



Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina

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ABSTRACT

Exotic plants are major constituents of species pools in modern landscapes. Managing succession for restoration of degraded ecosystems thus requires an understanding of novel trajectories unfolding in mixed, native/exotic plant assemblages. We examined trends in native and exotic species abundance over 20 years of old-field succession on set-aside farmland in the Inland Pampa, Argentina. Changes in plant cover and species richness were annually monitored on adjacent permanent plots established in different years (1978–1989). Both native and exotic species occurred in early, mid and late successional stages, exhibiting similar life-form replacement patterns, from annual forbs, through annual to perennial grasses. Exotic plant richness declined with plot age. Yet, four exotic grasses remained dominant through succession (50–70% cover), with plots initiated in later years showing increased exotic cover. While native perennial grasses occurred from the onset of succession, increasing from 5 to 12 spp/plot, they only showed transient peaks below 30% cover. Cluster analysis of 113 plot-year samples identified alternative community states for early, mid and late successional stages, which were connected by a complex network of interweaving dynamic pathways. Depending on the plot, vegetation dynamics comprised directional temporal trajectories as well as nondirectional pathways, and arrested community states dominated by exotic grasses. Our results illustrate the overwhelming role of exotic species in modern old-field succession, and their potential to hinder recovery of native communities on former agricultural land. Community states with novel, native/exotic plant mixtures could be managed to deliver specific ecosystem services (e.g. forage production, carbon sequestration). However, meeting conservation goals may require active restoration measures, including exotic plant removals and native grass seeding.

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1. Introduction

Efforts to conserve and restore native vegetation in degraded habitats are hampered by the lack of long-term data on secondary succession unfolding in novel ecological scenarios (Pickett et al., 2001; Suding et al., 2004). Modern successional pathways are influenced by species pools, habitat conditions and biotic interactions that are no longer the same that shaped the original communities. In present-day anthropogenic landscapes, native plant communities have been reduced to small, semi-natural remnants, whereas exotic plants have become widespread (Foley et al., 2005; Kareiva et al., 2007). Invasion by exotic species may alter patterns of vegetation recovery in disturbed sites (Cramer et al., 2008), even where native species are able to recolonize through natural dispersal (Foster, 1999; Meiners et al., 2002; Corbin and D'Antonio, 2004; Kulmatiski, 2006). Knowledge of the character of succession in invaded habitats can be used to inform restoration (Lockwood and Pimm, 1999; Prach et al., 2001) by identifying

pathways of vegetation change leading towards desirable states (Young, 2000; Cramer et al., 2008). In particular, there is a need to better understand successional trajectories in mixed, native/exotic communities, and to identify novel vegetation states that may provide various management opportunities and ecosystem services (Young et al., 2001; Foley et al., 2005).

Exotic plant species may contribute to community dynamics at different stages of succession. The realized 'successional niche' (Pacala and Rees, 1998) of native and exotic species will reflect life history attributes represented in the respective species pools (Daehler, 2003; Huston, 2004), as well as interactions during the assembly process (Corbin and D'Antonio, 2004; Cramer et al., 2008). Fig. 1 depicts simplified successional patterns for exotic vs. native plant dominance, assuming that species can be roughly assigned to 'early' and 'late' successional niches (Pacala and Rees, 1998). Firstly, exotic plants often behave as ruderal species invading disturbed sites (Rejmánek, 1989; Daehler, 2003; Fig. 1a), but are eventually displaced by slow-growing native perennials (Meiners et al., 2002; Sarmiento et al., 2003). Second, exotics may reach dominance after a transient period of prevalence by native colonists (Fig. 1b), a pattern that may reflect invasion by long-lived,

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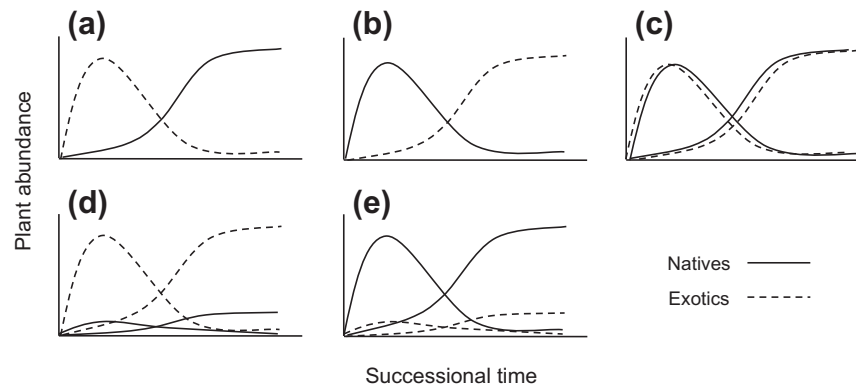


Fig. 1. Simplified models for successional dynamics of native vs. exotic plants. (a) Exotics acting as pioneer species; (b) long-lived exotics become dominant in later seral stages; (c) exotics with different life forms outperform natives throughout succession; (d) natives and exotics coexist across all seral stages; (e) exotics chronically present but contributing little to community dominance.

exotic species (e.g. Vitousek and Walker, 1989; Meiners et al., 2002). Third, as exotic species pools often comprise functionally diverse taxa (Grime, 1998; Huston, 2004), exotics may share the dominance with equivalent native species at different seral stages (Fig. 1c). Indeed, exotics could locally coexist with natives through various mechanisms (Pacala and Rees, 1998; MacDougall et al., 2009). Fourth, exotics with different life strategies might displace their native counterparts throughout succession (Fig. 1d), due to their higher fitness under current environmental conditions (Daehler, 2003; MacDougall et al., 2009). Lastly, exotics might be chronically present whilst having little influence on community dynamics (Fig. 1e; cf. Ortega and Pearson, 2005). These patterns assume that native species typical of different successional stages are not limited by seed availability at the disturbed site. However, in fragmented landscapes, dispersal limitation of native species could reinforce exotic dominance through succession (Seabloom et al., 2003; MacDougall and Turkington, 2005; Standish et al., 2007).

