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Simulating the effects of different disturbance regimes on *Cortaderia selloana* invasion

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ABSTRACT

Disturbances favour plant invasions because they provide a pulse of resources for seedling establishment and growth. However, little attention has been paid to the importance of the different disturbance regimes in the extent of invasion. In this paper we asked to what extent invasion depends on spatial and temporal patterns of disturbance. By using the spatially explicit model FATELAND, we simulated how *Cortaderia selloana*, a large-wind dispersed perennial grass invading Mediterranean grasslands, responds to different medium-term (up to 55 years) disturbance regimes. The different scenarios combine disturbance frequency, extent of disturbance and temporal and spatial disturbance variability, and they roughly mimic real situations of habitat management and disturbances in cultural landscapes.

The model predicted that the proportion of invaded area would increase with disturbance frequency. The extent of the disturbance overcame the importance of frequency. Aggregated disturbances randomly distributed in space had a more positive effect on invasion than scattered disturbances at repeatedly fixed locations. Whether the disturbances regularly occurred in time or were irregularly distributed did not influence the percentage of invaded landscape. Our simulation analysis unambiguously supports the hypothesis that disturbances are essential for the persistence and expansion of *Cortaderia sellona*. The high amount of seed rain from a few individuals (e.g., gardens) make this species very sensitive to landscape changes produced by different disturbance patterns (e.g., land abandonment, habitat management or rubbish dumping). Our results can contribute to redirect land management options.

1. Introduction

Invasions by alien species are one of the global change factors threatening the conservation of native species and the integrity of ecosystems worldwide (Vitousek et al., 1996; Mack et al., 2000; Levine et al., 2003) with important economic costs (Higgins et al., 2000; Pimentel et al., 2000; McNeely, 2001). The potential of an alien plant species to invade natural ecosystems depends on the number and frequency of the propagules introduced (i.e., propagule pressure), the species life-traits, and the invasibility and resistance of the recipient ecosystem to invasion (Lonsdale, 1999). One of the factors increasing ecosystem invasibility is disturbance (Burke and Grime, 1996; Alpert et al., 2000). Several studies have shown a higher

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abundance of alien plant species, or a better performance of particular plant taxa, in human-disturbed habitats than in natural ones (Hobbs and Huenneke, 1992; Pysek, 1994; Robinson et al., 1995; Lambrinos, 2002). Disturbances provide both "windows of opportunity" (sensu Myster, 1993) for the entrance of alien propagules and increases in the quantity of resources per capita, including space for establishment and growth (Hobbs and Huenneke, 1992; Davis et al., 2000). Furthermore, human-disturbed areas are also often associated with human activities (e.g., agriculture, gardening, road systems, tourism) that promote the arrival of alien species (Frenot et al., 2001; Hansen and Clevenger, 2005).

Disturbances are complex. Disturbance regimes better explain the set of spatial and temporal disturbance characteristics occurring in a territory, including extent, shape, frequency, season, intensity and severity, among others (Sousa, 1984; Moloney and Levin, 1996). Though the disturbance regime has been successfully explored in many ecological contexts (e.g., Moloney and Levin, 1996; Pausas, 1999; Lloret et al., 2003), it has rarely been applied to the invasion process by alien plants (Vujnovic et al., 2002; With, 2002; Huston, 2004), despite that it is a driver of fluctuating resource availability (Davis et al., 2000; Davis and Pelsor, 2001), and thus it may increase invasibility.

To consider both the spatial and temporal aspects of a disturbance regime on invasion, a simulation approach is appropriate because it allows working at large spatial and temporal scales (Higgins and Richardson, 1996). Most of the models used for predicting the rate of plant invasion (Marco et al., 2002; Cannas et al., 2003) are based on the arrival of the new species in an empty (bare) land (Higgins et al., 1996). However, this situation is not always realistic; usually, invasion starts in a vegetated area. Therefore, simulations should be based on the life history and competitive attributes of both the invading species and the dominant species in the "host" ecosystem (Cannas et al., 2003).

