Research

Comparing short and long-distance dispersal: modelling and field case studies

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Dispersal is a factor of great importance in determining a species spatial distribution. Short distance dispersal (SDD) and long distance dispersal (LDD) strategies yield very different spatial distributions. In this paper we compare spatial spread patterns from SDD and LDD simulations, contrast them with patterns from field data, and assess the significance of biological and population traits.

Simulated SDD spread using an exponential function generates a single circular patch with a well-defined invasion front showing a travelling-wave structure. The invasive spread is relatively slow as it is restricted to reproductive individuals occupying the outer zone of the circular patch. As a consequence of this dispersal dynamics, spread is slower than spread generated by LDD. In contrast, the early and fast invasion of the entire habitat mediated by power law LDD not only involves a significantly greater invasion velocity, but also an entirely different habitat occupation. As newly dispersed individuals soon reach very distant portions of the habitat as well as the vicinity of the original dispersal focus, new growing patches are generated while the main patch increases its own growth absorbing the closest patches. As a consequence of both dispersal and lower density dependence, growth of the occupied area is much faster than with SDD.

SDD and LDD also differ regarding pattern generation. With SDD, fractal patterns appear only in the border of the invasion front in SDD when competitive interaction with residents is included. In contrast, LDD patterns show fractality both in the spatial arrangements of patches as well as in patch borders. Moreover, values of border fractal dimension inform on the dispersal process in relation with habitat heterogeneity. The distribution of patch size is also scale-free, showing two power laws characteristic of small and large patch sizes directly arising from the dispersal and reproductive dynamics.

Ecological factors like habitat heterogeneity are relevant for dispersal, although its importance is greater for SDD, lowering the invasion velocity. Among the life history traits considered, adult mortality, the juvenile bank and mean dispersal distance are the most relevant for SDD. For LDD, habitat heterogeneity and changes in life history traits are not so relevant, causing minor changes in the values of the scale-free parameters.

Our work on short and long distance dispersal shows novel theoretical differences between SDD and LDD in invasive systems (mechanisms of pattern formation, fractal and scaling properties, relevance of different life history traits and habitat variables) that correspond closely with field examples and were not analyzed, at least in this degree of detail, by the previously existing models.

Understanding how species are distributed in space is a central issue in ecology and evolutionary biology. Numerous aspects are involved in species distribution patterns, like life history traits (including dispersal), intrinsic population processes, habitat suitability and disturbance, among others. Of these factors dispersal is one of the most important in determining a species' spatial distribution, as it can determine for example the success of a biological invasion (Viard et al. 2006), or explain the present genetic population structure of a species that underwent major paleoclimatic events (Petit et al. 1997).

Ecological and evolutionary implications for species of either following a short distance dispersal (SDD) or a long distance dispersal (LDD) strategy have been pointed out (Bolker and Pacala 1999, Levin et al. 2003, Snyder and Chesson 2003, Soons and Ozinga 2005, Rosindell and Cornell 2009). In addition, there is a growing consensus in that different modes of dispersal, namely, SDD and LDD yield very different spatial distributions (Xu and Ridout 1998, Higgins and Richardson 1999, Clark et al. 2001, Cannas et al. 2003, 2006, Gilbert et al. 2004). In particular, spatial models have shown that simulating LDD with

power-law functions generate patchy patterns with not well-defined epidemic fronts, which are more complex and realistic than those produced by the patterns of dispersal modelled with exponential functions (Mollison 1977, Minogue 1986, Shaw 1994, 1995). Cannas et al. (2003, 2006) showed that the exponential function is more appropriate to simulate SDD than LDD.

Although Shaw (1995), Filipe and Maule (2004), Wingen et al. (2007) and Soubeyrand et al. (2008) compared some aspects of SDD and LDD in the epidemic or genetic context, a comprehensive comparison between SDD and LDD driven spatial distribution patterns of non-pathogen organisms is still in need. In this paper we perform such comparison by summarizing our previous modelling and field work on SDD and LDD terrestrial plant invasion systems of central Argentina, and by showing new results from invasive plants dispersion worldwide.

Methods

The basic model

We present here previous and new results obtained using a model we developed for plant biological invasions. Here we will give a brief account but further model details are given in Marco et al. (2002, 2008) and Cannas et al. (2003, 2006). The field model was defined on a square grid containing square sites. Each site contained at most a single individual of a given age. The spatial length scale was set to the size of one adult individual (5×5 m). The value of all variables at a given (discrete) time t depended on the value of the variables at time $t-1$. The time scale was set to match the minimal reproductive interval, typically one year for woody species. Life history traits included were: d, mean seed dispersal distance (in grid units), q, annual adult survival probability, t_m, age of reproductive maturity (in years), n, mean seed production (seeds/plant), f_g, mean germination probability, and P_n, juvenile survival probability.

An occupied site $a_i(t) \neq 0$ was updated according to the following rule:

$$a_i(t) = \begin{cases} a_i(t-1) + 1 & \text{with probability q} \\ 0 & \text{with probability } 1-q \end{cases}$$

Given an empty site i at time $t-1$, that is, $a_i(t-1) = 0$, and considering germination and juvenile survival as two independent events, the site was colonised at time t, that is, $a_i(t) = 1$, with a probability $p_i(t)$ given by

$$p_i(t) = 1 - (1 - f_g P_n)^{s_i(t)}$$

where $s_i(t)$ was the number of propagules received by the site i at time t; $p_i(t)$ was the probability that at least one propagule survives to reach the reproductive stage. s_i was obtained by counting the propagules received by the site i coming from the rest of the sites containing a reproductive individual at time t, i.e. those that $a_j(t) > t_m$. Propagule dispersion from an individual was described by the dispersal function f(r), where $r = \sqrt{x^2 + y^2}$ was the distance to the parental individual. The function f(r) describes the fraction of the total number of propagules produced by a single individual dispersed per unit area to a cell located at a

distance r; f(r) was assumed to be isotropic (i.e. it did not depend on the orientation) and normalised in the whole plane. One important inclusion was the juvenile bank. The juvenile bank was defined as the collection of seedlings that germinate and establish under the canopy, surviving in the shade, until a gap in the canopy appears, and seedlings can resume their growth and eventually reproduce (Silvertown and Lovett-Doust 1993). Let t_j be the average age of the juvenile bank of the species. If the individual died at time t it was replaced by another individual of age tj. If the species did not have juvenile bank then $t_j = 0$ and the cell became empty. Habitat heterogeneity and interaction between species like competition were easily incorporated into the model, by altering the probability of site occupation as a function of spatial location (Marco et al. 2002).