Examining the prevalence of these broad patterns is important because of their varied management implications (Suding et al., 2004; Cramer et al., 2008). However, few long-term studies have focused on exotic plant dynamics during succession. Work conducted in North American old fields show that early exotic colonisers are usually replaced by native perennial grasses or woody plants after ~10–20 years of succession (e.g. Inouye et al., 1987; Collins, 1990; Meiners et al., 2002; Kotanen, 2004; but see Gross and Emery, 2007). Native vegetation recovery has been also observed in cultivated fields of the tropical Andes (Sarmiento et al., 2003). In contrast, in systems such as California annual grasslands (Seabloom et al., 2003), oak savannas in Canada (MacDougall and Turkington, 2005), New Zealand semi-natural grasslands (Wilson et al., 2000), Australian eucalypt woodlands (Standish et al., 2007) and Mediterranean old fields (Domenech et al., 2005), exotic plants appear to have taken over historically disturbed sites, establishing novel vegetation states (Cramer et al., 2008). Whereas most successional studies to date have relied on ‘space-for-time’ substitutions, continuous surveys on permanent plots have been lacking for assessing the role of exotics at various stages of succession (Pickett et al., 2001; Meiners et al., 2002).

We examined 20 years of vegetation changes during old-field succession in the Inland Pampas of eastern Argentina, a landscape extensively transformed to agriculture. Prior work in this system focused on early-successional stages driven by exotic annuals (D’Angela et al., 1986; Facelli and D’Angela, 1990; Omacini et al., 1995). Here, we document long-term trends in plant cover and species richness to determine the extent to which exotic and native plants dominated different stages of succession on set-aside farmland. Specifically, we asked: (1) What is the life-form profile and

overall rank-abundance of exotic and native species? (2) Do exotic and native species show different life-form replacement patterns over time? (3) Is there a predictable, directional shift in dominance from exotic to native plants during succession?, or Is there any evidence that native vegetation recovery might be halted? (4) What alternative community states occur at different stages of succession, and what kind of trajectories connect those vegetation states?

Our analysis was based on annual vegetation surveys conducted during 1979–2004 in eight old-field plots established over a 12-year period. We focused on life-form (defined by species’ growth form and life span) abundance patterns because these may provide a more realistic goal for vegetation restoration (as opposed to restoring specific taxa), where the original flora has been profoundly disrupted by land-use history (Lockwood and Pimm, 1999). Vegetation trajectories were further examined at the species level in order to identify alternative community states at different stages of old-field succession.

2. Methods

2.1. Study site

The study was conducted at Estancia San Claudio, a farm managed by the University of Buenos Aires located in the Inland Pampa, Buenos Aires, Argentina (36° 00’ S, 61° 5’ W). The climate is temperate subhumid, with ~1022 mm annual precipitation for the last 25 years. Mean monthly temperatures vary from 7.2 °C in July to 23.8 °C in January. Soils in cultivated upland sites are Typic Hapludolls (or Haplic Phaeozem, FAO system) developed from loess materials, with a deep and well-drained upper horizon, rich in organic matter (Soriano, 1992). The landscape is a mosaic of crop fields, sown pastures and semi-natural grasslands used for livestock grazing. The original vegetation was a mesic grassland made up of a diverse mix of perennial tussock grasses (Parodi, 1947; Soriano, 1992). Relict (unplowed) native grasslands are scarce and largely confined to corridors along old railway tracks and roadsides. The regional flora comprises many naturalized, nonnative species mostly from central Europe and the Mediterranean (Rapport, 1996; Ghersa and León, 1999; Prinzing et al., 2002). Exotic species represent about 25% of the regional vascular flora (Rapport, 1996).

The study system comprised 10 adjacent plots located at the centre of a 290-ha field, which was cultivated for at least 60 years. Since the beginning of the study in 1978, crop rotations involved wheat, maize, sunflower and soybean. In 1990–1995, the field was turned into pasture and managed for cattle. Each year between

1978 and 1989, excepting 1985–1986, one 40 × 100 m plot was left fallow and fenced to exclude domestic grazing (Table 1). Newly fenced plots were adjoined by their longest side, forming a large strip of uncultivated habitat surrounded by crop land. The closest remnant of unmanaged native grassland with a rich mixture of perennial grasses (~34 species) was located 5 km north-west of the study site. However, many native grass species persist as small, fragmented populations embedded in the agricultural matrix (e.g. Poggio et al., 2010). Thus, propagules of native species were available in the surrounding landscape, though probably in low numbers. Old-field vegetation was sampled annually in late spring (December), allowing for the high richness of winter-spring species. At the time of sampling, summer species just started flowering but were identifiable by vegetative traits. In each plot, the percent cover of all vascular plant species was estimated for 20 quadrats (1 m²) placed at random along four parallel transects; these estimates were averaged before analysis. Sampling was interrupted during a period of severe floods in 1985–1986. For the present study, we used data from eight plots, excluding plots C and D, which were accidentally burned shortly after abandonment; for the same reason, sampling in the oldest plots (A and B) was discontinued. Thus the number of replicates for any given age ranged 2–8 plots (Table 1).

2.2. Data analysis

Plant species were classified as native or exotic according to their geographical origin. Exotics were all species originating from other continents, including taxa from Eurasia, Africa, Australia and Central America. Species were ranked in order of relative abundance based on their average cover across all plant surveys (=113 plot-year samples). An overall species rank-abundance distribution was then constructed to assess exotic and native species presence amongst dominant, subordinate and transient (rare) species (Grime, 1998). Species were also classified by growth form into forbs and grasses (all monocots), and by life span into annuals (including biennials) and perennials, which resulted in four major life-form groupings. A maximum likelihood χ^2 test was performed to test whether native and exotic species pools differed with respect to the proportions of these life forms.

The overall pattern of succession was examined by taking each plot as a replicate. For each successional age (number of years since last crop), the mean cover (\pm standard error) and species number (richness) of native and exotic plant groups were computed for plots reaching that age in different calendar years (D'Angela et al., 1986; Omacini et al., 1995). We looked for consistent trends in native and exotic plant groups within and among plots using linear mixed models (Pinheiro and Bates, 2002; Crawley, 2007). Changes in plant cover and richness were evaluated as a function of plot age (1–20 years) and year of abandonment (coded 1–8),

Table 1
Plots used to study patterns of vegetation recovery during old-field succession in the Inland Pampa, Argentina.