Cortaderia selloana (Schultes) Asch. & Graebner) (pampas grass) is a perennial, tussock grass native to South American pampas (Argentina, southern Brazil, and Uruguay) that has been introduced in many regions of the world as a garden plant because of its showy plumes, and also for dryland forage, soil amendment, and windbreaks (Harradine, 1991). In many regions, including some Mediterranean ecosystems, *C. selloana* (*Cortaderia* hereafter) has become invasive (Bossard et al., 2000; Lambrinos, 2001, 2002). In Spain, this species has escaped into wetlands, oldfields and coastal grasslands. More specifically, in the protected coastal wetland areas of Catalonia (NE Spain), this species has become a major conservation concern because its invasion of oldfields prevents their restoration back to wetlands where some rare or endemic species occur. *Cortaderia* can reach 2–4 m in height, forming a large fountain-like tussock with sharply serrated leaves. The inflorescence consists of showy plume-like heads at the end of a stiff stem. Each plant can produce about a million wind-dispersed viable seeds (Connor and Edgar, 1974; Lambrinos, 2002). Invasion by *Cortaderia* can drastically alter ecosystem properties (e.g., flammability, diversity, food webs), as has been demonstrated for the morphologically similar *Cortaderia jubata* (Lem.) Stapf (Bossard et al., 2000; Lambrinos, 2000).

We used a spatially explicit model to explore *Cortaderia* invasion patterns in relation to several disturbance regimes that mimic relevant management scenarios occurring in the Catalonian region (NE Spain), also typical of other Mediterranean basin areas. Our main questions were: (1) To what extent does invasion depend on disturbance frequency? (2) Do different temporal patterns of disturbance (i.e., regular vs. irregular) modify invasion? (3) Is the extent of the disturbance more relevant than the disturbance frequency? (4) Do changes in the spatial variability of the disturbance (i.e., random vs. fixed and aggregated vs. sparse occurrence of disturbance) affect invasion? To our knowledge this is the first time that different components of a disturbance regime are disentangled to predict their effect on the degree of community occupancy by a wind-dispersed alien plant.

2. Methods

2.1. *Modelling*

We used a spatial-explicit version of FATE (Moore and Noble, 1990) called FATELAND as implemented in the LASS modelling environment (Pausas and Ramos, 2004, 2006; available at www.ceam.es/lass). FATE is a non-spatial semi-quantitative vegetation dynamics model specifically designed for disturbance-prone ecosystems. FATE was elaborated for Australian communities and later tested for Mediterranean ecosystems (Pausas, 1999; Lloret et al., 2003). FATE is based on the life history traits of individual plants at stand level where several species may coexist. Vegetation dynamics are qualitatively predicted from simple parameters describing species traits. The model runs at annual time steps and simulates cohorts of plants that pass through a series of four discrete stages: propagules, seedlings, immature and mature plants. In FATE there are three levels of light availability (low, medium, high) determined by the vertical structure of the vegetation (stratum). Germination and survival are determined on the basis of these light availability levels, and changes in light availability are due to species overtopping one another (for further details see Moore and Noble, 1990; Pausas, 1999; Cousins et al., 2003).

FATELAND incorporates the spatial component missing in FATE; that is, FATELAND corresponds to a 2-dimensional array of cells, and the FATE model operates in each cell. Different species may co-occur in each cell. FATELAND also includes a spatially explicit dispersal module and a disturbance module. Thus, FATELAND is especially appropriate for modelling spatio-temporal dynamics in disturbed ecosystems. While FATE is a full deterministic model, in FATELAND, stochasticity is included throughout the dispersal module, which is based on the probability of dispersal (p) according to the negative exponential equation: $p = A \times \mathrm{Exp}(k \times \mathrm{Distance}/\mathrm{MaxDistance})$, where Distance is a random number between 0 and MaxDistance, MaxDistance is the maximum distance to the edge of the landscape, and k and A are the species-specific input parameters for modelling dispersal (Table 1); k provides the shape of the curve and A the magnitude of the dispersal. A fecundity value is used as a number of iterations in this dispersal module. Disturbance is simulated as the removal of all vegetation from the disturbed cell, following a set of designed spatial and temporal disturbance scenarios (see below).