Interactive model

Interaction between the invader and native species was included as competition for suitable sites, allowing germination and establishment (competition for space, Silvertown et al. 1992, Marco and Páez 2000). The final occupant was chosen with a probability that depends on the state and use of the resources in the site. In the SDD case study, *Lithraea ternifolia* establishes either in shallow soil or rock crevices as well as in deep soil, compared to *Gleditsia triacanthos*, which needs deep soil (Marco and Páez 2000). Soil parameters were coded as a dummy variable (0 = rocky ground and 1 = deep soil), and were chosen with some spatial distribution at the beginning of the simulation and kept fixed throughout. Site occupancy was then defined by soil state and species characteristics: if soil value = 1, the occupants were chosen with equal probability, but if soil value = 0, then *L. ternifolia* occupies the site (see Cannas et al. 2003 for details). For LDD, we simulated one possible kind of habitat heterogeneity for seed colonisation, defining 10, 20, 30% of habitat as unsuitable. Unsuitable sites were modelled as single sites having zero probability of receiving seeds from anywhere in the system. Since we assumed no propagule limitation, this situation is also equivalent with a scenario of seeds finding an unsuitable site for establishment and further reproduction. The number of unsuitable sites was equal to a fraction m of the total number of sites, and their location was randomly chosen at the start of the simulation and kept fixed thereafter. We explored a range of m between 0 (no unsuitable sites) and 0.3. For simulating interactions, if more than one species colonises the site, final occupation depended on species traits, for example, if a site was occupied by a species with juvenile bank, the site remained occupied by the same species after death of the occupant individual. More details of the interactive case are given in the Supplementary material Appendix 1.

Dispersal distribution functions f(r)

The difference between SDD and LDD is based on whether the dispersal function f(r) (or redistribution kernel in the language of Kot et al. 1996) has an exponentially bounded tail or not; the former (SDD) implying finite expansion velocities (Kot et al. 1996). In a general sense this means that the distribution is short ranged if the kernel has a

moment generating function; otherwise, it is long ranged (Kot et al. 1996). In particular, LDD is observed if some of the moments $\int r^n\, f(r)da$ are infinite (extremely fat tailed kernels), where the integral extends over the infinite plane and da stands for a surface area element. An example of short ranged dispersal is given by the negative exponential function

$$f(r) = \frac{2}{\pi d^2} e^{-2r/d}$$

where $d = \int r\, f(r)da$ is the mean dispersal distance (first moment). This function appropriately describes the dynamics when species have short ranged dispersal strategies (Marco et al. 2002, Cannas et al. 2003). We simulated long ranged dispersal mechanisms using a power law function:

$$f(r) = \begin{cases} \dfrac{A}{r^a} & \text{if } r \geq {}^1/_2 \\ 0 & \text{if } 0 \leq r \leq {}^1/_2 \end{cases}$$

where A is a normalisation constant and $\alpha > 2$. When $3 < \alpha \leq 4$ there is a finite mean dispersal distance, but moments of higher order (including the variance) are infinite. When $2 < \alpha \leq 3$ the mean dispersal distance is not defined. Finally, for $\alpha > 4$ the global spatial pattern of spread is similar to the short ranged one (Cannas et al. 2006). The use of this power law has been useful when dealing with organisms dispersed by LDD (Cannas et al. 2006, Marco et al. 2008). Biologically speaking, inclusion of the power law means that dispersion from a given focus is allowed to reach with finite probability any point of the whole area considered, even when the mean dispersal is finite and much smaller than the area size (Cannas et al. 2006). In other words, such probability decays very slowly with the distance to the focus.

Spatial pattern analysis

Simulations began with a single mature individual located at the centre of a square area or starting from a row of individuals randomly aged between 1 and t_m, along a line $y = 0$ at the bottom of the area, with varying configurations of resident species when an interactive case is considered. We defined a patch as a set of contiguous occupied sites. The border set of a given patch was defined as the list of all the occupied sites lying at its border. Spatial pattern analysis of species spread was based on the statistics of propagation front or patches of occupied sites and their borders. When a scale-free, fractal pattern appeared, we calculated the fractal dimension of patches and their borders using the box-counting algorithm. We plotted the number of boxes $N(l)$ of linear size l as a function of l; the fractal dimension was defined as $N(l) \propto l^{-D}$. We fitted the curve using the least square method. We analysed the scale-free geometry of patches for time scales smaller than the time needed to fill the whole area. After this time most of the simulation area was covered by the main patch while the few secondary patches that remain isolated were located near the border. The simulations were repeated between 20 and 200 times to obtain averages of the different quantities of interest at every time step. To investigate the sensitivity of the spread velocity and spatial pattern to the main life history traits considered relevant to invasive spread (longevity, juvenile bank, age of first reproduction (t_m), and propagule pressure) we performed several simulations, changing values of these traits while keeping the others fixed. We also assessed habitat suitability and interaction among invader and native species effects.