Plot	Last crop	Year ^a	Sampling (plot age)	<i>n</i>
A	Sorghum	1978	[1] 2–7 [8,9] 10	7
B	Maize	1979	1–6 [7,8] 9	7
E	Maize	1982	1–3 [4,5] 6–17	15
F	Maize	1983	1–2 [3,4] 5–20	18
G	Sunflower	1984	1 [2,3] 4–20	18
H	Wheat	1985	[1,2] 3–19	17
I	Sunflower	1988	1–16	16
J	Sunflower	1989	1–15	15

^a Year in which the plots were abandoned from agriculture. Each plot was annually sampled for plant cover in December (late spring), except for successional ages shown in brackets. *n* = number of data points per plot used in the analyses.

with both these factors modelled as random effects. The year of abandonment (see Table 1) could affect succession through initial conditions, climatic history and propagule availability, including the influence of previously established plots (Pickett et al., 2001), and reflected the temporal sequence in which the plots were established at the study site (Facelli and D'Angela, 1990; Omacini et al., 1995). A significant 'plot effect' would thus be interpreted as a consistent trend in average plant cover or richness among study plots, irrespective of plot ages. The number of data points for a given plot varied between 7 and 18 (Table 1). Furthermore, our study design implied a certain amount of temporal autocorrelation within plots. Hence, we used a first-order autoregressive correlation structure (Pinheiro and Bates, 2002) to model the effect of successional age on vegetation variables. The model goodness-of-fit was examined through the correlation between predicted and observed values, and was tested using approximate likelihood-ratio tests (Crawley, 2007). Residual analyses revealed non-linear trends in the cover of various plant groups, which were accounted for by including a quadratic term for plot age. Analyses were conducted using the *lme* function in the *lme4* package of the R statistical software (Bates et al., 2008).

We used hierarchical cluster analysis to identify alternative community states during succession (Austin, 2005). All vegetation censuses (*n* = 113 plot-year samples) were classified through the furthest-neighbour method using a cut-off point of 25% of the maximum group distance (McCune and Mefford, 1999). This method applies an agglomerative algorithm in which the compositional distance between groups of samples (clusters) is defined by the greatest pairwise distance between members in each group. The procedure emphasizes differences between clusters and is best suited for dissecting complex datasets into clear-cut units (Greig-Smith, 1983; Austin, 2005). We used Sørensen's quantitative distance measure, which is appropriate for heterogeneous data sets. Species occurring in less than 5% of the samples were excluded, yielding 99 species for analysis. To summarize the dynamic relations among vegetation states, we calculated transition probabilities from the particular temporal paths followed by each study plot. The transition probability (*p*) between two states, or clusters, was computed as:

$$p_{m-n} = K_{m-n}/T_m$$

where K_{m-n} is the number of plots that moved from state 'm' to state 'n' between two consecutive years, and T_m is the total number of samples classified into state 'm'. We also calculated the probability of a plot remaining in a given state for two consecutive years as the number of times a plot remained within cluster 'm' from one year to the next divided by the total number of samples in that cluster. This allowed us to identify vegetation states in which succession might be temporarily arrested, as well as to detect community states that were revisited at different times within the time-frame of study (nondirectional trajectories). Note that since end-point samples along a given plot trajectory, by definition, did not change their community state at the time of last sampling, *p* values for some states may not sum up to 1.

3. Results

3.1. Composition of the successional flora

Exotic species were a major component of old-field communities. We recorded a total of 149 herbaceous species, of which 40% were introduced to the original pampas. Although exotics occurred in all life-form groupings (Fig. 2a; see Supporting data Table S1), the life-form composition of the native and exotic species pools differed substantially ($\chi^2 = 33.9$, $P < 0.0001$, $df = 3$). From a total

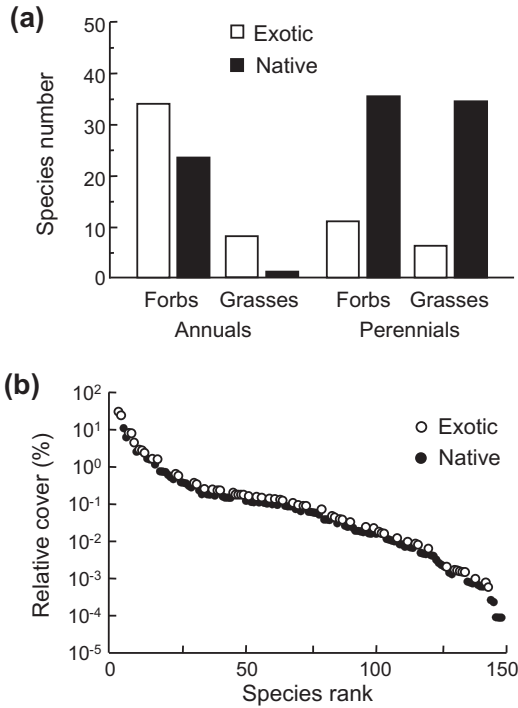


Fig. 2. Overall contribution of native and exotic species to the successional flora. (a) Number of native and exotic species by life form and life span. (b) Species rank-abundances from the relative mean cover of all species recorded in 113 plot-year samples (exotics slightly displaced for clarity).

of 59 exotics, most (71%) were annuals and 60% were annual forbs (Fig. 2a). In contrast, the native species pool (89 spp) was dominated by perennial taxa (74%). Old-field plots harboured 23 native perennial grasses (including 12 other monocots); most native species were annual or perennial forbs (Fig. 2a; Table S1).

Exotics occurred throughout the species rank-abundance distribution. Indeed, abundance curves for native and exotic species were strikingly similar (Fig. 2b). Overall, the two most abundant species were the exotic grasses *Cynodon dactylon* and *Lolium multiflorum*. Among the top 16 ranked species (>1% mean cover), 10 were exotics and seven were annual/biennial taxa (five exotic). The highest ranked native was the short-lived perennial *Bromus*

catarticus, which only attained half the cover of the top two exotics. Other native grasses of the pristine pampas were placed much lower (below the 30th species) in the rank-abundance distribution.