We built an artificial landscape of 70 × 70 (4900) square cells, each one equivalent to 3 × 3 m, with two species types: "Grass" and "Cortaderia" (Table 1). Grass type would include different herbaceous species commonly co-occurring with *Cortaderia* in Spain. In these grasslands, graminoid species are dominant (e.g., *Festuca arundinacea* Schreber, *Elymus pungens* (Pers.) Melderis, *Cynodon dactylon* (L.) Pers.), although forbs also occur (e.g., *Trifolium pratense* L.). The Grass type species is assumed to usually establish a short-term persistent seed bank (based on species closely-related to those found in the study area; Grime et al., 1988). Since they represent an early successional stage, we assume a low-to-moderate ability to recruit under closed canopy (i.e., at low resource levels, Table 1). We also assume that the Grass type has less dispersal ability than *Cortaderia*; the dispersal parameters for the latter species were derived from Saura and Lloret (2005). The *Cortaderia* type represents the attributes of the invasive species *Cortaderia selloana*. This species produces a great amount of long-distance dispersed seeds (Connor and Edgar, 1974; Lambrinos, 2002; Saura and Lloret, 2005). We assume that "Grass" plants have a large self-replacing ability, resulting in a longer life-span than *Cortaderia*. Although *Cortaderia* sprouts after aboveground removal, we did not include this life history trait in the modelling because our disturbances simulated drastic events in which all living plants would be totally removed. Empty cells may occur after disturbances or plant death. All the landscape is potentially available for invasion by *Cortaderia*, if the establishment conditions are appropriate (Table 1).

2.2. Scenarios

The initial situation corresponds to a landscape in which all the cells are occupied by "Grass" plants, and *Cortaderia* occurs in a narrow front (1 cell wide) in one border of the landscape. This mimics the case found in many natural invaded zones near urban areas where *Cortaderia* is used as an ornamental plant. From this initial landscape we applied three sets of disturbance scenarios (A, B, C) within a 55-year timeframe by combining different spatial and temporal disturbance patterns (Table 2). In all cases, the disturbance started at year 5.

Table 1 – Main species attributes used for modelling the invasion of Cortaderia selloana in a landscape dominated by the species type "Grass"

Traits	Grass	*Cortaderia*
Lifespan (years)	100	25 ± 3
Age at maturation (years)	2	4
Innate dormancy? (years)	Yes (2)	No
Germination rate	Low, Medium, High	None, Low, Low
Seedling survival	No, Yes, Yes	Yes, Yes, Yes
Immature survival	No, Yes, Yes	Yes, Yes, Yes
Mature survival	No, Yes, Yes	Yes, Yes, Yes
Dispersal capacity (A)	0.3	0.9
Dispersal shape (k)	−2.4	−6.9
Fecundity	1 500	15 000

The three values for germination and survival refer to low, medium and high resource levels. See the method section for further details.

(A) Scenarios of increasing disturbance frequency. We selected regular and sparse disturbance scenarios from no disturbance (A0) to 5 (A5), 10 (A10), 20 (A20) and 40 (A40) disturbances of 30 randomly chosen cells at each disturbance event. Therefore, the disturbance frequencies were (from A5 to A40): every 10, 5, 2 and 1 year, and the inter-disturbance periods were 9, 4, 1 and 0 years, respectively.

(B) Scenarios of increasing disturbance frequency and decreasing extent of each disturbance (i.e., number of disturbed cells). Five (B5), 10 (B10), 20 (B20) and 40 (B40) disturbances of 120, 60, 30 and 15 cells respectively. Note that the total number of disturbed cells for the simulated timeframe is the same (i.e. 600 cells) in each scenario. Disturbance frequency and inter-disturbance periods were as in (A) above.

(C) Scenarios with changing disturbance patterns combining the following temporal and spatial patterns:

Temporal disturbance patterns:

- Regular temporal pattern (CR) – Five disturbances at regular intervals of time (every 10 years). The first disturbance is at year 5 and the last one at year 45. Thus the inter-disturbance periods consist of 9 years.
- Irregular temporal pattern (CI) – The first disturbance is at year 5 and then at years 23, 25, 43 and 45. Therefore, the sequence of inter-disturbance periods is 2, 18 and 2.