Field species data

The mountain forests studied covered most of the mountains of central Argentina up to 1400 m. Native dominants are *Lithraea ternifolia* and *Fagara coco*. At present, native forest areas have been diminished by clearcutting, grazing and urbanisation, and invasion by many woody alien species is common (Marco and Paez 2000). *Lithraea ternifolia* and *F. coco* are trees up to 15 m in height, able of germinating and establishing in shallow soils and rock crevices. Both species produce small, dry drupes that fall and remain near the parental tree, do not have vegetative reproduction, and germination and seedling establishment need full sunlight and moderate moisture conditions (Marco and Paez 2000). The most frequent invaders are *Gleditsia triacanthos*, *Ligustrum lucidum* and *Ulmus minor*. The North American *G. triacanthos* and the Chinese *L. lucidum* invaders are trees up to 15 m height. Both species present vegetative reproduction. The big, indehiscent pods produced by *G. triacanthos* are locally dispersed by gravity (Schnabel and Hamrick 1995), while the small, fleshy drupes of *L. lucidum* are bird dispersed. Although bird dispersion has been proposed as LDD, most bird movements are restricted to short distances (Westcott and Graham 2000), so we considered *L. lucidum* as a SDD species. Both species produce fruits in high numbers every year, and present a dense juvenile bank (Marco and Paez 2000). *Ulmus minor* is a European tree introduced as ornamental species in the region around the mid 20th century. Reproduction is by seeds. We found no evidence of vegetative reproduction in the field. Fruits are samaras released in high numbers and dispersed by wind. Values for life history traits considered determinants of plant spread (Higgins and Richardson 1996, Rejmanek and Richardson 1996, Marco and Paez 2000) were estimated for the species (Supplementary material Table A1). Detailed data obtention is available in Marco et al. (2002, 2008), Cannas et al. (2003). We studied the spatial pattern of spread of trees using aerial photographs, taken in 1970 (1:5000), 1987 (1:20 000), and 1996 (1:5000). Photographs were interpreted using a stereoscope, detected trees were checked in the field, and propagation front or patches finally drawn on scanned photographs using standard processor images. Photograph edges were not used in the interpretation to avoid image distortion. An estimation of error in the photograph interpretation was made by identifying individual trees in the photograph and then checking if they were correctly assigned to the species. The area was mapped, surveyed in detail, and then checked in the field, covered 5 km^2 of a low mountainous system (ca 1100 m), with predominantly deep soils and few rocky outcrops. Rate of spread was calculated by estimating the square root of the area successively covered in 1970, 1987, and 1996.

Simulations and case studies

Short-distance dispersal

SDD was simulated using the negative exponential function showed above. Values of the life history traits used are in Supplementary material Table A1. The propagation front $y = h(x)$ for each species was defined as the farthest occupied site y from the starting point for every coordinate x.

We defined the mean front position starting with a line of individuals as

$$\bar{h} = \frac{1}{L_x} \sum_{x=1}^{L_x} h(x)$$

We averaged $\bar{h}$ over different initial conditions and different sets of random numbers, for all species, for an area of width $L_x = 80$. Several tests performed for different area widths showed that the results did not change significantly for widths over 80 sites. We used the asymptotic speed V of the averaged spread front to estimate the velocity of spread. We calculated population density profiles ρ along the propagation direction y as the average density profiles for non-reproductive (ρ_1) and reproductive individuals (ρ_2) (see further model details in Supplementary material Appendix 1). We simulated the interactive invasion system constituted by the invasive species *G. triacanthos*, *L. lucidum* and the natives *L. ternifolia* and *F. coco*, using different configurations of invaders and natives in the simulation field.

Long-distance dispersal

We calculated the mean fractal dimension D_P of patches (excluding the main patch) as a function of time, where the averages were taken at fixed times over several simulation runs, and the mean fractal dimension D_B of the patch borders. Patch size is defined by the number of sites in each patch. We calculated the relative frequency histogram P (s) of patches with size s (excluding the main patch). P (s) was calculated in an area of 1024×1024 sites at a stationary stage but at a time when less than 50% of the sites were occupied. We determined this by tracking the density of occupied sites as a function of the simulation time. After this time most of the simulation area was very soon completely covered (Cannas et al. 2006). We also calculated P (s) of patches with size s with reproduction restricted to the founder parent (i.e. no local proliferation after LDD outside the original patch). The results for P (s) were averaged for every value of s and every time step in a sample of M independent runs, M being between 100 and 200.

We studied the spatial pattern of spread of *U. minor* using aerial photographs from a forest area of 7 ha located in a low mountain region of central Argentina. The seven hectares surveyed comprise a whole hillside of low slope. In 1970 there was only a patch of few trees planted, considered as the first dispersal focus in the studied area. Number and area covered of patches generated from the first focus were calculated for 1987 and 1996, and the fractal patch dimension (excluding the main patch) and the fractal dimension of patch borders were calculated following the box-counting method using square boxes of side equivalent to 5 m spanning to 150 m.

Results and discussion

Simulations and field study cases

Spatial patterns and velocity of propagation for the basic model

Patterns generated by SDD are radically different from patterns produced by LDD. With SDD the spatial spread produces a circular compact patch with a defined, simple invasion front, surrounded by a few isolated individuals and very small patches. In contrast, with LDD, the spatial pattern promptly develops into a complex structure of small patches of different size surrounding the main patch. Individuals are dispersed all over the field at early simulation steps, and as they also begin reproduction, patches tend to coalesce (see details of pattern formation in Cannas et al. 2003, 2006). Figure 1 shows an example of patterns generated by SDD (Fig. 1a) and LDD (Fig. 1c) simulations. Simulated patterns show great similarity with field patterns, for example with dispersion of *Robinia pseudoacacia*. *Robinia pseudoacacia* is a North American native tree now invading worldwide, that produces seeds but mainly disperses by root sprouts (Motta et al. 2009). This vegetative strategy is an extreme form of SDD, generating extended compact clones that invade dense native forests (Peloquin and Heibert 1999) (Fig. 1b). On the other hand, patterns simulated by LDD resemble closely the spread of *U. minor*, an invasive tree that disperses by wind, a typical LDD strategy (Fig. 1d).

With SDD, the propagation front increases at constant velocity and shows a travelling wave structure (Supplementary material Fig. A1). The density profiles for *G. triacanthos*, and other invasive species show a wide band of non-reproductive individuals covering about half of the area of the propagation front, characterised by a sharp peak in the corresponding density profile (Cannas et al. 2003). The width of this area (ca 20 grid units) is larger than the mean dispersal distance (d = 3 grid units in this example), so the front advances only when non-reproductive individuals in the front begin reproduction. In real populations, individuals occupying the borders of the circular patch experience less intraspecific competition and have greater access to light, nutrients, and pollinators, and thus are in better conditions to begin reproduction (Burguess et al. 2006). For *G. triacanthos*, V predicted from simulations with homogenously suitable habitat and no interaction was 9.6 ± 0.1 m yr^{-1}, while field calculated spread velocity ranged between 2.5 and 4 m yr^{-1}. For *L. lucidum*, field calculated spread velocity ranged between 11 and 12.5 m yr^{-1}, slightly lower than the 13.6 ± 0.1 m yr^{-1} predicted by the model. Discrepancies between simulation and field V values are due to the effect of habitat and interactions.