3.2. Overall pattern of succession

Total plant richness decreased over successional time (Table 2). On average, old-field communities experienced a net loss of about one species per year. After 15 years of succession, richness decreased from about 42 spp to less than 25 spp/plot. This trend was largely explained by a decline in annual species (from 26 to 6 spp/plot, $r^2 = 0.85$, $P < 0.0001$). Perennial plant richness averaged 18 spp/plot showing no temporal trend ($r^2 = 0.04$). Both exotic and native plant richness decreased along succession (Table 2, Fig. 3a).

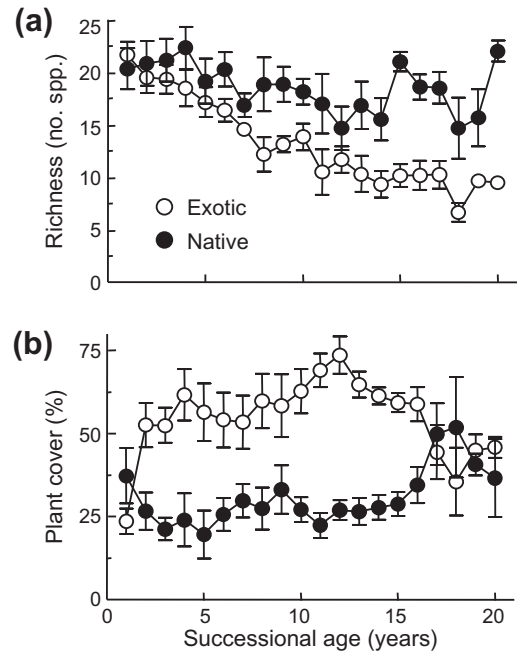


Fig. 3. Trends in total plant richness (a) and absolute cover (b) of native and exotic species during old-field succession in the Inland Pampa. Data show means ± SE for plots reaching a given age in different years ($n = 2-8$).

Table 2

Linear mixed-effect models for the influence of successional time (age) and year of abandonment (plot) on native and exotic plant richness and absolute cover in old-field communities of the Inland Pampa, Argentina. For each model ($n = 113$), values show partial linear coefficients for each factor, correlation coefficient between predicted and observed values (r) and likelihood-ratio statistic (LR). Non-significant quadratic terms ($P > 0.10$) were excluded from final models.

Life form	Species richness				Plant cover				
	Age	Plot	r	LR	Age	Age ²	Plot	r	LR
All species	-0.93***	-0.25	0.562	28.90***	3.98***	-0.15***	3.09***	0.706	60.30***
All natives	-0.22*	-0.16	0.251	7.45*	-2.03*	0.12***	0.18	0.334	9.39*
All exotics	-0.71***	-0.08	0.749	93.14***	5.96***	-0.27***	3.03*	0.588	36.85***
Native annual forbs	-0.26***	-0.03	0.628	56.79***	-3.27**	0.13***	0.37	0.564	43.27***
Exotic annual forbs	-0.57***	-0.14	0.791	111.15***	-2.84***	0.09***	-0.76*	0.623	43.95***
Native annual grasses	-	-	-	3.01 ^{ns}	-	-	-	-	3.11 ^{ns}
Exotic annual grasses	-0.05***	-0.05	0.405	20.34***	3.64***	-1.64***	-2.22**	0.518	29.52***
Native perennial forbs	-0.19***	-0.13	0.453	23.69***	-1.53***	0.08***	-0.17	0.391	18.96***
Exotic perennial forbs	-0.15***	-0.05	0.548	39.84***	-0.90***	-	1.79**	0.592	36.43***
Native perennial grasses	0.24***	0.04	0.501	30.29***	2.82**	-0.08*	0.09	0.487	24.31***
Exotic perennial grasses	0.06***	0.21**	0.641	32.13***	5.71***	-0.19***	3.25**	0.808	101.99***

* $P < 0.05$.
 ** $P < 0.01$.
 *** $P < 0.001$.

The net species loss rate was significantly higher for exotics than for natives (difference between slopes, $F_{1, 222} = 22.2$, $P < 0.0001$). As a result, in older communities native plant richness doubled the exotic richness (Fig. 3a).

Total plant cover increased up to 85–90% after seven years of succession and remained so in older communities. Regardless of plot age, total plant cover tended to be higher in study plots that initiated succession in more recent years (Table 2). Exotic species consistently accounted for a large fraction (>50%) of the total plant cover, nearly doubling the native cover for the first 16 years of succession (Fig. 3b). Yet exotic plant cover depicted a quadratic pattern with a tendency to decrease in older communities (Table 2, Fig. 3b). Native species only matched the cover of exotics at the beginning and in later stages of succession.

3.3. Trends in exotic vs. native plant richness

The richness of all forb species groups decreased over time (Table 2), but this trend was especially pronounced for exotic annual forbs, which were the most diverse group during early succession (Fig. 4a and c). The richness of annual grasses was consistently low, regardless of plant origin (Fig. 4b). Both native and exotic perennial grasses significantly increased their mean richness with plot age (Table 2, Fig. 4d). However, native grasses outnumbered their exotic counterparts throughout the study; exotic grasses generally comprised only 4 spp/plot, whereas native perennial grasses increased from nearly 5 to 12 spp/plot (Fig. 4d).