Spatial disturbance patterns:

- Aggregated (Q10f) – a fixed block of 10 × 10 cells (100 cells, ca. 2% of the landscape) located in the centre of the landscape is disturbed every disturbance year; the remaining landscape is not affected by disturbance.
- Aggregated random (Q10r) – a block of 10 × 10 cells (100 cells, ca. 2% of the landscape) is randomly located within the landscape every disturbance year.
- Sparse fixed (Q1f) – 100 cells are randomly chosen at the first year of disturbance and the same cells are disturbed every disturbance year.
- Sparse random (Q1r) – 100 randomly chosen cells are disturbed every disturbance year.

These simulations mimic several disturbance regimes associated with specific human activities, including conservation management (Table 3). Dumping resulting from periurban development is common in coastal wetland areas of Catalonia (NE Spain), producing a pattern of small, scattered disturbed areas (Table 2, CI Q1 scenarios). Agricultural activities eliminate *Cortaderia* from the invaded communities but a few individuals remaining in the field margins can invade when the field is abandoned again. The temporal pattern of these abandoned fields is irregular, and the size of the areas

Table 2 – Details of the different disturbance scenarios used to simulate Cortaderia selloana invasion with FATELAND

Scenarios	Temporal pattern of disturbance[a]	Spatial pattern of disturbance	Location of the recurrence	# Disturbed years	# Cells disturbed (in each disturbed year)	Inter-disturbance periods (year)
Increasing the disturbance frequency						
A0	–	–	–	0	0	–
A5	Regular (10)	Sparse	Random	5	30	9
A10	Regular (5)	Sparse	Random	10	30	4
A20	Regular (2)	Sparse	Random	20	30	1
A40	Regular (1)	Sparse	Random	40	30	0
Increasing the disturbance frequency and decreasing the number of disturbed cells						
B5	Regular (10)	Sparse	Random	5	120	10
B10	Regular (5)	Sparse	Random	10	60	5
B20	Regular (2)	Sparse	Random	20	30	2,3
B40	Regular (1)	Sparse	Random	40	15	1,2
Changing the disturbance patterns in space and time						
CRQ10f	Regular (10)	Aggregated	Fixed	5	100	9
CRQ10r	Regular (10)	Aggregated	Random	5	100	9
CIQ10f	Irregular	Aggregated	Fixed	5	100	2, 18
CIQ10r	Irregular	Aggregated	Random	5	100	2, 18
CRQ1f	Regular (10)	Sparse	Fixed	5	100	9
CRQ1r	Regular (10)	Sparse	Random	5	100	9
CIQ1f	Irregular	Sparse	Fixed	5	100	2, 18
CIQ1r	Irregular	Sparse	Random	5	100	2, 18

a The disturbance frequency is in brackets when the temporal pattern is regular.

is relatively large (aggregated disturbance pattern) (Table 2, CIQ10 scenarios). Vegetation removal to create habitats suitable for animal feeding (birds, rabbits) is a common practice in these protected areas and tends to be reproduced at the same locations (Table 2, DR), while the size of the vegetation clearing or flooding depends on the animal targets (Table 2, CRQ1 and CRQ10 scenarios).

Although FATELAND has some stochasticity (due to the dispersal module only), the core model (FATE) is deterministic. Preliminary analysis with FATELAND showed that the simulations with different initial random seed numbers produce very similar results; the variability of replications is thus very low. For this reason, replicated simulations are unnecessary and are not performed in the present work. In any case, to avoid any differences due to stochasticity, all simulations were started with the same seed number for the random generator.

3. Results

Simulation results show that *Cortaderia* tends to disappear from a landscape with no disturbances (A0, Fig. 1; see also Fig. 3 below). When the disturbance frequency is increased, the invaded area increases (Fig. 1). The same occurs when the disturbance size is increased while its frequency is kept constant (preliminary analysis not shown). Increasing the disturbance frequency but reducing the amount of area affected by each disturbance produces small differences (Fig. 2), although infrequent large disturbances (B5) generate pulses of more invaded area than frequent small disturbances (B40). That is, starting with a large number of cells (B5) leads to an increase in the invaded area regardless of frequency. A5 and A10 with 30 initially disturbed cells do not lead to invasion while the same frequency with 120 cells at the beginning does lead to invasion.