When LDD is simulated using the power law function, and as the pattern generated does not present a defined spread front, it is not possible to calculate V in the same way that in the SDD case. However, the square root of the area covered by the spreading trees can be calculated over time giving an estimation of V. Velocity of the propagation front with LDD is expected to grow exponentially with time (Kot et al. 1996).

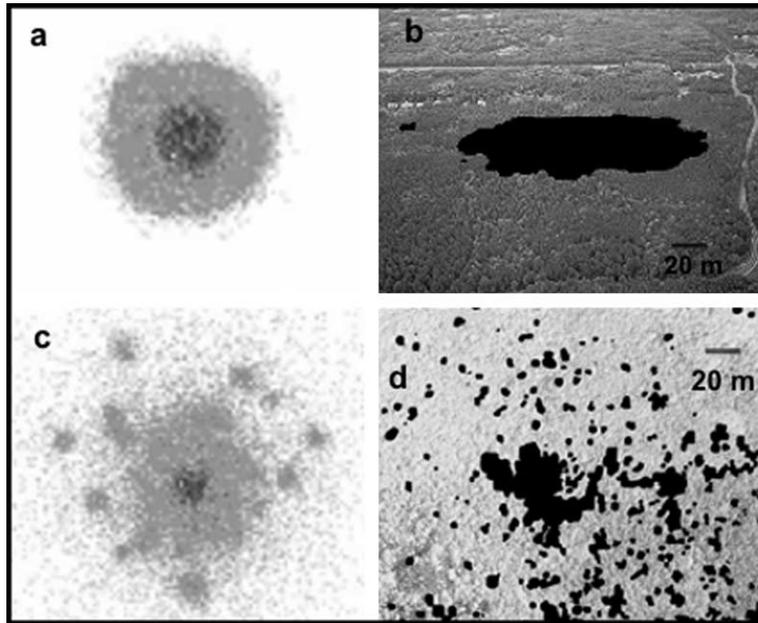Results from simulations using LDD and *U. minor* parameters (Fig. 2a) resembled closely the early invasive

Figure 1. (a, c) Snapshots of the spread from a single focus at the centre of a square area with L = 200, d = 5 and tm = 7. The dark dots correspond to reproductive individuals while the light grey ones to non-mature individuals. The simulation started with a mature individual at the focus. (a) Spread of a species with SDD (inverse exponential function), 15 yr after t_m; (c) spread of a species with LDD (power law function, a = 3.11 ...) and juvenile bank, 12 yr after t_m. (b, d) Spatial spread of invasive trees (black areas) in forests (grey ground), (b) *Robinia pseudoacacia*, SDD by clonal propagation, invading native pine forests; (d) *Ulmus minor,* LDD by wind, invading mixed forests. Photograph in Fig. 1b courtesy of Albany Pine Bush Preserve Commission.

steps in the field (Fig. 2b). The initial establishment of *U. minor* in the area studied occurred around 1950. By 1970, just the initial patch was present, and the area was still covered by native forests, dominated by *L. ternifolia* and *F. coco*. In 1987 ca 74 patches were scattered through the whole area, but in 1996 the number of patches had more than doubled. The increase in area covered by the patches was even more dramatic. By 1987 patches excluding the initial one covered a small fraction of the whole area and were mainly representing individual trees. During the next 10 yr the increase in covered area was exponential, occupying nearly 8000 m^2 out of 7 ha of total forest area and still increasing. The slower rate of patch generation compared to area covered increase reveals that after a certain time, few new patches are generated but the increase in area is mainly due to patch growth and coalescence. This is the same mechanism of spatial pattern formation found in the simulations (Cannas et al. 2006), and the exponential rate of increase of the spatial extent of the population agrees with the expected for a system with LDD (Kot et al. 1996). V of *U. minor* propagation calculated as the square root of area covered between aerial surveys in 1987 and 1996 was 77 m yr^{-1}. In simulations with LDD it was not possible to calculate V since the transient time is too short and complete habitat occupation is reached in few time steps. Simulations considering a single species spreading in a uniform field give a faster habitat occupation compared to real examples where spread of species is influenced by variables like habitat heterogeneity and interactions with other species, as we will show below.