The year of plot abandonment had only a small influence on plant species richness. As indicated by a significant ‘plot’ effect

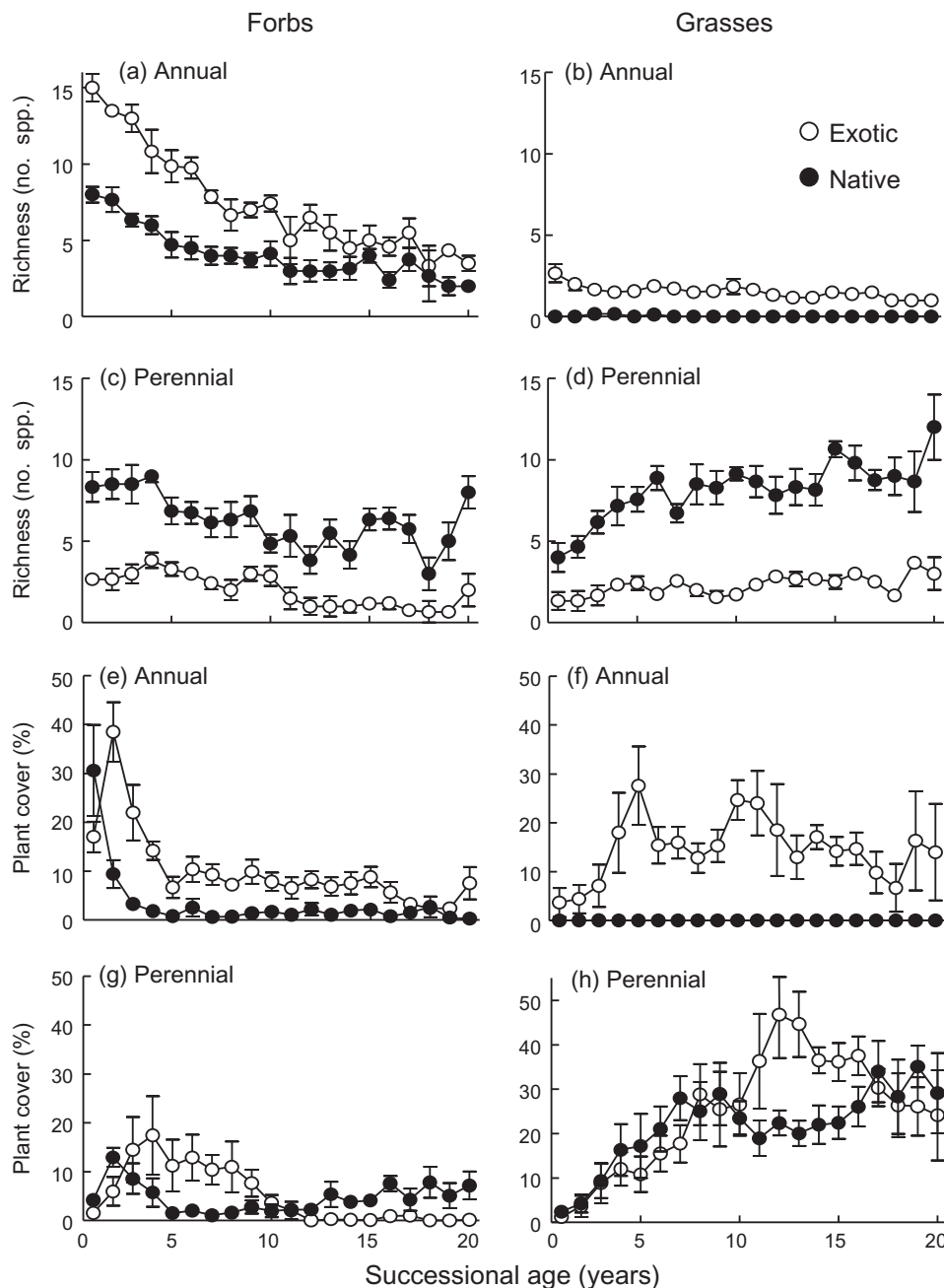


Fig. 4. Successional trends in plant richness (a–d) and absolute cover (e–h) of native and exotic species grouped by life form and life span. Annual forbs (a and e), annual grasses (b and f), perennial forbs (c and g) and perennial grasses (d and h). Data show means \pm 1 SE, as in Fig. 3.

(Table 2), on average, the richness of exotic perennial grasses increased in more recently established plots (e.g. I and J), relative to that observed in plots abandoned in earlier years (e.g. A and B, see Table 1).

3.4. Changes in exotic vs. native plant abundance

There was an overall trend for annual forb species to be replaced by perennial grasses (Table 2, Fig. 4e–h). Both exotic and native annual forbs declined abruptly within two years of succession, although exotics persisted at higher cover values (Fig. 4e). Conversely, after a rapid early increase, exotic annual grasses remained a major component of these plant communities within the time-frame of study (Fig. 4f). The perennial vegetation matrix was made up of both native and exotic species. Exotic perennial forbs were more abundant than their native counterparts during earlier stages of succession, whereas the reverse was true in later stages (Fig. 4g). Exotic perennial grasses depicted a strong unimodal pattern over time (Table 2) and dominated mid-successional communities (Fig. 4h). Native perennial grasses increased up to 25–30% within 10 years of succession and then levelled-off, becoming slightly more prevalent in older plant communities (Fig. 4h).

Only three native grasses attained substantial cover (>10%) during succession (Fig. 5). Tussock grasses common in the pristine grassland generally exhibited very low cover (<3%) in our study plots (see Table S1). Exotic species with different life forms played a dominant role at different stages of succession (Fig. 5). The broad-leaved forbs *Carduus acanthoides* and *Hypochaeris radicata* prevailed in early and mid-successional stages. The perennial grasses *C. dactylon*, *Sorghum halepense* and *Festuca arundinacea* be-

came dominant in mid to late-seral stages, even though they colonized shortly after abandonment. Lastly, the annual grass *L. multiflorum* exhibited a persistent, cyclical pattern, with peaks up to 45% cover occurring every 5–7 years of succession (Fig. 5).

The year of abandonment significantly affected the cover of exotic species per plot. A positive 'plot' effects on exotic perennial grasses and forbs (Table 2) indicated that, on average, these groups became more abundant in those plots initiating succession in more recent years. Conversely, the negative plot effect for exotic annual forbs and grasses signified that these pioneer groups attained lower covers in newly established plots (Table 2).

