukes and Mooney 1999; Sankaran et al. 2004). Successful invasions by exotic trees draw attention towards biogeographic and phylogenetic constraints that might have limited the presence of trees in the original grasslands (Ricklefs and Schluter 1993; Mack 2003). Hence, questions regarding the historical existence of treeless grasslands as well as present shifts in woody cover may be integrated within a common framework, by emphasising the role of multiple processes that control vegetation structure at different spatio-temporal scales.

In this chapter, we examine the ongoing process of tree invasion in South American Pampa grasslands. In doing so, we consider two broad phenomena, namely, the dynamics of native woody species across grassland/forest boundaries and the spread of exotic trees over heterogeneous habitat mosaics. We argue that the latter occurs primarily through "diffuse" ecotones created by anthropogenic landscape fragmentation. Overall, grassland invasion by either native or exotic tree species represents the assembly into a local community of a novel life form that managed to pass various ecological "filters" (Funk et al. 2008; Fig. 5.1). Our central thesis is that human activity facilitates woody species establishment in grasslands by altering assembly filters for either exotic or native tree taxa. We shall use the term "invasion" to denote the successful addition of a new species to a recipient system, regardless of whether it was introduced from other continents or expanded its range from an adjacent biogeographic zone (see Vermeij 2005).

We focus on the humid Pampas of Argentina, the largest portion of the Río de la Plata grasslands, which also comprise the Campos of Uruguay and southern Brazil (Soriano 1992). Woody invasions in the Campos have recently been assessed by others (De Patta Pillar et al. 2009). We begin by discussing grassland invasion by woody plants in the light of a hierarchical model of community assembly. Second, we introduce the main biogeographical features of the study region, before revisiting hypotheses for the absence of forests in the Pampas. We close the section with a consideration of multi-causal constraints to the presence of trees in pristine grassland. Third, we summarise empirical evidence from different scenarios of tree invasion in Pampa grasslands. We conclude by suggesting how facilitative interactions between exotic and native woody taxa could play a key role in accelerating a state shift towards a novel, woody-dominated ecosystem.
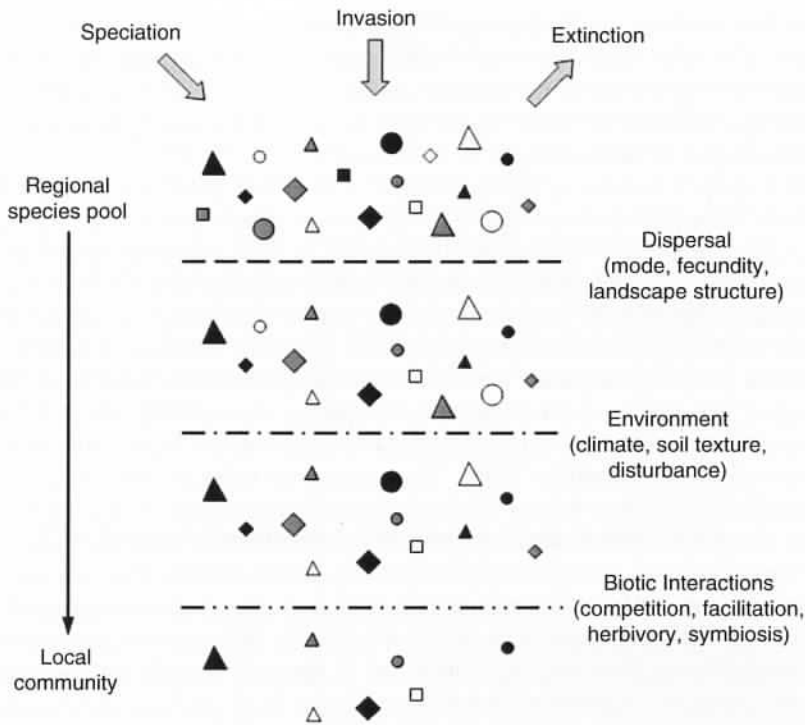
Fig. 5.1 Hierarchical model of community assembly. *Horizontal lines* represent ecological filters for species addition to a local grassland community. *Small symbols* denote herbaceous species; *large symbols* denote tree species, including native species of wet subtropical origin (*white*), native species from dry savannas (*grey*), and introduced exotic species (*black*)

5.2   Woody Invasions as Hierarchical Assembly Processes

The assembly of new species into a local community is hierarchically constrained by dispersal from the regional species pool and niche limitations created by habitat conditions and biotic interactions (Ricklefs and Schluter 1993; Funk et al. 2008; Myers and Harms 2009). Factors affecting the chances of successful species establishment can be seen as a series of ecological "filters" (Fig. 5.1). Only species in the regional pool having certain adaptive traits will be able to pass these filters (Keddy 1992; Funk et al. 2008; see also Theoharides and Dukes 2007). Assembly filters roughly correspond to processes operating at different spatio-temporal scales.

Species may be added to a regional pool as a result of speciation processes or by immigration from another region (Ricklefs and Schluter 1993). Biotic exchanges at large biogeographical scales are aided by human transport (Williamson 1996; Theoharides and Dukes 2007), which may act to enrich the phylogenetic background of a regional flora (Mack 2003). Exotic invasions are a manifestation of the re-shuffling of regional species pools caused by human activities on a global scale. In this context,

the absence of woody life forms in a grassy ecosystem may just reflect the evolutionary history of the flora, including major events deep in the regional past (Ricklefs and Schluter 1993; Mack 2003). It also suggests that native trees growing in nearby forest habitats may not have the "right" functional traits to establish successfully in a grassland environment (Bredenkamp et al. 2002; see Fig. 5.1).

For a species to occur at a given locality, it must first arrive via dispersal from available propagule sources (Fig. 5.1). The chance of seed arrival is a function of landscape configuration, including site isolation, as well as species fecundity and dispersal mode (anemochory, zoochory, etc.) of the focal species. The existence of appropriate vectors (e.g. frugivorous birds) can be critical for animal-dispersed species. Seed dispersers interact strongly with landscape structure in determining the spatial pattern of dispersal, both within and across biomes (Nores et al. 2005). Propagule "pressure" (i.e. the quantity and frequency of propagule arrival) has been indicated as a primary determinant of exotic invasions that is highly influenced by human activity (Williamson 1996). Low propagule pressure may increase the chances that an invading species will be eliminated by stochastic events (Simberloff 2009). Exotic tree species that were planted at several points within a region, produce large seed crops with a short age at maturity, and are readily dispersed by wind or animals (e.g. cattle, birds) may exhibit high invasion potential (Rejmánek and Richardson 1996; Lamarque et al. 2011). Conversely, native woody species found in grassland/forest ecotones might have yet to disperse in sufficient numbers to become established in grassland habitats.

Species lacking the functional traits to cope with local habitat conditions will fail to become established or to persist in the long term (Fig. 5.1). Therefore, successful invaders should be pre-adapted to abiotic conditions in the recipient system (Williamson 1996; Mack 2003). This involves the ability to tolerate various environmental stresses (e.g. frost, drought, waterlogging), which can be recurrent features of certain localities. For instance, soil aridity or low temperatures may limit the presence of trees in natural grasslands (Bredenkamp et al. 2002). Climate fluctuations may create resource opportunities for episodic seedling recruitment as observed for resident savanna trees (Sankaran et al. 2004). Natural disturbances may act to facilitate or prevent exotic species establishment (D'Antonio et al. 1999; Chaneton et al. 2002). For instance, effects of burning and grazing on woody encroachment are mostly idiosyncratic and context-dependent (Hobbs 2000; Bond 2008), although some invasive taxa like *Pinus* spp. appear to thrive in frequently disturbed habitats (Simberloff et al. 2010).

Only a small fraction of the species arriving at a site do establish persistent populations without being excluded by interactions with other species (Fig. 5.1). Biotic limitations to establishment can reflect either negative impacts from competitors and consumers (e.g. seed predators) or the absence of specific mutualists (Crawley 1987; Levine et al. 2004). Elton (1958) regarded the network of resident species interactions as the prime barrier against invaders (cf. Levine et al. 2004). Tree seedling growth in grasslands can be strongly limited by competition from herbaceous plants (Davis et al. 1998). Selective removal of the grass cover may release resources and increase woody recruitment (Sankaran et al. 2004). Exotic trees with high growth

rates at the seedling stage appear to be better equipped for invading undisturbed grasslands (Rejmánek and Richardson 1996; Lamarque et al. 2011). Lastly, positive interactions (facilitation) between woody invaders, or between tree seedlings and resident plants, may be important as a means of ameliorating the effects of physical or biotic stress during tree establishment (e.g. Tecco et al. 2006; Smit et al. 2006).