Recurrent disturbances in the spatially constant (fixed) scenarios produce a declining tendency in *Cortaderia* occupancy along the simulation time period (bottom graphs in Fig. 3). In contrast, the same recurrence in randomly located positions generates an increasing *Cortaderia* occupancy (upper graphs in Fig. 3). The number of cells occupied by *Cortaderia* for the whole simulation period is significantly higher in the random than in the fixed-location disturbance scenarios (Fig. 4, $p < 0.0001$). Furthermore, aggregated patterns of disturbance (Q10) favour invasion with respect to sparse disturbances (Q1) (Fig. 4, $p = 0.02$). The magnitudes

Table 3 – Examples of the relevance of the temporal and spatial patterns of the disturbance scenarios to which Cortaderia selloana is subjected

Temporal	Spatial	
	Sparse disturbance (Q1)	Aggregated (clumped) disturbance (Q10)
Regular disturbance (CR)	Fauna habitat management (patch clearing)	Fauna habitat management (e.g., flooding for water birds, mowing and seeding to obtain grain)
Irregular disturbance (CI)	Litter, solid or rubbish dumping	Land abandonment

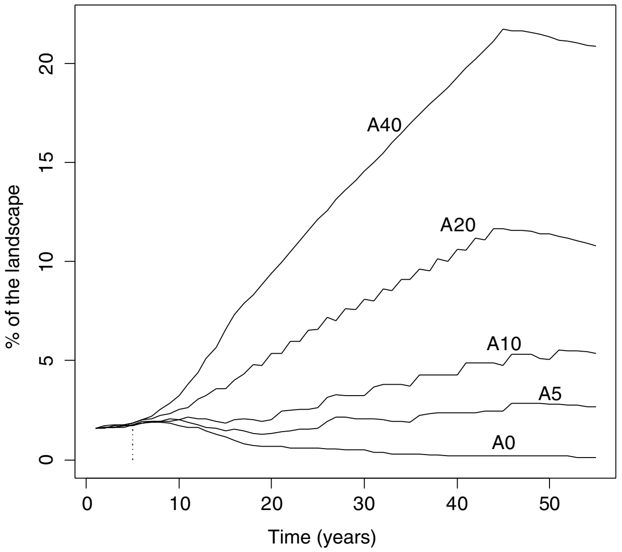

Fig. 1 – Proportion of the landscape occupied by *Cortaderia selloana* during the 55 years of simulation with no disturbance (A0) and with 5, 10, 20 and 40 disturbances (see Methods and Table 2a). In each disturbance event, 30 cells were disturbed. In all cases (except for T0), the disturbances started in year 5, while the last disturbance occurred between years 43 and 50, depending on the scenario.

of the changes in invasion patterns are higher between fixed and random disturbance locations than between aggregated and sparse disturbances (Fig. 4). The area occupied by *Cortaderia* is not significantly different when comparing the simulation with different inter-disturbance periods (i.e., regular vs. irregular scenarios, Fig. 3). Therefore, changes in the temporal disturbance pattern have lesser implications on the invasion dynamics than changes in the spatial disturbance pattern.