Scale-free characterization of dispersion patterns

When dispersing alone in a uniform habitat, a SDD species generates a non-fractal pattern spread, characterized as described above, by a main patch of rather smooth border and few smaller patches (see Fig. 1a, b, for simulated and field examples respectively). Invasive patterns of SDD species have shown a non-fractal border (Marco et al. 2002). The rather smooth patch border changes to a fractal border when there is interaction between the invader and a native or resident species (Cannas et al. 2003). LDD, in contrast, presents a scale-free pattern even in absence of interactions (Fig. 1c, d). To characterize the LDD patch border pattern, we calculated the fractal dimension of patches (D_P), and the fractal dimension of patch borders (D_B). Due to the fast spread, D_P from simulations showed a continuous curve of increase over time, characterized by cyclic rises coincident with periodic increments in offspring production every 7 yr, the age of reproductive maturity. In 24 simulated years, D_P increased from 0.8 to 1.7. D_P of *U. minor* field spread calculated from the digitized aerial images taken in 1996 (Fig. 1d), i.e. 26 yr later from the first patch spread, was 1.30 ($R^2 = 0.93$, n = 9). This D_P value agrees well with simulation D_P values, considering that the age of reproductive maturity of *U. minor* is ca 10 yr. In another field example, alpine treeline in Glacier National Park (USA) formed by several wind-dispersed tree species present a typical patchy structure (Zeng and Malanson 2006). From a multispectral remote sensing image with 1 m spatial resolution showed in Zeng and Malanson (2006, Fig. 1a), we calculated D_P and found a value of 1.4 ($R^2 = 0.99$, n = 8). This treeline system occurs
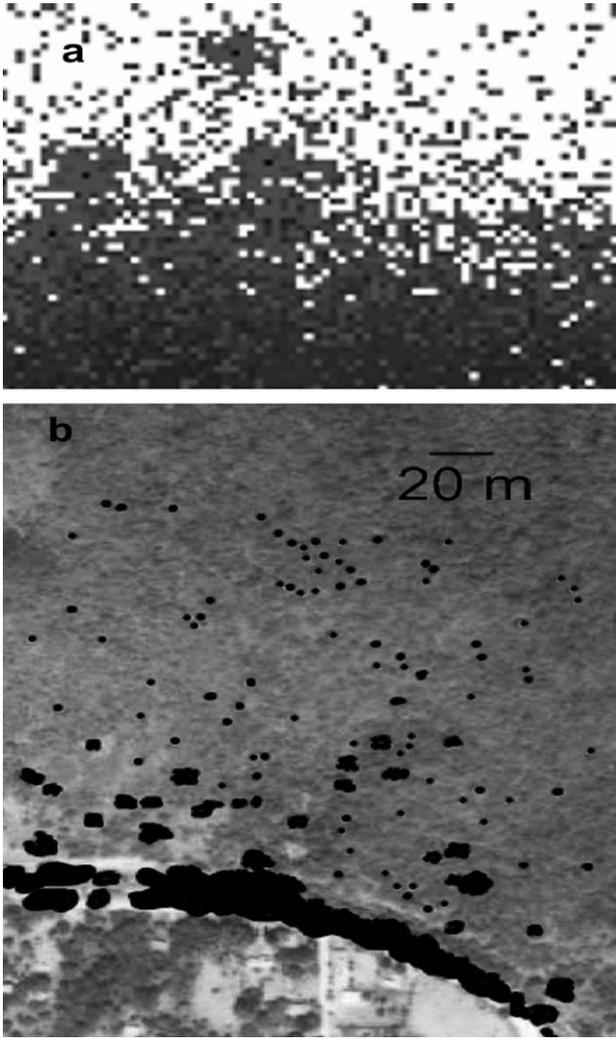
Figure 2. (a) Snapshots of the spread of a species using LDD ($\alpha = 4$) and *U. minor* parameters (Supplementary material Table A1), from a row of mature individuals (bottom), at $t = 30$ yr. Black dots correspond to reproductive individuals while the grey ones to non-mature individuals. (b) Spatial spread of *U. minor* (black areas) surrounded by a mixed forest of other invasive and native species (grey ground), during its early invasion (ca 30 yr) into the area from a row of planted trees (stretched out black areas at the photograph bottom).

in a hard environment where seedling mortality is very high and survival has been proposed to be facilitated by positive feedbacks in a self-organized process mediated by the influence of already established trees (Zeng and Malanson 2006). Although the D_P found is consistent with LDD dispersion, its lower value may reflect a constraint in effective LDD through restrictions in seedling establishment.

We had previously found that the mean fractal dimension D_B of patch borders from simulations as a function of α ranged more or less constantly between 1.6 and 1.8 for $2 < \alpha \leq 3$ (mean dispersal distance not defined), and it decreased monotonically for $3 < \alpha \leq 4$ (mean dispersal distance defined) (Cannas et al. 2006). This means that, with less restricted dispersal distances, greater and more or less constant D_B values are found, probably due to the fast

coalescence and integration of new patches in the periphery of the main patch. D_B of main patch border from the digitized aerial images of *U. minor* field spread in 1996 was 1.88 ($R^2 = 0.93$, n = 9) (Cannas et al. 2006), agreeing well with simulated D_B values found for $2 < \alpha \leq 3$. From the Zeng and Malanson (2006) example mentioned above, D_B value found was 1.15 ($R^2 = 0.397$, n = 12), again showing a lower value compared with simulations and *U. minor* results. This lower D_B may indicate constraints in effective LDD, as explained above.

The patch size distribution P (s) of diverse LDD systems presents a disrupted distribution characterized by two different power laws P (s) $\sim s^{-\beta 1}$ and P (s) $\sim s^{-\beta 2}$ at small and large patch areas s separated by a crossover region (Fig. 3 and Cannas et al. 2006, Marco et al. 2008). We also have showed that the small area section of P (s) is generated by random dispersal and aggregation of reproductively immature individuals. The large area section corresponds to larger patches generated by reproduction of previously dispersed individuals by LDD forming their own patches
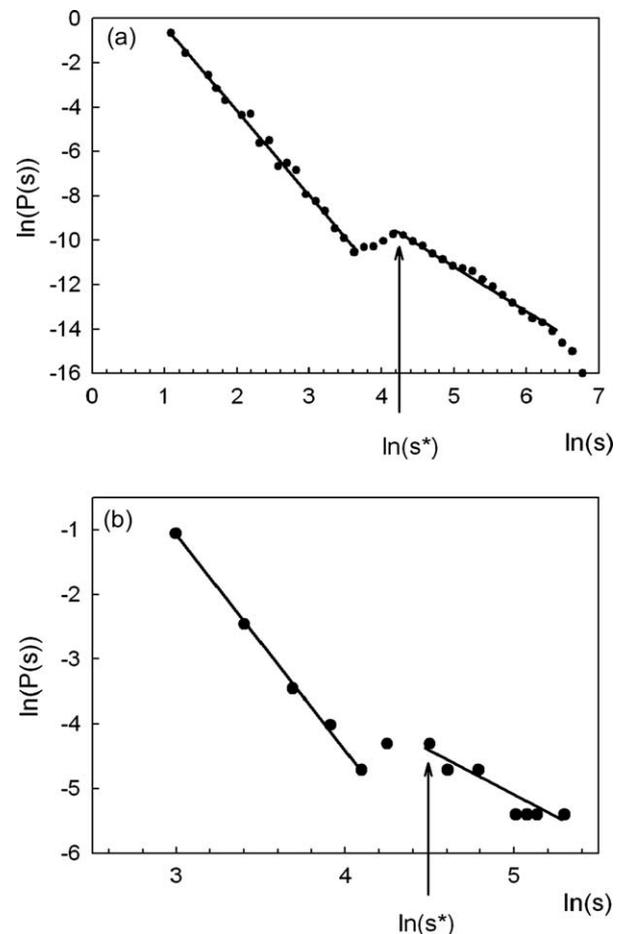