It follows that grassland invasions by woody species (native or exotic) should be seen as multi-causal processes that integrate the effects of several putative factors acting at various scales. The existence of treeless grasslands such as the humid Pampas could be traced back to the influence of historical processes that shaped the composition of the regional pool as well as to the roles of propagule pressure, environmental stress, disturbance, and biotic interactions (Fig. 5.1). Tree invasion of primary grasslands begs the question of which filters were modified and what were the intervening causes.

5.3   The Humid Pampas: A Phytogeographic Overview

The temperate humid Pampas extend over *c.* 400,000 km² between 31 and 38 °S in east-central Argentina (Fig. 5.2). The Pampean phytogeographic province is surrounded by the Espinal province, a belt-shaped system of open woodlands and savannas (Cabrera 1958, 1976; Cabrera and Willink 1980). Native forests also occur along riparian corridors of the Uruguay and Paraná rivers, which extend from the subtropical Paranaense province into the northern part of the Pampas (Nores et al. 2005). Precipitation decreases from the north-east to the south-west of the region (1,000–500 mm/year). Rainfall occurs throughout the year, with mild summer water deficits in the east, and more severe, winter dry periods in the west. Mean annual temperature is 18 °C, although frosts are common in winter (Soriano 1992). The landscape developed on Andean loess deposits and alternates vast flat areas with gently rolling hills. Rocky outcrops form the Tandilia and Ventania ranges (1,500 m a.s.l.) in the southern Pampas (Fig. 5.2). The dominant soils in the wetter, eastern areas are Mollisols with a heavy argillic B horizon, while towards the west, soils are mostly Entisols with a coarse, sandy texture (Soriano 1992).

The origin of the Pampas flora reflects the influence of the Neotropical and Antarctic realms (Cabrera and Willink 1980; Ribichich 2002). The primary vegetation corresponds to mesophytic grasslands with a mix of C_3 and C_4 perennial grasses (Burkart 1975; Soriano 1992). Common genera include *Stipa, Poa, Piptochaetium, Melica, Briza, Bothriochloa, Aristida, Panicum,* and *Paspalum.* Exotic herbaceous forbs are common throughout the region (Ghersa and León 1999; Perelman et al. 2001; Burkart et al. 2011). The Pampas comprise five phytogeographic districts (Fig. 5.2), differing in the degree of landscape transformation by humans (Baldi et al. 2006):

Mesopotamic pampa—This is most humid and warmer section of the Pampas. The vegetation structure and composition have strong affinities with the Espinal and Chaco provinces (Cabrera 1958, 1976; Soriano 1992). This district is surrounded by
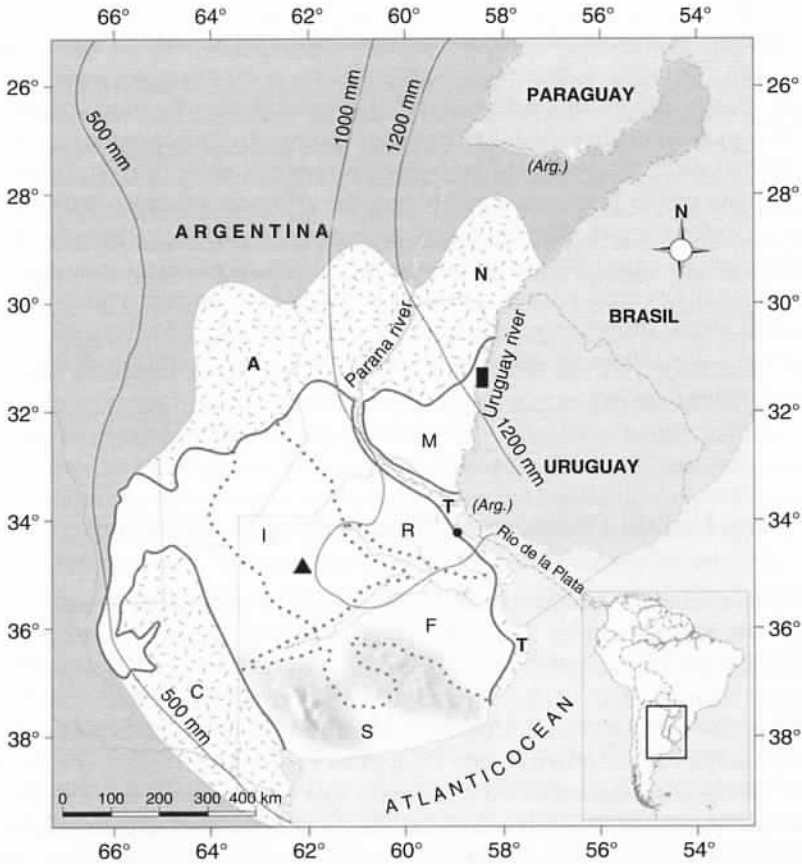
Fig. 5.2 Limits of the Pampa grasslands and Espinal woodlands in east-central Argentina. Phytogeographic districts (*dotted lines*) of the Pampa province (*thick line*) are denoted by different letters: *M* Mesopotamic pampa; *R* Rolling pampa; *F* Flooding pampa; *I* Inland pampa; *S* Southern pampa. Districts of the Espinal province (*stippled area*) are denoted by *bold-type letters*: Ñ Ñandubay; *A* Algarrobo; *C* Caldén; *T* Tala. *Lightly shaded areas* within S show the Ventania and Tandilia mountain ranges. *Symbols* indicate the location of long-term research sites: El Palmar National park (*rectangle*) and Estancia San Claudio (*triangle*)

different types of forest formations, including subtropical gallery forests along the Uruguay and Parana riverbanks. Grasslands are dominated by C_4 tussock grasses and several native shrubs. Palm trees (*Butia yatay*) are scattered across large grassland areas, creating a conspicuous savanna-like physiognomy. Wildfires likely were a recurrent disturbance agent in the past, but nowadays have been largely suppressed.

Rolling pampa—This section of the Pampas has been the most deeply transformed by rowcrop agriculture, cattle husbandry, and human settlement since the Europeans arrived in the mid-1500s. Darwin (1893) described the grasslands as being heavily

invaded by exotic thistles. The potential vegetation is a "flechillar" with a species-rich mixture of C_3 and C_4 tussock grasses (Cabrera 1976; Soriano 1992). Yet seminatural grasslands occupy only a small fraction of the area, and no relicts of native grassland exist today (Parodi 1947; Burkart et al. 2011).

Inland pampa—The eastern side of the district is a mosaic of croplands and rangelands. Native grasslands are confined to relictual fragments extending along abandoned railway tracks and secondary roadsides (Soriano 1992). In contrast, the western side comprises extensive natural grasslands, which are mainly used for cattle grazing. Prescribed burning is used as a management tool in the drier western areas. The dominant community is a steppe-like "flechillar" with tall-tussock grasses forming dense, species-poor, homogeneous stands (Burkart et al. 2011).

Flooding pampa—The area comprises extremely flat, flood-prone landscapes devoted to domestic grazing on natural grasslands and sown pastures (Soriano 1992). Crops have been sown only in the most elevated areas. Grazed grasslands are dominated by short tussock and prostrate grasses and harbour high numbers of low-growing exotic forbs. The C_3/C_4 native grass ratio increases southward (Perelman et al. 2001). Periodic floods and soil salinity limit plant species richness in lowlands areas.

Southern pampa—This is the cooler and drier section of the Pampas. The landscape mosaic is dominated by winter crops, pastures, and natural grassland remnants. In unploughed, well-managed grazed sites the grassland is made up of a species-rich ensemble of C_3 grasses and forbs, thriving within a matrix of tall bunchgrasses (Soriano 1992). Montane grasslands occurring on rocky outcrops and elevated hills (>500 m) contain high species richness and many endemisms.

All five pampean districts are in contact with the Espinal province (Fig. 5.2). The Espinal comprises xerophytic forests, parklands, and savannas (Cabrera 1976). The climate is warm and humid in the north, and temperate semiarid in the west and south sections. Annual precipitation varies from 1,200 mm in the north to less than 500 mm in the south-west. Mean temperatures range between 20 and 14 °C. The tree overstorey has varying densities, being dominated by *Prosopis* and *Acacia* species (Fabaceae, Mimosoideae). Tree species richness declines southwards. Woody species have a neotropical lineage, including *Celtis*, *Schinus*, *Jodina*, and *Geoffroea*. Much of the original vegetation has been modified by logging and livestock management, and presumably by fire suppression as well. The Espinal can be divided into four main districts (Cabrera 1976).