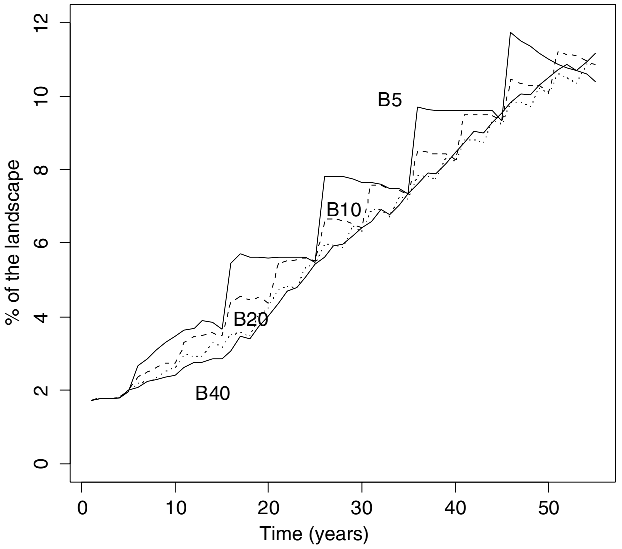

Fig. 2 – Proportion of the landscape occupied by *Cortaderia selloana* during the 55 years of simulation with 5, 10, 20 and 40 disturbances involving 120 (B5), 60 (B10), 30 (B20) and 15 (B40) cells respectively. See Table 3b for more details.

Overall, the total area occupied by *Cortaderia* through the whole simulation period is relatively low (Fig. 3). The total cumulative area occupied by this species (area under the curves in Figs. 1–3) is positively correlated with the disturbed area ($p < 0.001$) estimated as the proportion of the accumulated disturbed area throughout the simulations (Fig. 5). On the other hand, the abundance of Grass was always very high (close to 100% in all scenarios) and was not related to the disturbed area (not shown).

4. Discussion

One of the goals of biological conservation is to identify the key processes that govern plant invasibility (Vermeij, 1996). Our results support the hypothesis that disturbances are essential for the persistence and expansion of *Cortaderia*. Without any disturbance, *Cortaderia* invasion would be transient; in less than 30 years the species would probably disappear because of the lack of safe sites for seedling establishment. The relationship between community invasibility and disturbance has been addressed for many alien plants by experimentally manipulating disturbances as single events, analysing gradients of disturbance or comparing disturbed and non-disturbed areas (Burke and Grime, 1996; Smith and Knapp, 1999; Alpert et al., 2000; Lake and Leishman, 2004). However, in realistic situations, invasion is triggered by successive disturbances across the landscape (D'Antonio et al., 1999). Our results suggest that the larger (or more frequent) the disturbances are, the larger the invaded area will be. The increasing cumulative curves observed in the random simulations suggest a strong founder effect, reinforced by the large size attained by *Cortaderia* adults, which may outcompete native herbs and grasses. The higher variability of *Cortaderia* occupancy observed in fixed simulations is simply due to the mortality caused by disturbances occurring on sites that were occupied by *Cortaderia* after a previous disturbance.

Both the absence of a soil seed bank and the lack of resprouting after our drastic simulated disturbances highlight the importance of seed rain from remnant individuals for colonising disturbed patches. This dependence on disturbance at early stages of development suggests that young *Cortaderia* individuals are scarcely able to establish in well-developed grasslands. Thébaud et al. (1996) also showed that competition with plant neighbours has a significant impact on the performance of *Conyza* species invading European oldfields. However, other kinds of disturbance such as herbivory by mammals (e.g., rabbits) have been shown to reduce invasion by *Cortaderia* (Lambrinos, 2002), as also found in other alien plants in Mediterranean communities (Kruger et al., 1989; D'Antonio, 1993).

The results also point out that the spatial pattern of the disturbance plays a role in the invasion rate (With, 2002): the aggregated pattern of disturbance (Q10) favours *Cortaderia* invasion with respect to the sparse pattern (Q1). Small disturbances are easily and quickly colonised by native herbs and grasses that have low dispersal ability and that inhibit the establishment of alien plants. In contrast, large disturbed