Figure 3. Size distribution of patches P (s). (a) P (s) for LDD simulations for $t_m = 7$ yr and $\alpha = 3.33 \ldots$, where s is given in number of sites. (b) P (s) for field spread of English elm, where s is given in m². P (s) curves are characterised by power laws P (s) $\sim s^{-\beta 1}$ and P (s) $\sim s^{-\beta 2}$, corresponding to patches of small and large areas. β values are given in the text. s* indicates the estimated average minimum size of a patch generated by a single individual by reproduction and localised dispersal in the simulations (a) and in the field (b).

by localized dispersal and recruitment, followed by growth and coalescence of neighbouring patches. The large area section begins around Ln (s) = 4 (Fig. 3), a patch size compatible with a young patch originated by reproduction from a patch founder parent, followed by localized dispersal in different systems (tree invasion and cell cancer invasion) (Marco et al. 2008). Large area patches arise only at times greater than first reproduction and thus appear only when reproduction is effective (Cannas et al. 2006, Marco et al. 2008). When individuals recruited after a dispersal episode do not reproduce, the small patch area scale power law still appears but the large area power law is not defined, since it is a direct effect of local reproduction following LDD dispersal (Cannas et al. 2006, Marco et al. 2008). The effect of reproductive restriction after dispersal is even more clearly seen in an example from an invasion of *Cortaderia selloana* (silver pampas grass), in central Argentina. This invasive giant grass produces hairy seeds that disperse by wind, and normally forms wide and closed canopies over extensive areas in short invasive periods. However, in a field situation where seedling recruitment after initial invasion in 1999 was prevented by periodic lawn mowing but preserving adult *C. selloana* tufts, secondary patches did not appear. Thus, tuft spatial arrangement still reflects the first stages of LDD pattern formation. A representative part of the invaded area, from 2008 satellital images provided by Córdoba Province Government, is compared with patterns generated by LDD simulations at early times, before secondary reproduction occurs (Fig. 4a, b). We calculated D_p for the field pattern and found 0.77 ($R^2 = 0.95$, n = 13), agreeing with D_p values at early times in LDD simulations before reproduction begins (Marco et al. 2008). Spatial pattern is slightly clumped (variance/mean index = 1.2), in agreement with snapshots of LDD simulations at early times (Cannas et al. 2006). As patch formation was prevented, it is not possible to calculate P (s) in this example.

Influence of ecological and life history traits on SDD and LDD patterns of spread

Habitat characteristics

SDD simulations performed considering habitat heterogeneity showed a decrease in spread velocity compared to homogeneous habitats. For example, V for *G. triacanthos* decreased from 4.4. m yr^{-1} for suitable soil to 1.9 m yr^{-1} for unsuitable, rocky soils, comparing well with field estimations (Cannas et al. 2003). Interactions among species, in this case, as competition for colonisable space, have profound effects on both velocity and spatial patterns of spread. We studied the common invader tree species *L. lucidum* and *G. triacanthos* invading native *L. ternifolia* forests in central Argentina (Marco et al. 2000). When using the model with SDD for interacting species, both V and the smoothness of the spread front changed. In this case, V decreased, and the smooth spread front was replaced by a wide spread band area of rough borders with fractal dimension, as the result of the patch formation generated by invader species introgression into the native forests. As the spread front of the invader moved along the simulation area, a wide band of introgression was formed, many patches of *L. ternifolia* were replaced by the invader, and after some time, the whole area was invaded. In 300 yr, the dense native forest was replaced by a pure and dense forest
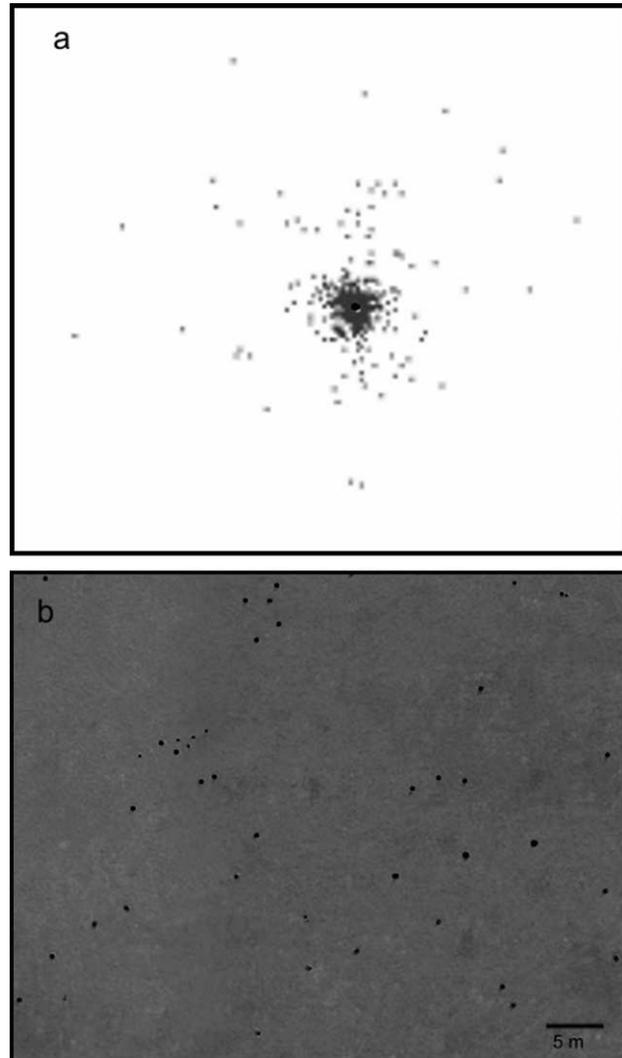

Figure 4. (a) Snapshots of the LDD spread from a single focus at the centre of a square area with L = 200, d = 5, tm = 7, and α = 3.11 …, at yr = 3 after first reproduction from a single individual and before next reproductive event. Isolated dots are non-reproductive (immature), single individuals. (b) Invasion of the giant grass *Cortaderia selloana* in a field where reproduction after first dispersal has been prevented. Black points are *C. selloana* single adult tufts. The initial invasion focus was located ca 1.5 km south to the area shown in the figure, and consisted of several plants grown together with ornamental purposes.

of invading trees (Marco et al. 2002, Cannas et al. 2003). With interaction, the propagation front still increases at constant velocity and shows a travelling wave structure, but the sharp peak in the density profile corresponding to the non-reproductive individuals (Supplementary material Fig. A1) no longer appeared (Cannas et al. 2003). This means that with interaction, the invasion advance is not restricted by waves of reproduction of immature individuals beginning reproduction, since in this case the invasion front is mostly composed by reproductive individuals. V estimates from simulations were lower and more realistic when interaction was included, agreeing well with field values (Marco et al. 2002, Cannas et al. 2003, 2004). The interacting border presents a fractal dimension that is a

monotonic increasing function of V. Thus highly indented borders may be indicative of higher invasion velocities (Cannas et al. 2004).