Ñandubay district—The northern section of the Espinal (Fig. 5.2) comprising low forests (<10 m height) dominated by *Prosopis algarrobillo* (ñandubay) and *Prosopis nigra* (algarrobo negro). Other common woody species include *Acacia caven* (espinillo), *Geoffroea decorticans* (chañar), *Aspidosperma quebracho-blanco*, *Celtis tala* (tala), *Schinus molle* (molle), *Jodina rhombifolia* (sombra de toro), and *Scutia buxifolia* (coronillo). There is a well-developed shrub understorey. The herbaceous layer comprises a diverse community of C_4 grasses, forbs, and bromeliads (see Cabrera 1976).

Algarrobo district—The western section of the Espinal corresponds to a once extensive xerophytic woodland (see Fig. 5.2), which has been largely lost to logging and agriculture. There remain a few relics of native forest in which the dominant trees are *Populus alba* (algarrobo blanco), *P. nigra*, and several other species shared with the Ñandubay district, except *P. algarrobillo* (Cabrera 1976).

Caldén district—The southern section intergrades with the western Inland pampa along a wide ecotone (Fig. 5.2). The dominant species is *Prosopis caldenia* (caldén), which forms open woodlands and savannas with a sparse shrub layer and 35–50 % grass cover. This area has been severely degraded by cattle grazing and wood extraction, and therefore the actual limits with the Pampas are a source of controversy (cf. Cabrera 1976; León and Anderson 1983). Common subdominant woody species include *Prosopis flexuosa* (algarrobo), *P. nigra*, *G. decorticans*, *J. rhombifolia*, and *Schinus* spp. (incienso). The grass layer (flechillar) comprises several bunchgrasses including *Elyonurus muticus, Piptochaetium stipoides, Poa ligularis, Poa lanuginosa*, and various species of *Setaria* and *Stipa* (Cabrera 1976).

Tala district—It extends southward as a narrow coastal forest along the lower section of the Paraná river and the coast of Buenos Aires on the Atlantic (Parodi 1940; Cabrera 1958, 1976; Fig. 5.2). The so-called "talares" are xerophytic hardwood forests growing on well-drained coastal dunes or calcareous soils formed on ancient marine (shell) deposits. Forest patches intermingle with lowland grasslands (Soriano 1992). The community is dominated by a deciduous thorny tree, *C. tala* (Ulmaceae), and contains a mixture of woody natives such as *S. buxifolia, A. caven, Stellaria longifolia, J. rhombifolia, P. alba, Phytolacca dioica* (ombú), and *Sambucus australis* (sauco). The original forest has been deeply fragmented by logging and few patches remain undisturbed (Cabrera 1976). In some areas, the forest was cleared during colonial times (Garavaglia 1999a). Forest remnants are being colonised by nearly 20 exotic tree species, of which the evergreen *Ligustrum lucidum* is the worst invader (Cagnoni et al. 1996; Ribichich and Protomastro 1998).

5.4   Why Were There No Trees in the Pristine Pampas?

The existence of treeless natural grasslands in virtually all continents has attracted much controversy (Bredenkamp et al. 2002; Bond 2008). Broadly speaking, explanations for the lack of trees in grassy steppes and prairies can be divided into "bottom–up" and "top–down" arguments. The former emphasise the influence of climatic conditions and abiotic stress on tree growth potential, whereas the latter focus on the role of woody biomass consumption by fire and herbivores (Bond 2008). On the one hand, the global distribution of forests would be limited by macroclimatic aridity and soil texture (Walter 1967; Whittaker 1975). On the other hand, there is little doubt that human-induced fire suppression and reduction of native herbivore populations provide opportunities for woody encroachment on grassy vegetation (Sankaran et al. 2004; Bond 2008; Bond et al. 2005). We notice,

however, that both these perspectives implicitly assume that ill-adapted tree genotypes would be available in the regional pool, and hence focus on environmental and biotic filters to species assembly (see Fig. 5.1). We shall come back to this point later in this section.

Vegetation scientists have often regarded the Pampa grasslands as an anomaly, since other regions with similar temperate humid climates typically support deciduous or mixed forests. Were the Pampas a climatically determined (primary) grassland or an anthropogenic one? (Schmieder 1927; Parodi 1942; Ellenberg 1962; Walter 1967). It has also been questioned why is that forests do not occur naturally in the Pampas when many introduced tree species grow spontaneously in old fields, along road verges and fencelines, and within forest plantations (Parodi 1942; Ellenberg 1962; Ghersa et al. 2002). In the following, we briefly revisit traditional ideas for the paucity of trees in the pristine Pampas. We stress that hypotheses thus far have largely been articulated around single causes. We then integrate the various putative causes for the existence of treeless Pampa grasslands within a multi-causal, hierarchical framework.

5.4.1   Single-Cause Explanations for Treeless Grasslands

Perhaps the most frequently cited cause for the paucity of trees in temperate grassy systems is the occurrence of seasonal drought (Bredenkamp et al. 2002). For instance, the absence of trees in Eurasian primary grasslands and North American prairies has been associated with an aridity gradient. Where conditions become too dry, forests and woodlands give way to grassland. It is then common to find trees where the local moisture regime is more favourable for tree growth, like in river valleys or flood plains immersed within steppe or prairie zones (Bredenkamp et al. 2002). This is indeed a common feature of the Rolling pampa landscape, where woody species typical of the Espinal occur along tributaries of the Paraná river (Walter 1967; Ghersa and León 1999).

A related hypothesis states that the root systems of resident grasses exert strong competition for water, limiting the establishment of tree seedlings (Parodi 1942). There is much experimental evidence that grass competition can significantly reduce seedling or sapling growth under water-limiting conditions (Davis et al. 1998; Sankaran et al. 2004; Riginos 2009). This suggests that the regeneration niche of the trees would overlap with that of resident grasses (Facelli and León 1986; Bond 2008). Taken together, a negative water balance during part of the year and the higher competitive ability of grasses would determine the existence of natural "climatogenic" grasslands, and the Pampas would be no exception (Walter 1967). Forestry practices provide stress-free microsites for seedlings, which explains why many planted tree species grow well in the humid Pampas.

Some researchers have pointed out the role of soil texture in tipping the competitive balance for water between grasses and trees (Walter 1967). Heavy, clayed soils may favour grass dominance by limiting tap-root penetration, whereas trees

would become dominant in lighter, sandy soils. In the Pampas, the ecotones between grassland and woodland (Espinal) roughly correspond with transitions from heavy loessic soils to coarser-textured soils (Cabrera 1976; Yazawa 1989). The combination of fine-textured soils and summer drought would make it difficult for tree seedlings to establish in bare-soil spaces among grass tussocks (Parodi 1942). This seemingly strong effect of soil texture on life-form balance may account for the sharp boundaries between xerophytic forests (talares) and grasslands on the north-eastern side of the Rolling and Flooding pampas (Ribichich and Protomastro 1998; see Fig. 5.2).

Temperature has been proposed to control the presence of trees in some regions. In particular, frost periods may limit seedling recruitment for subtropical woody taxa. For instance, according to Bredenkamp et al. (2002), it is not aridity that excludes trees from Southern African grasslands. The cooler climates prevailing in some temperate grasslands, especially during the winter, would exclude subtropical trees. Many cold- and frost-tolerant tree species from the northern hemisphere and Australia do grow well when planted in these grasslands (e.g. *Eucalyptus camaldulensis, Platanus acerifolia, P. alba*). Some of these species even become invasive (e.g. some pines and acacias). However, native trees do not survive when planted, as they are killed by winter frosts. This suggest that while aridity excludes cold-resistant trees from temperate steppes, low temperatures (and frost) may exclude subtropical trees (Bredenkamp et al. 2002). Such a causal scenario might explain why, when occurring at higher latitudes, trees originating in the subtropical Paranaense province remain confined to mild riparian habitats, without invading adjacent Pampa grasslands (Cabrera 1958; Nores et al. 2005).

Fire has been invoked as a major determinant for the absence of woody plants in grassy biomes worldwide (Bond et al. 2005). In particular, frequent burning used by early human societies for land clearing, hunting, and agriculture has been implicated in the origin of anthropogenic (secondary) grasslands in western Europe (see Bredenkamp et al. 2002). Some authors have suggested that fires set by native American Indians were the cause for the existence of treeless North American prairies (Christy 1892). This hypothesis was extended to South American grasslands, on the basis that burning was found to be a common practice among native Indians, at least, during the early period of European settlement in the Pampas (Schmieder 1927; Ellenberg 1962; Henning 1988). In this light, the Pampa grasslands would be anthropogenic, rather than a natural vegetation type in equilibrium with climate and soil conditions. This notion has been rejected for reasons that will soon become clear (Parodi 1942; Walter 1967; Soriano 1992).