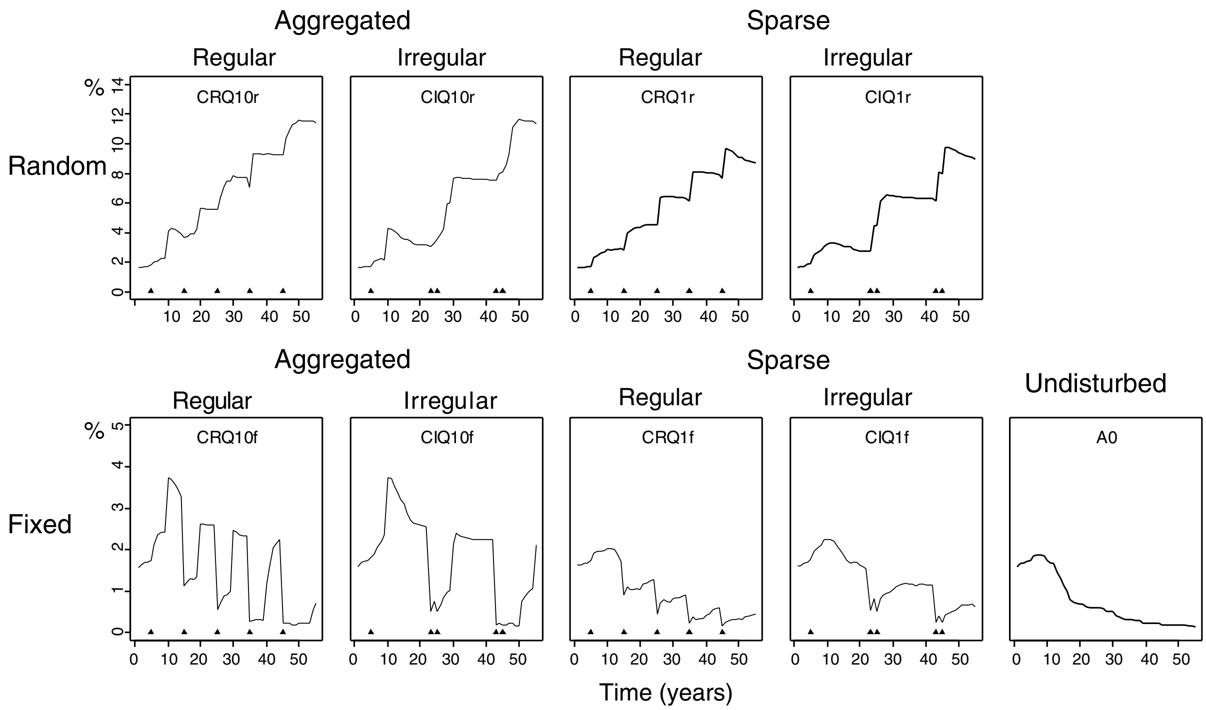

Fig. 3 – Proportion of the landscape occupied by *Cortaderia selloana* during the 55 years of simulation with different disturbance spatial-pattern scenarios. (Note the different vertical scales in the upper and lower figures). Upper figures represent the random (r) spatial disturbance pattern scenarios, and lower figures represent the fixed (f) spatial disturbance pattern scenarios. Black triangles indicate the time of disturbance. DR = disturbance at regular intervals, DI = disturbance at irregular intervals. Q10 = aggregated disturbances, Q1 = sparse disturbances. Note that A0 represents the scenario with no disturbance. More details on the disturbance regimes are given in the text (Methods) and in Table 2c.

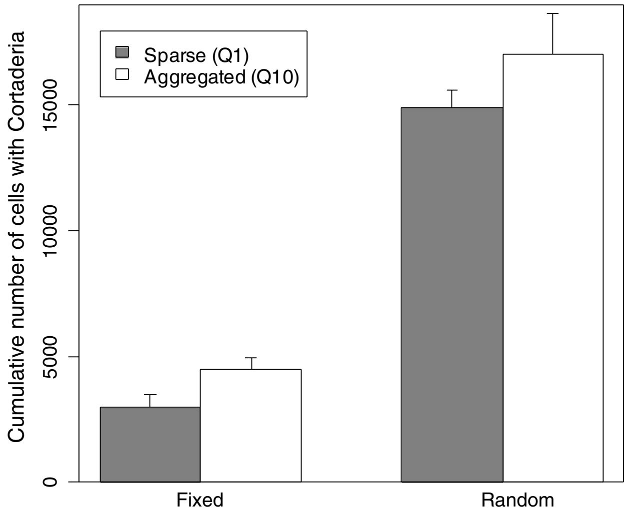

Fig. 4 – Mean area of invasion (+ standard deviation) of *Cortaderia selloana* for the whole simulation period (55 years) expressed as the total (cumulative) number of cells with *Cortaderia* (i.e., area below the curve in Fig. 3) for the scenarios with fixed and with random spatial disturbance, for aggregated disturbances of 10 × 10 cells (Q10) and for isolated cells representing sparse disturbances (Q1). Both factors are significant (ANOVA Fixed vs Random: $p < 0.0001$, Q10 vs Q1: $p = 0.02$).