3.5. Vegetation states and successional pathways

Cluster analysis produced 10 groups of samples (or vegetation states), which corresponded to early, mid and late successional stages, according to plot ages and mean floristic distances among clusters (Fig. 6; Table S1). Each cluster included samples from different study plots. Succession initiated from three alternative 'early' states dominated by exotic and native forbs (Fig. 6; Table S1). The 'mid' successional stage comprised four clusters with plots ranging 3–19 years old. These communities were variously dominated by annual and perennial exotic species, and a few native grasses (Table S1). 'Late' vegetation states comprised three clusters of plots ranging 6–20 years old, which were characterized by perennial grasses or forbs, and occurred in different localities within the study area (Fig. 6). Only one state (L3) contained a high proportion of native species, and these were typical of lowland habitats. Most vegetation states had exotics among their dominant species, whereas those dominated by native spe-

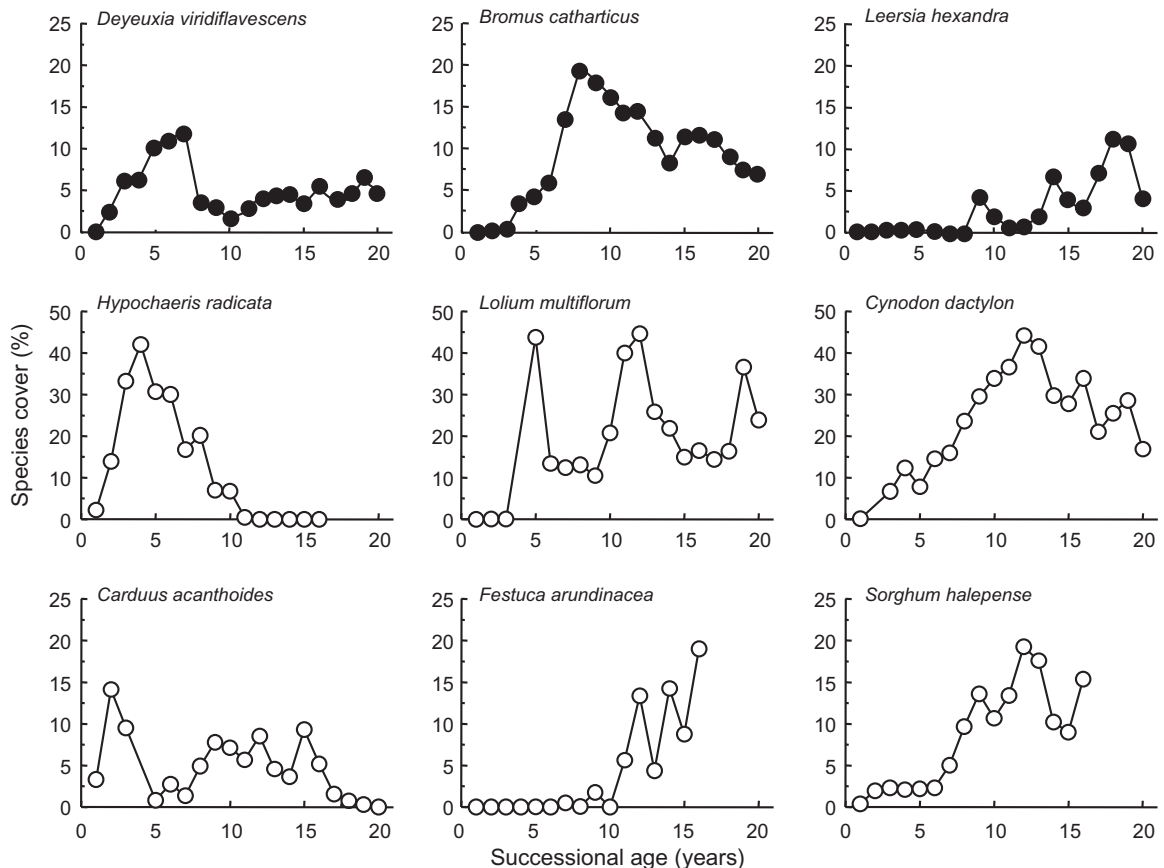


Fig. 5. Dynamics of dominant native and exotic plant species during old-field succession. Data show mean cover per plot for native (solid symbols, upper panels) and exotic (open symbols, middle and lower panels) plant species. Error bars were omitted for clarity.

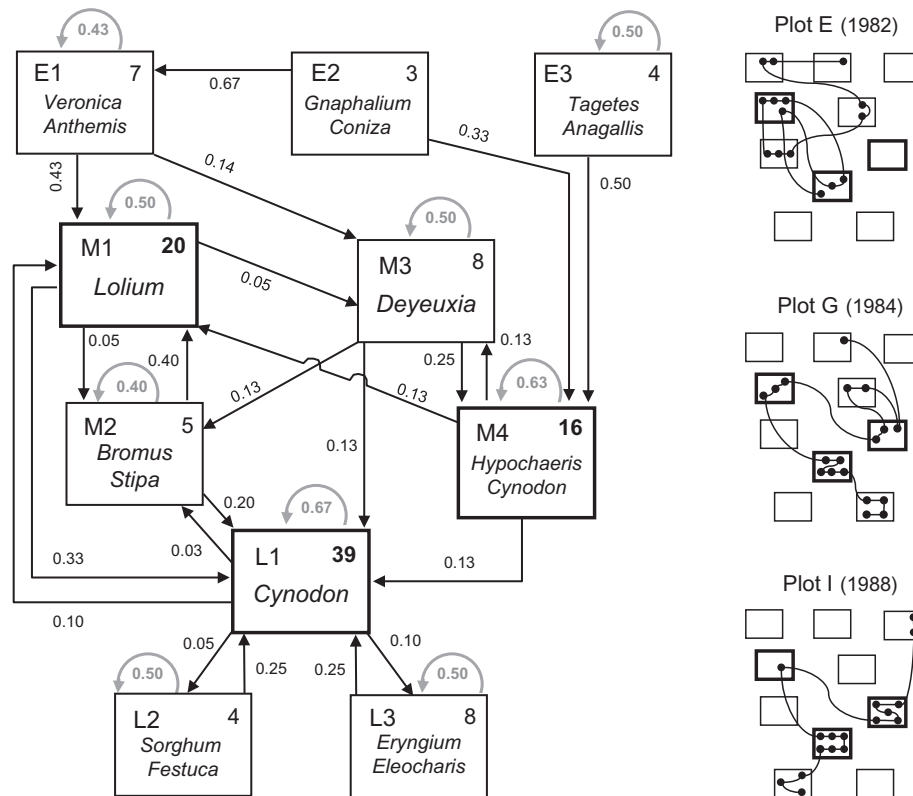


Fig. 6. Summary model for 20 years of succession on set-aside farmland in the Inland Pampa. Boxes represent early (E), mid (M) and late (L) successional community states identified by cluster analysis, with states labelled by their main indicator species. Thick lines highlight states comprising the largest number of samples. Arrows depict transitions between states and their associated probabilities; bow arrows show the probability of a plot persisting in the same state between consecutive years. Insets: successional paths followed by three representative study plots.