The other top–down force with the potential to control vegetation structure is herbivory, especially by large-bodied grazers and browsers (Johnson 2009). Temperate South American grasslands developed without supporting high densities of large vertebrate herbivores since the late Pleistocene extinctions (Burkart 1975; Barnosky and Lindsey 2010). However, a rich fauna of megaherbivores roamed the region for much of the Tertiary (Webb 1978). Did plant consumers play a role in precluding the expansion of trees onto grassy plains in the Pampas? May be, although megaherbivores coexisted with open woodlands and gallery forests in

areas like the Great Chaco and Patagonia. Medial Miocene to Pliocene fossil faunas became dominated by pampas and steppe adapted forms, while gallery forests likely persisted along stream borders (Webb 1978). Since the megafauna extinctions of southern South America coincided with the drying of the climate and occurred after the arrival of early humans (some 13,000 year BP; Barnosky and Lindsey 2010), and even so the region remained covered by grassland up to the present (Tecchi 1983; Prieto 1996), there is no compelling evidence that extinct herbivores were a primary driver of the prehistoric paucity of trees in the Pampas (cf. Johnson 2009).

A final hypothesis for the absence of forests emphasises the geomorphological youth and changing climatic history of the Pampas (Parodi 1942; Iriondo 1999; Iriarte 2006). There is strong fossil evidence from phytoliths (Tecchi 1983), pollen records (Prieto 1996), and faunal assemblages (Tonni et al. 1999) that grassy vegetation occupied the Pampas from the early Miocene and through the Quaternary. The late Pleistocene (c. 14,810–10,000 ^{14}C year BP) of the Pampas was defined by drier and cooler conditions (Iriondo 1999), as shown by the presence of C_3-dominated psamophytic steppes (Iriarte 2006). These conditions prevailed until the onset of a humid period in the early Holocene (c. 10,000–6,600 ^{14}C year BP), which saw the emergence of extensive wetlands and the replacement of C_3 pooid by C_4 panicoid grasses (Iriarte 2006). Dry steppes were displaced by humid grasslands (Prieto 1996, 2000). During the mid-Holocene, around 6,600 ^{14}C year BP, began a new period of dryness, which led to the expansion of halophytic vegetation in flat lowlands. After c. 4,000 ^{14}C year BP, a decline in halophytes signals the onset of more humid and stable climatic conditions, characteristic of the late Holocene to the present (Prieto 1996; Tonni et al. 1999). Overall, evidence suggests that the Pampas are a relict of drier past climates. Recurrent drying–wetting cycles might have also acted to constrain the presence of tall woody plants.

5.4.2 A Multi-causal Perspective: Putting History and Ecology Back Together

Hypotheses for the paucity of trees in the humid Pampas have referred to either proximate causes (e.g. tree seedlings cannot successfully compete with grasses) or distant causes (e.g. the Pampas are a relict of a drier past climate). Yet single-cause explanations may fail to account for the absence of tree life forms in grassland (Bond 2008), as for biotic invasions in general (Theoharides and Dukes 2007). Moreover, univariate models of vegetation structuring are inconsistent with modern ecological theory, which embraces the role of long-term evolutionary and historical processes as well as local niche relations in shaping present-day community patterns (Ricklefs and Schluter 1993; Valiente-Banuet et al. 2006; Fig. 5.1). We stress that the former absence of trees in the Pampas likely resulted from multiple interacting factors (i.e. filters) operating at disparate scales. Limitations to tree occurrence were probably fourfold.

Species pool—It appears that the regional species pool for the Pampas did not contain autochthonous trees with evolved adaptations to the local environment. Yet the region was surrounded by forests of subtropical affinity since pre-historic times (Webb 1978; Cabrera and Willink 1980). It is unknown why the dry woodland and wet forest lineages did not give rise to a "Pampas tree genotype". We may think of two reasons. First, there might have been strong phylogenetic constraints to the evolution from northern South American ancestors of temperate tree genotypes adapted to cool, subhumid climates (see Mack 2003). Southern lineages from the Antarctic domain were confined to the Andes after the last glacial period and the emergence of vast semiarid steppes in Patagonia (Markgraf et al. 1995). Second, the unstable climatic and geological conditions that characterised the Pampas from the late Tertiary through the Quaternary (Webb 1978; Prieto 1996, 2000; Iriarte 2006) could make it difficult for any marginal or founder long-lived tree population to develop the "right" suite of adaptive traits. Moreover, prior to the late Pleistocene mass extinctions, resident megaherbivores also probably helped to maintain a treeless grassy biome (Webb 1978; Johnson 2009).

Seed dispersal—Even if pre-adapted tree genotypes were available in past species pools along the margins of the Pampas, successful invasion by trees could have been precluded by low dispersal rates and hence low propagule pressure. Dispersal limitations to native trees could reflect lack of seed sources, as determined by the northward retreat of tropical forests during the late Tertiary–early Quaternary period of increased aridity in southern South America (Markgraf et al. 1995). Further, low seed arrival may result from reduced activity of dispersal agents. Birds may act as long-distance dispersers, but may fail to transport tree seed into grassland areas with few perch structures (Milton et al. 2007).

Abiotic stress—Although several tree species were actually present in the broader regional pool of the Pampas (encompassing the ecotones with Espinal woodlands and Paranaense riparian forests), most seemed to lack the functional traits to establish and reproduce in a temperate subhumid environment (Fig. 5.1). Provided enough seed of either xeromorphic or subtropical tree genotypes was dispersed into adjacent grasslands, then colonisation would have been impeded by heavy soils, drought, or frosts, especially during periods when climate was much drier than at present (Prieto 1996, 2000). Such niche limitations should create demographic bottlenecks during early life stages, thus reducing the chances of invasion (Bond 2008). Indeed, native trees from savanna and gallery forests generally do not survive when planted, as they are often killed by winter frosts.

Biotic interactions—The potential for woody species from adjacent communities to establish in the Pampas was also probably limited by competition from resident grasses (Parodi 1942; Walter 1967). Tussock grasses strongly suppress tree seedling growth and survival in humid grasslands (Mazía et al. 2001; Chaneton et al. 2004), and may indirectly prevent seedling emergence by providing cover to granivorous rodents (Mazía et al. 2010). These factors alone only rarely repel invasion, unless immigrating species are propagule-limited (Levine et al. 2004; Lockwood et al. 2005),

which is the case at increasing distance from seed sources. In addition, root symbionts such as mycorrhizal fungi must be available for successful recruitment of many trees. Dominant tree taxa in the Espinal belong to the Fabaceae and require certain *Rhizobium* strains for nitrogen fixation. Thus, absence of specific soil microbial partners can add another, often underestimated barrier to tree invasion (see Simberloff et al. 2010).

Overall, we expect that low propagule pressure, abiotic stresses, biotic resistance, and a paucity of specific symbionts might have exerted a synergistic influence in slowing tree invasion rates (Crawley 1987; Lockwood et al. 2005). These factors operated under a higher-level constraint, that is, the palaeoclimatic history of the region and its long-term influence on species pool evolution.

5.5 Contemporary Patterns and Mechanisms of Tree Invasion

The original treeless physiognomy of the Pampas began to change dramatically with the arrival of European settlers to the Río de la Plata in the mid-1500s. Human activity was instrumental in shaping all four stages of the process of invasion by tree species alien to South America, from transport through colonisation and establishment, to landscape spread (Theoharides and Dukes 2007). Species pool limitations were overridden by the introduction of temperate tree genotypes pre-adapted to the Pampas environment. Since the seventeenth century trees and other woody species became conspicuous features of "estancias" in the northern (Rolling) pampas. Frequency of planted trees in urban and countryside areas increased between the eighteenth and nineteenth centuries (Garavaglia 1999b), with both native and exotic species being introduced for living fences, shade, wind barriers, and as ornamental plants (Ghersa and León 1998, 1999). Native woody species included *Acacia bonariensis* (añapindá), *Parkingsonia aculeata* (cina-cina), *P. dioica* (ombú), and *C. tala* (tala), while early exotics were *L. lucidum*, *Gleditsia triacanthos* (acacia negra), *Melia azedarach* (paraíso), *Morus alba* (mora blanca), and *Phoenix canariensis* (palmera), and later *Eucalyptus* spp. Pollen records for *G. triacanthos* in the eastern Rolling pampa date back to the late 1700s (Prieto et al. 2004). This process reshaped the regional pool by adding species with novel functional traits (Fig. 5.1).