In the case of LDD, population density decreased with an increasing percentage of unsuitable habitat. The reduction in density was linearly related to reduction in habitat suitability ($y = -0.085x + 1.05$, $R^2 = 0.92$ with $\alpha = 2.55$, $y = 0.0083x + 0.45$, $R^2 = 0.99$ with $\alpha = 3.33$) (Fig. 5). We found that the general LDD pattern is maintained, although D_B values are increased in presence of habitat heterogeneity (Fig. 6).

Life history traits

Life history traits like life span, juvenile bank, age of first reproduction (t_m), and propagule number and dispersion have been proposed as important factors in biological invasions (Higgins and Richardson 1996, 1999, Rejmánek and Richardson 1996, Clark et al. 2001). In this section we report and discuss our findings on the effect of potentially relevant life history traits on SDD and LDD patterns.

When SDD was considered, among the life history traits studied, the presence of a juvenile bank and relative longevity of native and invader were the main factors influencing patterns of spread. In SDD simulations, presence of invader's juvenile bank guarantees invasion
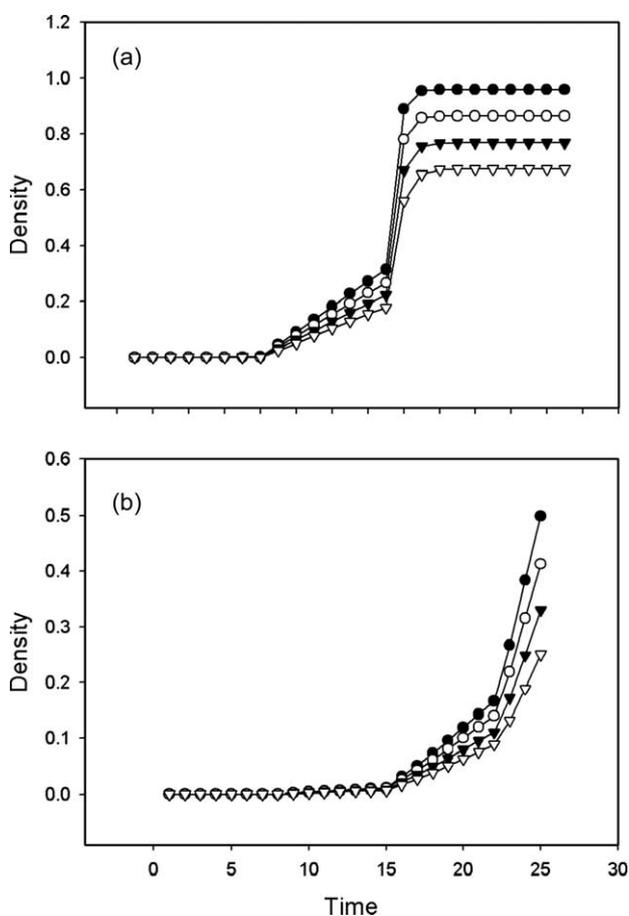

Figure 5. Population density without juvenile bank, considering different percentages of habitat unsuitability (0, filled circles; 10, empty circles; 20, filled triangles; 30%, empty triangles), for $\alpha = 2.5$ (a) and $\alpha = 3.3$ (b).
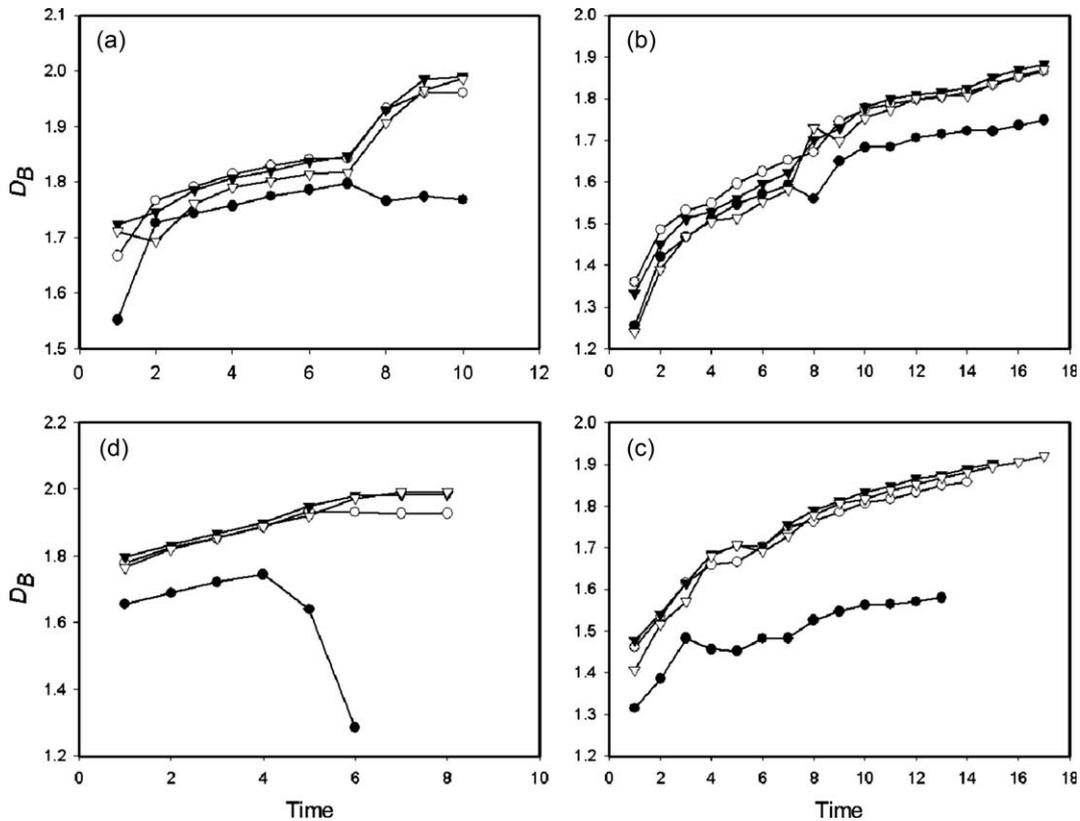
success when native species life span is set as significantly greater compared with longevity of invaders (a common situation in invaded forests such as the *L. ternifolia* system already mentioned (Marco and Páez 2000)). If the invader's juvenile bank is withdrawn from simulations, the alien species no longer excludes the native but a coexistence regime is established instead. However, in this case, the native species may go extinct if longevities of both invader and native species are similar (Cannas et al. 2003). The presence of a juvenile bank is a common feature of SDD invasive species such as *G. triacanthos* and *L. lucidum*, explaining in great part their success as invaders at field (Marco et al. 2002). The juvenile bank was a major factor influencing population dynamics in *G. triacanthos*, contributing with 56% to population growth in a field work performed in the same habitat (Marco and Páez 2000). The juvenile bank also plays an important role in forest species' regeneration of the Meliaceae family (Becker and Wong 1985) that includes invasive species like *Melia azederach* (Marco et al. 2002). Other life history traits have a smaller influence on SDD patterns of spread. In SDD simulations for an invader species with juvenile bank the velocity of invasion V depended linearly on d, the mean dispersal distance, and decayed logarithmically with t_m for small values of it ($t_m < 7$ yr). For higher values of t_m we found that V is approximated by the inverse of t_m (Cannas et al. 2003). The least influential of the life history traits considered on V was propagule pressure. We estimated it as the mean number of seeds produced by the invasive species (Marco and Páez 2000), incorporated into the colonization probability function, since what ultimately determines invasion success is both seed production and seedling establishment and survival (Marco and Páez 2000, Marco et al. 2002). We assessed the sensitivity of V to variations of the mean seed production while maintaining d and t_m fixed, for different values of the product Psfg. V grew logarithmically with n, at least for large values of n characteristic of invasive species (Cannas et al. 2003). This means that propagule pressure may be a secondary factor in determining V in forest systems, where later recruitment stages following seed production exert major effects (Silvertown et al. 1993, Marco and Páez 2000).