cies (E2, M2, M3 and L3) comprised a small (<7%) fraction of all samples (see Fig. 6).

Different study plots often followed alternative successional paths (Fig. 6: insets), but there still were repeatable vegetation states. Communities dominated by the exotics *L. multiflorum* and *C. dactylon* were central to the system's dynamics; together, these comprised 67% of all samples (Fig. 6; Table S1). The *Lolium* (M1) and *Cynodon* (L1) states occurred in all the trajectories, but appeared at different successional ages depending on the specific plot. The *Cynodon* states (M4 and L1) showed the largest internal 'loops' (Fig. 6), indicating that these communities retained their composition over several years.

4. Discussion

This long-term study assessed the potential for recovering native grassland communities through old-field succession. One possible outcome was that early-successional weeds, comprising both exotic and native annual forbs, would be replaced by native perennial grasses immigrating from seed sources scattered within the agricultural matrix (Poggio et al., 2010). We have monitored up to 20 years of vegetation changes in plots established over a 12-year time span. Exotic species not only dominated early seral stages but were also a major component of older communities, thus pervasively dominating succession on set-aside farmland (Fig. 1d). Although several native prairie grasses were present from the outset (Omacini et al., 1995), these remained relatively rare throughout the study. These results suggest that recovery of native grasslands in the Inland Pampa may not be just a matter of time (cf. Kotanen, 2004) but may require active restoration strategies (Suding et al., 2004; Cramer et al., 2008). This lack of recovery counters

the outcome of succession reported for other pampean grasslands in less fragmented landscapes, in which native plant communities were re-assembled within a few years after management cessation (Chaneton et al., 2001).

4.1. Rank-abundance status of exotic species

The similarity in rank-abundance structure between native and exotic species pools (Fig. 2b) illustrates the extent to which introduced species may contribute to create novel plant assemblages in disturbed habitats (Hobbs et al., 2006). Exotics occurred as dominant, subordinate and transient species, a pattern that would reflect the presence of both 'strong' and 'weak' invaders (Ortega and Pearson, 2005; MacDougall and Turkington, 2005). This suggests that exotic species may play various roles in 'modern' successional systems. The mass-ratio theory (Grime, 1998) posits that species in different abundance categories play distinct ecological roles. Dominant species would be major determinants of community structure. Subordinate species occupy interstitial microhabitats left by the dominants and together with the least abundant, transient species, may influence early community assembly and the potential recovery of late-successional plants (Grime, 1998; Corbin and D'Antonio, 2004).

4.2. Life-form dynamics of exotic and native plants

Most exotics were annual or biennial forbs with subordinate or transient roles at the whole-system level (Fig. 2). Exotic plant invasions are often associated with disturbances and high resource availability (Daehler, 2003; Huston, 2004; Blumenthal, 2006), and hence short-lived exotic species often prevail in early-successional

habitats (Rejmánek, 1989; Meiners et al., 2002). The initial dynamics of succession (see Fig. 4e) suggest that exotic annuals may perform better than native ruderal species in exploiting conditions created by agricultural disturbance. The Pampas have been invaded by a rich flora of fast-growing Eurasian forbs, which appear to be pre-adapted to current disturbance regimes (Rapport, 1996; Prinzing et al., 2002). An experiment combining seed and nutrient additions at the onset of succession showed that, in this system, exotic ruderal forbs outperform their native counterparts under resource-rich conditions (Tognetti and Chaneton, unpublished data).

Pioneer exotic forbs were mostly replaced by exotic grasses from disparate biogeographic origins. These included the annual *L. multiflorum* (Mediterranean), the prostrate clonal *C. dactylon* (Africa), the tall rhizomatous *S. halepensis* (Eastern Mediterranean), and the tussock pasture grass *F. arundinacea* (Europe), which made up novel but persistent community types (see also Kulmatiski, 2006). Native and exotic species displayed broadly equivalent life-form sequences occupying early, mid and late successional stages (Fig. 4e–h). These patterns are consistent with the view that exotic and native species may show similar population dynamics during succession (Meiners, 2007). The extended dominance by exotic plants in this old-field system was in stark contrast with trends reported for other temperate systems (Inouye et al., 1987; Collins, 1990; Prach et al., 2001; Meiners et al., 2002). Although only a few exotic grasses dominated late-seral stages, these species outperformed a richer assemblage of co-occurring native grasses (Fig. 4). Several native perennial grasses colonized after the cessation of agriculture, but they rarely attained dominance except for short periods (see Fig. 5; Omacini et al., 1995).