Widespread plantation of woodlots and tree lines increased the number of seed sources and hence propagule pressure. Main roads served as corridors for the early dissemination of introduced tree species. Planted trees created new habitat for wildlife, including native birds and mammals, which likely contributed to accelerate the spread of woody plants (Ghersa and León 1998). By the early 1800s, native trees of the Espinal like *G. decorticans*, *J. rhombifolia*, and *Prosopis* spp. could be found in small forest patches in northern and eastern sites of the Pampas (Garavaglia 1999a). On the northwestern Pampas ecotone, Espinal woody species were dispersed into dry grasslands by cattle herds driven by indigenous people (León and Anderson 1983). Rapid tree encroachment was facilitated by the land-use changes that dominated the Pampas in the late 1800s after the Indian wars (Tapson 1962). Before that,

burning of tall tussock grasslands by the aborigines (Darwin 1893) possibly slowed the spread of invasive woody plants.

During the 1900s, the profound anthropogenic transformation of the original landscape involved the division of the land by linear elements such as roads, fence-lines, channels, and railways. This created a network of seminatural vegetation cor-ridors that now harbour many exotic tree species (Ghersa et al. 2002). Bird species (e.g. *Turdus rufiventris*, zorzal) find perching sites along these corridors and in domestic woodlots, thus transporting the seeds of introduced woody plants across the landscape (Ghersa and León 1998). Riparian zones have also been invaded by frost-tolerant exotic trees such as *G. triacanthos*, *L. lucidum*, and *M. alba* (Ghersa et al. 2002), probably induced by directed, bird-mediated dispersal (Nores et al. 2005). Lastly, the modern Pampas landscape contains many human-disturbed areas of noncultivated or waste land, which are invaded by exotic trees like *G. triacanthos* and *Ulmus pumila* (olmo) forming dense forest patches (Facelli and León 1986; Mazía et al. 2001). Only the vast grazed plains of the Flooding pampa remained relatively free of woody invasions (Fig. 5.3).

Overall, anthropogenic landscape fragmentation generated a diffuse, reticulated "ecotone" between modified habitat patches and remnant grasslands. Whereas his-torical (biogeographical) boundaries with adjacent forested regions remained mostly stable, the ecotones created by human activity in the Pampas interior promoted encroachment of introduced woody species onto once treeless landscapes. In the remaining of this section, we review evidence for contemporary patterns of woody plant invasion in the Pampas. We highlight two separate phenomena, namely, woody encroachment across geographic ecotones and spread of exotic trees onto human-disturbed grasslands.

5.5.1 Dynamics Across Natural Grassland/Forest Ecotones

5.5.1.1 Humid Palm Savannas

Savannas dominated by the palm tree *B. yatay* occur on sandy soils in the eastern Chaco and Espinal provinces (Martinez-Crovetto and Piccinini 1950; Carnevali 1994). The largest area of *B. yatay* palm savannas extends over the watersheds of several streams that flow eastward into the Uruguay River, on the northern limit of the Pampas (Fig. 5.2). Stands with widely varying densities of *B. yatay* occur on the highlands and river terraces, while alluvial plains support tall grasslands and riparian subtropical forests (Cabrera 1976). Since the creation of El Palmar National Park in 1970, a large track of palm savannas has been protected under a policy of cattle exclusion and fire control. The area had previously been used for cattle ranching, and the savannas were structured by a tall palm tree layer and a short species-rich herbaceous layer (Martinez-Crovetto and Piccinini 1950). Scarcity of juvenile palms suggested that cattle were preventing palm recruitment (Dimitri and Rial 1955; Cabrera 1976). Hence, cattle exclusion should allow palm recruitment,
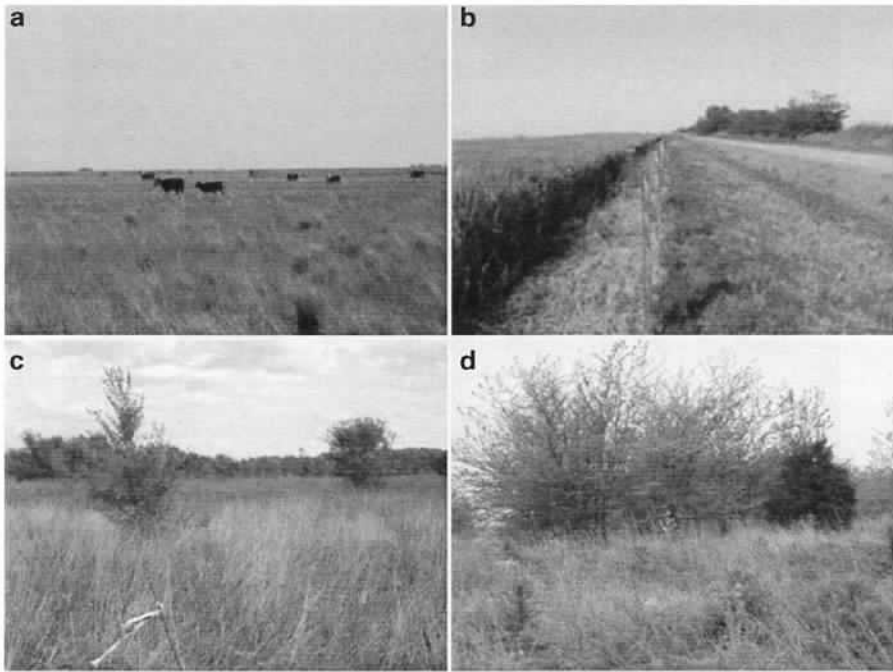
Fig. 5.3 Views of the Pampas. (**a**) Treeless landscape in the central Flooding pampa, (**b**) trees invading a roadside corridor in the Rolling pampa, (**c**) invasion of an old-field grassland by *Ulmus pumila* in the Inland pampa, (**d**) a thicket formed by *Gleditsia triacanthos* and *Ligustrum lucidum* (*dark tree*) in an old pasture field, Inland pampa (photos by E. Chaneton (**a, c, d**) and F. Weyland (**b**))

while maintaining the open savanna/grassland physiognomy. Yet palm savannas were rapidly encroached by native bushy species, whereas denser savannas have been invaded by both native and exotic tree species (Ciccero and Balabusic 1994; Goveto 2006; Fig. 5.4).

Tree encroachment on *B. yatay* savannas has been examined at the landscape and local (stand) scales. In 2000, a total of 26 tree species were recorded in the understorey at El Palmar (Table 5.1). Most invading trees are native to riparian forests and are distributed over the Paranaense or Espinal provinces (Cabrera 1976). In addition, palm savannas were invaded by tree species exotic to South America, especially *M. azedarach*. Among the encroaching tree species, the majority have their seeds dispersed by birds (Table 5.1). High-palm density savannas on lower terraces have been encroached by many tree species from nearby riparian forests, while sparser savannas on uplands have fewer trees and include hardwood species from the Ñandubay forests (Table 5.1; Fig. 5.4).

Current landscape distribution of three of the most common native trees, *Allophylus edulis*, *Myrcianthes cisplatensis*, and *Sebastiania commersoniana*, suggest that dispersal syndrome, adult palms, and fire frequency may all have a role in the encroachment process (Rolhauser et al. 2007). After 35 years of cattle exclusion

Fig. 5.4 Aspects of the *B. yatay* palm savannas in (**a**) cattle grazed and (**b**) protected areas at El Palmar National park. Cattle exclusion and fire control triggered invasion by both native and exotic tree species, especially in dense palm savanna stands (photos by A. Rolhauser)

and relative fire control, densities of *A. edulis* and *M. cisplatensis*, two bird-dispersed species, were found to decline with distance from the riparian forest edge. Since in 1970 trees were virtually absent from the palm savanna, the observed pattern is consistent with populations expanding as a front wave (Skellam 1951). For *M. cisplatensis*, the estimated distance of tree expansion in dense palm stands unburned

Table 5.1 Tree species recorded in the understorey of *Butia yatay* palm savannas at El Palmar National Park (Mesopotamic pampa)