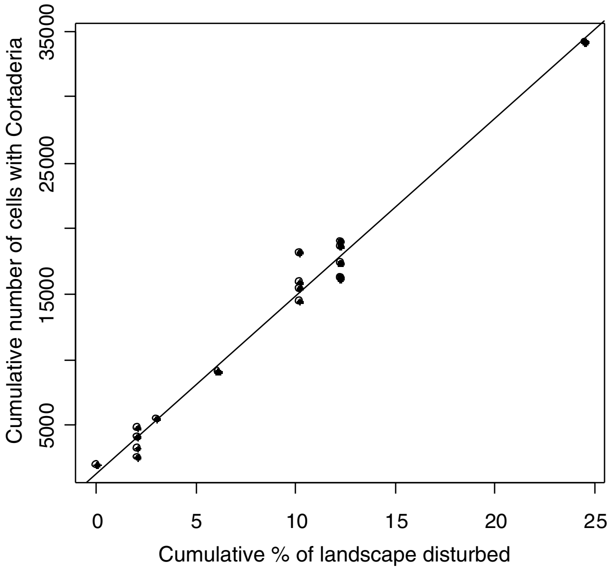

Fig. 5 – Relation between the cumulative percent of landscape disturbed for each disturbance scenario throughout the simulation period (55 years) and the total number of cells occupied by Cortaderia throughout the simulation period (i.e., area below the curve in Figs. 1–3; which is an indicator of Cortaderia selloana abundance for the whole period).

patches are easily colonised by *Cortaderia* because of its high seed production and long dispersal distances. The same rationale applies to previous spatially-explicit models (Moloney and Levin, 1996). After successful establishment and growth, *Cortaderia* plants achieve a large size and native herbs and grasses can hardly outcompete these large plants. The results also agree with the fluctuating resource availability hypothesis of invasibility because increases in resource availability due to disturbance reduce competition from resident vegetation, thereby increasing invasibility (Davis et al., 2000; Davis and Pelsor, 2001).

Moreover, our results suggest that invasion is more sensitive to changes in spatial patterns (i.e., spatial variability) than to changes in temporal patterns (i.e., temporal variability) of disturbance. Spatially random-distributed disturbances promoted more invaded area than fixed disturbances (Fig. 4), but regularity vs. irregularity of the disturbance occurrence through time did not modify the invasion pattern. In both regular and irregular scenarios, the whole available gap is similarly colonised by *Cortaderia* shortly after disturbance, and long before the next disturbance occurs. Other wind-dispersed alien species lacking a permanent seed bank would also be extremely dependent on the spatial distribution of the disturbances, and on the ability of the native vegetation to colonise gaps. Therefore, our simulations highlight the importance of spatial coupling between disturbance occurrence, seed dispersal mechanisms and competitive interactions between alien and native species. However, further studies for other species and situations are needed before we can make generalisations.

Our spatially explicit model provides new insights on the potential invasion of *Cortaderia*. Although field-testing would be needed to verify our findings, these new insights can be used to suggest management options. The use of *Cortaderia* in gardening close to natural areas should not be recommended especially if the adjacent natural areas are subjected to frequent and extensive disturbances. Similarly, in areas where *Cortaderia* is present, disturbances should be minimised to reduce *Cortaderia* expansion. If disturbances are inevitable, small disperse disturbances are preferred to large aggregated disturbances, because small disturbances are easily colonised by native species that may outcompete the invaders. As large gaps are difficult for native herbs and grasses to occupy, they provide a window for the establishment of *Cortaderia*. Because wind dispersal is a key process in the invasion of *Cortaderia*, any strategy preventing seed production and/or dispersal (e.g., inflorescence removal, selection of low fertility plants) could also help to reduce invasion. However given the difficulties in reducing disturbances in human-dominated landscapes, it would be better not to use *Cortaderia* for gardening outside of its native range.

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