The low abundance of perennial grasses typical of pristine pampas might be accounted for by different factors. First, seed-limited dispersal can determine the lack of recovery of native plants in extensively transformed landscapes (Seabloom et al., 2003; MacDougall and Turkington, 2005; Standish et al., 2007). It is then possible that distance to remnant seed sources and local propagule availability (D'Angela et al., 1988) would be limiting the chances of re-establishing native grass populations. This hypothesis was supported by seed addition experiments conducted at different stages of old-field succession (Tognetti and Chaneton, unpublished data). Second, rapid invasion by exotics may prevent re-colonization by native grasses through priority effects (Kulmatiski, 2006; Cramer et al., 2008). Moreover, exotic grasses may be better competitors than putative native dominants under current conditions (Daehler, 2003; MacDougall et al., 2009), which could explain why several native grasses failed to increase despite being present from the beginning of succession (Foster, 1999). This idea is consistent with a study in which the old-field initial composition was manipulated by sowing different mixtures of native and exotic species. Seed sowing allowed recovery of a native grass-dominated community, unless exotic perennial grasses were included in the initial mixture. The latter condition generated an alternative community state strongly dominated by introduced forage grasses (Tognetti and Chaneton, unpublished data). If exotics occupy similar niches as their native counterparts but exhibit higher fitness, then modern successional systems might offer little opportunities for coexistence of native and exotic species (MacDougall et al., 2009). The observed slow increase in native grass richness (Fig. 4d) further suggests that their full recovery could be enhanced by removing exotic grasses through prescribed disturbances (Young et al., 2001; Gross and Emery, 2007).

The same life-form sequence was broadly repeated among adjacent plots, although plots that initiated succession in more recent years exhibited increased dominance by exotic perennial grasses (Tables 1 and 2). We do not know what factors have driven this pattern, yet conditions favouring exotics appeared to have been reinforced in recent times. This temporal trend in invasion magni-

tude may reflect the influence of large-scale processes such as climatic change and agricultural intensification (Ghersa and León, 1999; Hobbs et al., 2006). Indeed, successional plots were invaded by *F. arundinacea* only after the surrounding field was converted into pasture in 1990–1994 (see Fig. 5). Local population processes including spread from adjacent plots (Pickett et al., 2001) likely contributed to accelerate grass invasions.

4.3. Trends in exotic vs. native plant richness

Total species richness decreased with successional age, being driven by the loss of both exotic and native forb species (Fig. 4). These pioneer plants emerge in early spring or autumn, and therefore their regeneration may be interfered by the increased cover of fast-growing exotic grasses (Fig. 5; Chaneton et al., 2001). This pattern was consistent with the faster decline of exotic annual forbs observed in newly established plots dominated by invasive grasses (see Table 2). The impact of exotic grass mixtures on the richness of short-lived plants may be associated with their ability to produce a thick litter layer in different seasons (Foster and Gross, 1997; Wilsey et al., 2009).

The overall loss of early-successional native and exotic forbs suggests that their dynamics might be governed by similar processes (Pacala and Rees, 1998; Meiners, 2007). However, the much faster decrease of exotic annuals (Fig. 3b) also suggests that different mechanisms could maintain native and exotic species richness. Wilsey et al. (2009) showed that short-term diversity losses in all-exotic plant assemblages were more pronounced than in equivalent, all-native assemblages. Competitive exclusion of weak invaders by exotic grasses may reflect lack of niche complementarity among species that did not share a coevolutionary history (Wilsey et al., 2009). The lower extinction rate of native annual forbs might be due to subtle differences in life-history strategy allowing them to persist by exploiting ephemeral resources in the presence of exotic grasses (MacDougall et al., 2009).

4.4. Alternative trajectories and community states

Whereas plant life forms showed broadly repeatable patterns across study plots, at the species level, individual plots followed various temporal trajectories (Fig. 6). Such differences in the predictability of successional pathways has been associated with the stochastic influence of environmental fluctuation and species dispersal (Pickett et al., 2001), as opposed to the deterministic sorting of functional traits (Fukami et al., 2005). Cluster analysis identified alternative community states connected by a complex network of interweaving pathways. The system dynamics comprised directional temporal trajectories as well as nondirectional loops, as depicted by plots returning to a community state already 'visited' in prior years (Fig. 6: insets). A striking example were the plots established during 1978–1983, in which vegetation dynamics was partly driven by fluctuations in *L. multiflorum* cover (Fig. 5). Further, old-field succession often became temporarily arrested when dominated by exotic grasses. The prevalence of *L. multiflorum* and *C. dactylon* during mid succession (Fig. 6) suggests a high degree of community inertia likely associated with the presence of highly competitive exotic species (von Holle and Simberloff, 2004). The greater directionality of succession in more recently established plots (1984–1989) might reflect the fact that those plots had a large cover of perennial grasses and a lower cover of annual forbs (Table 2).

4.5. Management implications

Patterns of exotic and native plant dominance in the Inland Pampa illustrate the overwhelming role that invasive species can

play in modern succession. Given the extent of the human footprint on the Earth's ecosystems (Kareiva et al., 2007), the kind of exotic plant-driven dynamics described here may become rather common, unless propagule sources for historically dominant native species are preserved and management efforts are directed to promote their re-establishment (Suding et al., 2004; Cramer et al., 2008). Our results suggest important lessons for the restoration of semi-natural vegetation on set-aside land. However, we concur with previous analyses in that restoration must be guided by clear goals (Lockwood and Pimm, 1999; Prach et al., 2001; Young et al., 2001).

If the goal were preserving native plant biodiversity, the pervasive occurrence of exotic species filling different successional niches may strongly hinder the possibility of recovering native communities through succession. In highly fragmented landscapes like the Inland Pampas, the system may have crossed a biotic 'threshold' towards an alternative state defined by a novel set of (exotic) plant species (Cramer et al., 2008). Thus, restoration would require large subsidies involving the addition of native grass seeds and the control of certain exotic species in order to accelerate succession. The challenge remains to identify successional states most susceptible to invasion by native grasses, provided seeds are added in sufficient quantities (Seabloom et al., 2003). We suggest that early community states might be targeted for sowing native grasses. Restoring native grass communities would be more feasible if measures are taken to prevent establishment by exotic grass species.

On the other hand, if we were interested in restoring ecosystem functions, then alternative vegetation states with novel plant mixtures could be managed to deliver specific services. It may thus be possible to restore desirable functions associated with certain plant functional groups, regardless of the species' origin (Lockwood and Pimm, 1999; Suding et al., 2004). For instance, in our system, fast-growing exotic grasses invading after a few years of succession may be encouraged for fodder production. This could be achieved using mowing, prescribed burns, or grazing animals as management tools to halt succession at desired states. We recognize that this approach may need a drastic shift in current perspectives on the role of exotic plants in modern ecosystems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.06.016.

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