Species name (family)	Distribution	Dispersal mode
Frequent in dense/sparse palm savannas		
Allophylus edulis (Sapindadeae)	P, E	Birds
Myrcianthes cisplatensis (Myrtaceae)	P, E	Birds
Sebastiania spp. (Euphorbiaceae)	P	Elastic dehiscence
Myrcia ramulosa (Myrtaceae)	P	Birds
Schinus longifolius (Anacardiaceae)	P, E	Birds
Sapium haemaospermum (Euphorbiaceae)	P	Birds
Melia azedarach (Meliaceae)	Exotic	Birds, bats
Frequent in dense palm savannas		
Hexachlamys edulis (Myrtaceae)	P	Gravity + mammals
Guettarda uruguensis (Rubiaceae)	P	Birds
Maytenus ilicifolia (Celastaceae)	P	Birds
Frequent in sparse palm savannas		
Acacia caven (Fabaceae)	E	Gravity + mammals
Prosopis affinis (Fabaceae)	E	Gravity + mammals
Occasional in palm savannas		
Acacia bonariensis (Fabaceae)	P, E	Gravity
Blephalocalyx salicifolius (Myrtaceae)	P	Birds
Celtis tala (Cannabaceae)	P, E	Birds
Erythrina crista-galli (Fabaceae)	P	Gravity + water
Nectandra angustifolia (Lauraceae)	P	Birds
Ocotea acutifolia (Lauraceae)	P	Birds
Pouteria salicifolia (Sapotaceae)	P	Gravity + water
Myrsine laetevirens (Myrcinaceae)	P	Birds
Scutia buxifolia (Rhamnaceae)	P, E	Birds
Fraxinus pennsylvanica (Oleaceae)	Exotic	Wind
Gleditsia triacantos (Fabaceae)	Exotic	Gravity + water + mammals
Ligustrum lucidum (Oleaceae)	Exotic	Birds
Magnolia grandiflora (Magnoliaceae)	Exotic	Birds
Prunus persica (Rosaceae)	Exotic	Gravity + animals

The occurrence of each species in other phytogeographic units and its dispersal mode are shown. *P* riparian habitats supporting forests of the subtropical Paranaense province; *E* Ñandubay forests of the Espinal province. *Exotics* refer to species not native from South America

over the previous 25 years (~2 km) was significantly longer than in either sparse palm stands or stands burnt within the previous 15 years (~1.5 km).

In contrast, the distribution of *S. commersoniana*, a self-dispersed species, exhibits no clear trend with distance from the forest edge. Density of this species is higher in dense than in sparse palm stands, where it is extremely rare. These patterns suggest that, under current conditions of cattle exclusion and fire suppression, palm trees would have facilitated tree encroachment. For bird-dispersed species, this may be partly generated by the palm trees acting as perches for dispersers. However, association of *S. commersoniana* with dense palm stands further suggests that other forms of facilitation or environmental control might be relevant. For *M. cisplatensis*,

burning appears to have limited tree encroachment rates in these savannas (Rolhauser et al. 2007).

Field experiments revealed the local influences of *B. yatay* and established adults of *A. edulis* and *S. commersoniana* on seed arrival and seedling performance of the latter two riparian species (Rolhauser et al. 2011). Seed traps and seedlings of both species were placed in open grassland patches, and beneath palm trees, *A. edulis* adults and *S. commersoniana* adults. Palm tree and grassland microsites were used to evaluate the influence of resident palm trees on early encroachment. Seed traps under palm trees captured more seeds of the bird-dispersed *A. edulis* than those in herbaceous patches, whereas no seeds of the self-dispersed *S. commersoniana* were trapped. Survival of *A. edulis* seedlings was lower under palm trees than in grassland, mainly because seedlings were more likely to be damaged by trampling and burrowing animals. Survival of *S. commersoniana* seedlings did not differ between palm trees and grassland.

Patterns of seed arrival and seedling performance under established *A. edulis* and *S. commersoniana* trees were used to examine intra- and interspecific effects during advanced stages of encroachment (see Rolhauser et al. 2011). *A. edulis* seed occurred massively under conspecific trees, but seedling growth was strongly suppressed under conspecific adults. *S. commersoniana* seeds were rare and were trapped only under *Sebastiania* trees. Seedlings of this species also showed reduced growth rates under conspecifics, but increased survival beneath heterospecific, *A. edulis* trees.

Species-specific influences of direct and indirect biotic interactions appear to be instrumental in the encroachment process (Rolhauser et al. 2011). Whereas palm trees may not affect the early dynamics of *S. commersoniana*, they exert animal-mediated indirect effects that may either boost or slow early encroachment by *A. edulis*. Further, seedlings of both riparian species grew better in heterospecific than in conspecific adult microsites, a pattern consistent with the "escape hypothesis" (Howe and Smallwood 1982). Lastly, *A. edulis* trees might facilitate establishment of *S. commersoniana* provided seeds arrive in *A. edulis* patches. The ongoing encroachment of dense palm stands by these riparian trees (Rolhauser et al. 2007) suggests that, under current management regimes, the role of palm trees as perches for frugivorous birds outbalances their role as attractors of disturbing animals. In contrast, lack of a long dispersal mechanism appears to limit the expansion of *S. commersoniana* across these savannas.

5.5.1.2 Espinal Semiarid Savannas

The vegetation physiognomy of the southern Espinal (Caldén district, Fig. 5.2) varies from typical *P. caldenia*-grass savannas to dense *P. caldenia* woodlands in relatively humid lowlands and open treeless grasslands on drier sandy soils (Cabrera 1976; Lerner 2005). Current limits between these plant associations as well as between the southern Espinal and the Pampas have been notoriously modified by human activity. Since the mid-1800s, land clearing for agriculture has kept pushing the Espinal forest boundary in both west- and southward directions

(Cabrera 1976). Also, domestic grazing promoted the encroachment of semiarid savannas and grasslands by native trees, mainly *P. caldenia* and *G. decorticans* (León and Anderson 1983; Distel et al. 1996; Peláez et al. 1992).

Livestock generally facilitates woody encroachment in the southern Espinal. The introduction of cattle likely increased seed dispersal of *P. caldenia* and *G. decorticans* (León and Anderson 1983), as these were dispersed by native herbivores such as *Lama guanicoe* (guanaco) and *Odococeilus bezoarticus* (pampa deer). Ingestion of seed pots by cattle enhances seed viability by preventing predation by bruchids, and also increases germination via scarification (Lerner and Peinetti 1996). Grazing indirectly enhances tree seedling recruitment by creating safe microsites where grass competition is relaxed, and this effect likely increased under domestic stocking rates (Villalobos et al. 2005). Further, grazing impacts would have shifted when sheep were replaced by cattle as main domestic grazer. Sheep removal presumably decreased consumption of tree seedlings, thus accelerating tree encroachment on overgrazed areas (Dussart et al. 1998).

In addition, domestic grazing modified the natural fire regime (Dussart et al. 1998; Fernández and Busso 1999) with varied impacts on grass/woody species dynamics. Fire facilitates recruitment of *P. caldenia* seedlings by reducing grass biomass and increasing soil temperature and nutrient content (Villalobos et al. 2007). However, frequent burning may prevent seedling development into older life stages (Bond et al. 2005). The current disturbance regime of the Espinal, which is characterised by a low frequency of wildfires, increases the chances of tree seedling establishment by providing enough time for tree development between fire events.

5.5.1.3 Coastal Xerophytic Forests

The *Tala* district of the Espinal forms a narrow, discontinuous strip of xerophytic forests bordering the northern and eastern Pampa grasslands (Fig. 5.2). The limits between the two vegetation types are abrupt and determined by soil properties (Parodi 1940; Cabrera 1958). The extent of these coastal forests has been progressively reduced through human disturbance (Arturi and Goya 2005). Although abundant *C. tala* seeds are dispersed from mature trees, seedlings are typically scarce within the forest. Seedling densities up to 10 plants/m² can be found, but they mostly die by early winter. High winter mortality is related to low frost tolerance, which may account for the lack of *C. tala* establishment in open areas, away from the forest understorey (Arturi and Goya 2005).

Fruits of *C. tala* are readily consumed by birds, which disseminate seeds away from the forest. It is not uncommon to find isolated trees (<50 cm height) in nearby ungrazed grasslands, but there is no evidence of grassland encroachment by this native tree (Arturi and Goya 2005). Given that seeds would be easily dispersed onto adjacent grasslands, competition from resident grasses may be preventing *C. tala* encroachment (Arturi and Goya 2005). However, roadsides, channels and fencelines, and forestry plantations are focal points for the natural spread of *C. tala*. Disturbances removing the herbaceous cover, and planted woods where grasses are suppressed by

canopy shading, both provide suitable microsites for tree seedling recruitment and survival.

Most *C. tala* forests are being heavily invaded by several exotic trees, including *L. lucidum*, *Ligustrum sinensis*, *M. azedarach*, *G. triacanthos*, *M. alba*, *Acer negundo*, *Fraxinus* sp., *Pinus* spp., and *Populus* spp. (Cagnoni et al. 1996). Patches of coastal forest may represent stepping stones for dispersal and subsequent invasion of adjacent grasslands by species like *L. lucidum* and *G. triacanthos*, which produce large seed crops and are dispersed by native fauna or cattle (Montaldo 1993; Ghersa and León 1999; see Table 5.1). Thus, a combination of anthropogenic disturbance and forested patches would promote grassland encroachment by either native or exotic tree species.

