



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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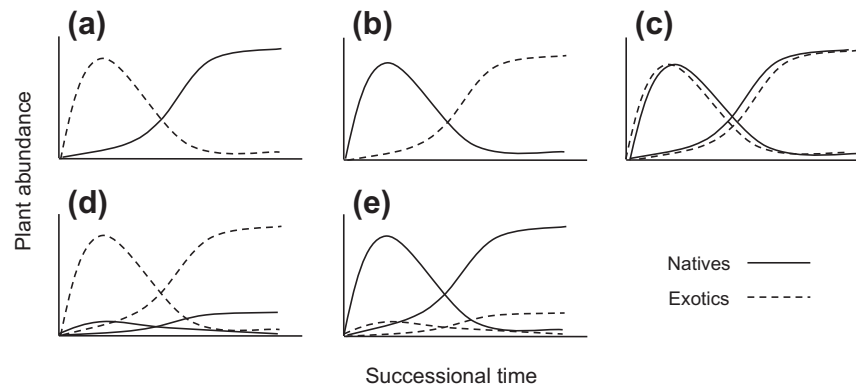


Fig. 1. Simplified models for successional dynamics of native vs. exotic plants. (a) Exotics acting as pioneer species; (b) long-lived exotics become dominant in later seral stages; (c) exotics with different life forms outperform natives throughout succession; (d) natives and exotics coexist across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

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