5.5.2   Invasion by Introduced Tree Species

5.5.2.1   Rolling Pampa: Exotic Trees in Agricultural Landscapes

The Rolling pampa is the main agricultural zone of Argentina and represents the most heavily transformed section of the Pampas (Ghersa and León 1999). At present, trees are virtually everywhere, and invasive species threaten to become problematic weeds too. By the end of the twentieth century, all fields had been converted into zero-tillage cropping, which involves growing glyphosate-resistant soybean transgenic cultivars (De la Fuente et al. 2006). This shift to no-till agriculture increased the likelihood of tree invasion, which was previously prevented by annual disturbance from tillage practices.

A recent survey of the area by Ghersa et al. (2002) recorded a total of 40 woody species, mostly trees, invading roadside and riparian corridors (Fig. 5.3b). The exotic trees *G. triacanthos*, *M. azedarach*, and *M. alba* showed the highest occurrence, and the former two species were also frequent components of weed communities in zero-tillage cropfields (Ghersa et al. 2002; De la Fuente et al. 2006). The current extent of woody encroachment indicates that the restoration of native grasslands in the Rolling pampa would be highly unlikely (see below) without targeted control of invasive tree species.

5.5.2.2   Inland Pampa: Tree Species Invasion in Old Fields

Factors limiting the establishment of exotic trees in grassland patches have been experimentally evaluated in a long-term study site in the eastern Inland pampa (Fig. 5.2). The area comprises planted woodlots and windbreaks with species like *Eucalyptus* sp., *L. lucidum*, *G. triacanthos*, *U. pumila*, and *Robinia pseudoacacia* (acacia blanca). As in other areas of the Pampas, trees have escaped from plantation and invade noncropped, ungrazed fields and peridomestic areas, as well as abandoned

railway corridors with relictual tussock grasslands (Facelli and León 1986; Mazía et al. 2001; Chaneton et al. 2004).

Early work documented the invasion of old-field communities by *U. pumila* from nearby woodlots (Facelli and León 1986; Fig. 5.3c). The magnitude of invasion was inversely correlated with the grass cover and plot age. Removal of resident grasses in a 4-year-old plot enhanced tree seedling recruitment. Still, copious arrival of wind-dispersed seeds partly counteracted the negative effect of grasses, as tree seedlings also occurred in intact vegetation plots (Facelli and León 1986). In another study, we manipulated vegetation cover in a 15-year-old seral community dominated by pasture grasses (Mazía et al. 2001). To control for propagule pressure and test different tree genotypes, we added seed of three exotic (*G. triacanthos*, *U. pumila* and *L. lucidum*) and one native species (*P. caldenia*). The experiment was replicated in understorey and treefall-gap microhabitats in a *L. lucidum* plantation. We asked whether woodlots provide suitable conditions for tree establishment, and may thus work as "stepping stones" for invasive tree species.

Only *G. triacanthos* and *P. caldenia* were recruited in grassland. Removal of herbaceous cover increased seedling emergence and first-year survival of both tree species. Yet, 5 years later, only *G. triacanthos* had established successfully in disturbed plots, whereas all *P. caldenia* seedlings failed to survive. Established trees were 4–5 m in height and produced abundant seed pots. Surprisingly, *L. lucidum* and *U. pumila* did not emerge from sown seeds, possibly due to low viability and/or seed predation (Mazía et al. 2001). These results confirmed that, once dispersal limitation is removed, resident plants remain a major barrier to tree invasion (Fig. 5.1). Further, how effective are local filters to invasion will depend on the specific identity of the tree coloniser, regarding its susceptibility to various biotic or abiotic stresses. Although *P. caldenia* occurs in the "marginal" species pool of the western Inland Pampa, this xeromorphic species apparently lacks the seed/seedling traits to regenerate in mesic grassland.

In the forest experiment, all four sown trees emerged in both gap and understorey conditions, but did not survive pass the first summer from emergence in understorey microsites. Survivorship of *G. triacanthos* and *P. caldenia* was high during 1.5 years in the forest gap. However, all seedlings eventually died with gap closure in the ensuing years (Mazía et al. 2001). Thus, while forest patches may not offer better conditions for tree establishment than old-field grasslands, they provide early recruitment opportunities that vary depending on species identity and microhabitat. The common presence of *L. lucidum* and *G. triacanthos* saplings in tree plantations suggests that increased seed arrival may enhance the chance of successful invasion of forest patches by these exotics.

Both anthropogenic and natural disturbances may favour exotic invasions (Hobbs and Huenneke 1992; D'Antonio et al. 1999). Studies in the Inland pampa show that disturbance effects on tree establishment can be context-dependent. In a large-scale, 4-year experiment, we examined the influence of two disturbance agents, burning and animal diggings, on *G. triacanthos* recruitment in a late-successional old field and a relict of native tussock grassland (Chaneton et al. 2004; Mazía et al. 2010). To adjust for propagule pressure, 40 seeds/m^2 were added in each of several sowing
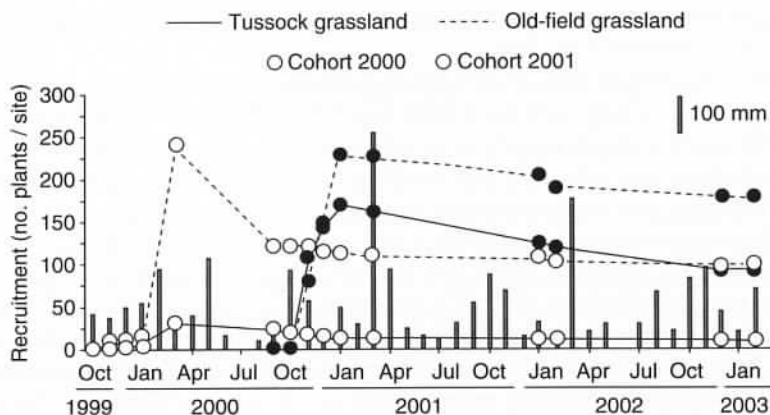
Fig. 5.5 Overall recruitment of *G. triacanthos* in old-field and relict tussock grasslands in the Inland pampa. Data show cumulative number of plants from two seedling cohorts (2000–2001) over 240 m². *Vertical bars (grey)* depict monthly rainfall (mm)

events to 12-m² plots, which were either burned or "burrowed" to simulate the digging activity of hairy armadillos (*Chaetrophractus villosus*) in a full factorial design (for details, see Mazía et al. 2010).

Emergence of *G. triacanthos* was fivefold higher in the old field than in the tussock grassland during the first, drier spring, but differences were reduced during the second, wetter spring (Fig. 5.5). Burning increased recruitment of the second-year cohort in both grasslands. Simulated armadillo disturbances prevented tree seedling emergence in the tussock grassland, especially in burned plots, and slightly increased recruitment in the old field (Fig. 5.6). Large- and small-scale disturbances thus promoted tree recruitment in the old field, whereas they exerted antagonistic effects in the relict tussock community (Mazía et al. 2010). Final establishment of *G. triacanthos* was twice as high in the old field as in the tussock grassland (Fig. 5.5). The greater resistance to tree invasion of the tussock grassland likely reflected the combined effects of grass competition and rodent granivory (Chaneton et al. 2004; Mazía et al. 2010). Indeed, seed loss to predators was higher in the tussock than in the old-field grassland (Fig. 5.7a), presumably because old fields offer a greater diversity of alternative food items to granivores. Hence, once propagule pressure is factored out, invasion by exotic trees becomes contingent on the recipient community, local disturbance regime, and annual rainfall patterns.

Recruitment of *P. caldenia* was similarly evaluated in the same grassland plots. Seedling emergence of *P. caldenia* from sown seed was abundant in both study grasslands. However, no seedling managed to survive beyond the first winter. Seed loss to granivores was greater in tussock than in old-field grassland (Fig. 5.7a). Rodent exclusion markedly increased *P. caldenia* emergence, while litter cover blocked seedling emergence within rodent exclosures (Fig. 5.7b). These findings show that different biotic factors may contribute to repel invasion by this native tree in both grasslands.
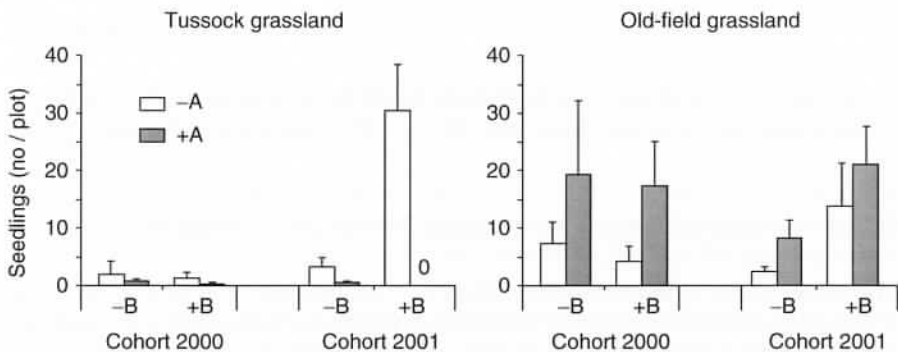
Fig. 5.6 Emergence of *G. triacanthos* under different disturbance regimes in old-field and relict tussock grasslands, Inland pampa. *Bars* show mean±SE (*n*=5) for two seedling cohorts emerged in a dry (2000) and a wet (2001) year. *B* burning; *A* armadillo diggings. There were significant effects of B×A×cohort (tussock $F_{1,16}$=9.46, $P<0.01$) and B×cohort (old field $F_{1,12}$=5.35, $P<0.05$)
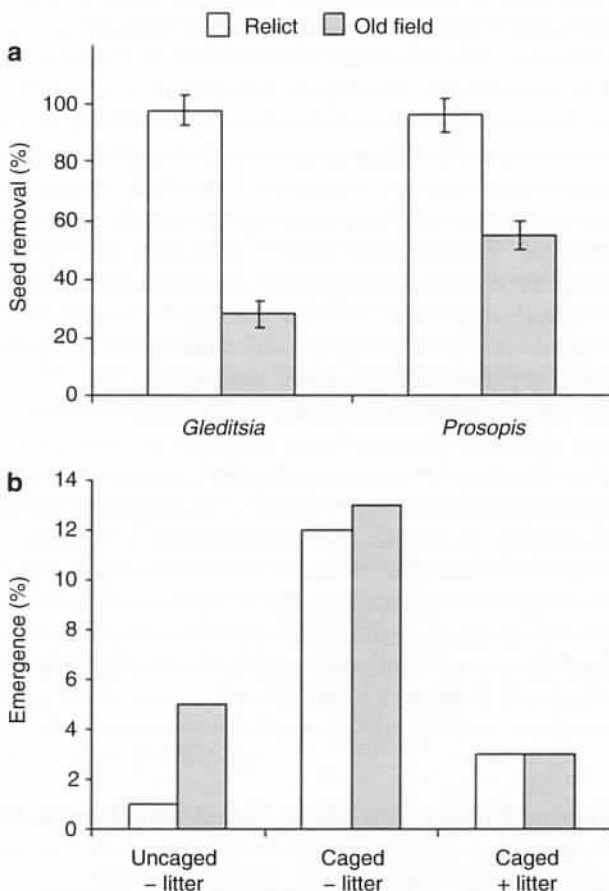
Fig. 5.7 (a) Removal of *G. triacanthos* and *Prosopis caldenia* seeds in old-field and relict tussock grasslands, Inland pampa. Site effect $F_{1,78}$=135.7, $P<0.0001$; site×species $F_{1,78}$=7.1, $P<0.01$. (b) Seedling emergence of *P. caldenia* as affected by rodent exclusion and litter cover. Relict, χ^2=30, $P<0.0001$; Old field, χ^2=21.8, $P<0.0001$ (both df=2)

In contrast, we found that even undisturbed grasslands were not fully immune to invasion by *G. triacanthos* (Mazía et al. 2001, 2010; Chaneton et al. 2004).

5.5.2.3   Southern Pampa: Pine Invasions in Montane Grasslands

The western limit of the Southern pampas forms a dynamic ecotone with the semi-arid Caldenal savannas (Cabrera 1976; Fig. 5.2). Present environmental conditions suggest that *P. caldenia* might have dispersed towards the east, although fossil pollen records indicate that the southeastern limits of the Espinal remained rather stable throughout the Quaternary (Prieto 1996). It has then been suggested that biogeographical barriers could have prevented colonisation of the Southern pampas by native trees (Arturi and Goya 2005).

Exotic tree species were introduced to the area since the early nineteenth century. Although the landscape physiognomy was drastically altered, trees were not originally reported to invade open grasslands. Widespread tree invasions in the Southern pampas began with *Pinus* and *Eucalyptus* plantations in the 1970s (Zalba and Villamil 2002). Successful tree introductions were mediated by an intensive selection process of ecologically pre-adapted genotypes. Historical (dendrochronological) records indicate that both *Pinus halepensis* and *Pinus radiata* were the most invasive forestry species, and that their landscape spread has been assisted by large fire events (Zalba and Villamil 2002). Factors promoting pine invasions after fire include massive seed crops and seedling recruitment, which continued for 12 years in the case of *P. halepensis* (Zalba et al. 2008). Grazing by feral horses has also been found to facilitate the spread of *P. halepensis* by reducing the competitive ability of native grasses outside plantations (Villalobos et al. 2011).

As shown for other southern hemisphere regions (Simberloff et al. 2010), the novel presence of pirogenic species (*Pinus*) increased the flammability of the system, enhancing the likelihood of tree establishment by relaxing the intensity of grass competition. Most importantly, attempts to restore grasslands on invaded sites have been highly encouraging. Four years after disturbance from intensive pine removal, native grasses replaced pioneer forbs without the need to augment grass seed availability through sowing (Cuevas and Zalba 2011). The reversal of tree-induced vegetation changes in the Southern pampas contrasts with the lack of recovery of native plant assemblages during old-field succession in the Rolling and Inland pampas (Ghersa and León 1999; Tognetti et al. 2010).

5.6   Conclusion: Future Trends in Grassland/Forest Dynamics

Biotic interchanges between adjacent regions have been common throughout the history of the Earth, and still are to be expected as a result of species' range expansions (Elton 1958; Vermeij 2005). However, natural shifts in biogeographical limits take time to develop and rarely involve long-distance dispersal events. By contrast,

human-assisted biotic invasions bridge large geographic scales, put in contact biotas with no co-evolutionary past, and occur at surprisingly fast rates (Williamson 1996; Vermeij 2005).

We have argued that in the humid Pampas pre-historic boundaries between natural grasslands and adjacent forest formations have remained largely stable, with little encroachment from native tree species. However, the last 300 years of human occupation have changed that pattern by creating a rural landscape mosaic with dynamic interfaces between cropland, forest stands, and grasslands (Vega et al. 2009). Anthropogenic activity has accelerated the addition of tree life forms to remnant grassy vegetation on a regional scale, by introducing woody genotypes with novel traits, by increasing propagule pressure and facilitating dispersal, and by altering disturbance regimes. These processes implied the removal of long-standing barriers to tree species establishment in open grassland (Fig. 5.1).

Furthermore, recent surveys suggest that the spread of exotic invasive trees might exert a cascading influence on the distribution of native woody species from adjacent forests. A screening of the central Pampas in 2×2 km cells using Google Earth revealed that trees occur in over 80 % of the cells. Interestingly, field observations indicate that many planted woodlots are being invaded by native forest species, such as *C. tala*, *A. caven*, and *S. australis*, and by widespread exotics, mainly *G. triacanthos*, *M. alba*, and *L. lucidum*. This pattern strongly suggests that tree patches increase the chance of directed immigration of other tree species via animal dispersers. The extent to which such spatial associations are only a matter of increased seed arrival or they reflect some kind of local facilitation to tree recruitment (Tecco et al. 2006; Rolhauser et al. 2011) is not as yet clear. It thus appears that several invasive tree species are past the initial lag-phase characteristic of invasion dynamics at landscape to regional scales (Williamson 1996), and that there might still be a substantial "invasion debt" (*sensu* Richardson and Rejmánek 2011) to be paid in the Pampas.

Historically, successional pathways in the study region have been driven by changes in grazing pressure, soil disturbance from cropping, and pasture ageing (Ghersa and León 1999; Chaneton et al. 2002; Tognetti et al. 2010). Despite obvious alterations of the original grassland composition, the herbaceous life form remained the primary state of the system. Grassland fragmentation and the pervasive introduction of exotic invasive trees have given way to novel, woody-dominated community states developing in old fields, noncultivated areas, and grassland relicts. The overarching implication is that the Pampa grasslands may be doomed, as they would be inevitably converted into savannas or parklands if energy subsidies are not applied to control tree encroachment.

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