With LDD, the juvenile bank plays a less influential role than in SDD. When the juvenile bank is present, population density shows slightly higher values at earlier invasive times (not shown). The general spatial pattern is maintained although the absence of the juvenile bank generates gaps (Fig. 7a), while the juvenile bank fills in these gaps (Fig. 7b). Filled gaps produce smoother patch borders, and due to the less complicated border, D_B values are smaller when the juvenile bank is present, as shown in Fig. 6a, b. Also, D_B fluctuates over time with a period equivalent to t_m (Cannas et al. 2006), reflecting the addition of new individuals in each cohort reproductive onset. In spite of causing differences in D_B, neither the juvenile bank nor t_m has significant effects on P (s). Figure 8 shows that the P (s) pattern with two power laws is maintained either in absence or presence of the juvenile bank, and also with different ages of first reproduction. Varying the age of saplings in the reproductive bank does not modify the P (s) pattern (not shown). Distance of propagule dispersion is a major life history trait that may define a species ability to colonise new

Figure 6. Fractal dimension of patch border (D_B) behaviour with time for LDD simulations, without juvenile bank, for $\alpha = 2.5$ (a) and $\alpha = 3.3$ (b), and with juvenile bank, for $\alpha = 2.5$ (c) and $\alpha = 3.3$ (d) considering different percentages of habitat unsuitability (0, filled circles; 10, empty circles; 20, filled triangles; 30%, empty triangles).

habitats. As we have shown, short and long-distance dispersers display very different invasive patterns. LDD patterns differ in some aspects when different values of the dispersal function are taken into account. Smaller α (extremely unrestricted dispersion) leads to a faster density growth, showing higher densities even at higher percentage of habitat unsuitability, compared with a higher α value (Fig. 5). Also, D_B varies with the value of α (Fig. 6). Comparing D_B values without juvenile bank and without habitat heterogeneity (Fig. 6a, b), a smaller α generates a faster saturating curve, attributable to the faster coalescence of secondary patches into the main patch. With juvenile bank, this effect is even more marked, with D_B values decreasing fast to an almost linear dimension (Fig. 6c). In contrast with D_B, the main general pattern of P(s) is maintained. The exponents of the power laws of P(s) appear to be almost insensitive to the dispersal range exponent α, the only appreciable effect being a change in the position and the width of the crossover range between the two power laws (Cannas et al. 2006).

SDD and LDD implications for modelling species spread

When SDD is the dispersal mechanism, mean dispersal distance d is important in determining invasion velocity. Invasion velocity increases linearly with increasing d. The

adoption of the negative exponential function as the seed dispersal curve, allowing for short distance dispersal only, and with a moment-generating function (Kot et al. 1996) allows for simulation results comparable to field values of SDD species. Using this function we found a well defined invasion travelling wave and local dispersal qualitatively similar to those obtained from applications of the reaction–diffusion model (Higgins and Richardson 1996, Marco and Páez 2000), integro-difference equation models (Van den Bosch and Metz 1996, Takasu et al. 2000) or the model coupling integro-difference equations with population matrices developed by Neubert and Caswell (2000).

However, when LDD process are involved, utilization of bounded or partially bounded distribution functions like the exponential decay impairs both the predictive and explanatory aspects of the models. For example, when modelling the spread of an invasive moth using exponentially bounded dispersal functions Gilbert et al. (2004) found incongruities between the observed invasion rates, spatial pattern configuration and fractal characterization. The main difficulty is the failure in reflecting the early invasion of the entire habitat. As we have shown, this problem is circumvented by the use of 'fat tailed' distribution functions for propagule dispersal, like the power law.

An interesting feature of the power law functions is their relationship with self-organising processes. As they indicate the invariance of some system property over a range of temporal and spatial scales, it is increasingly accepted that
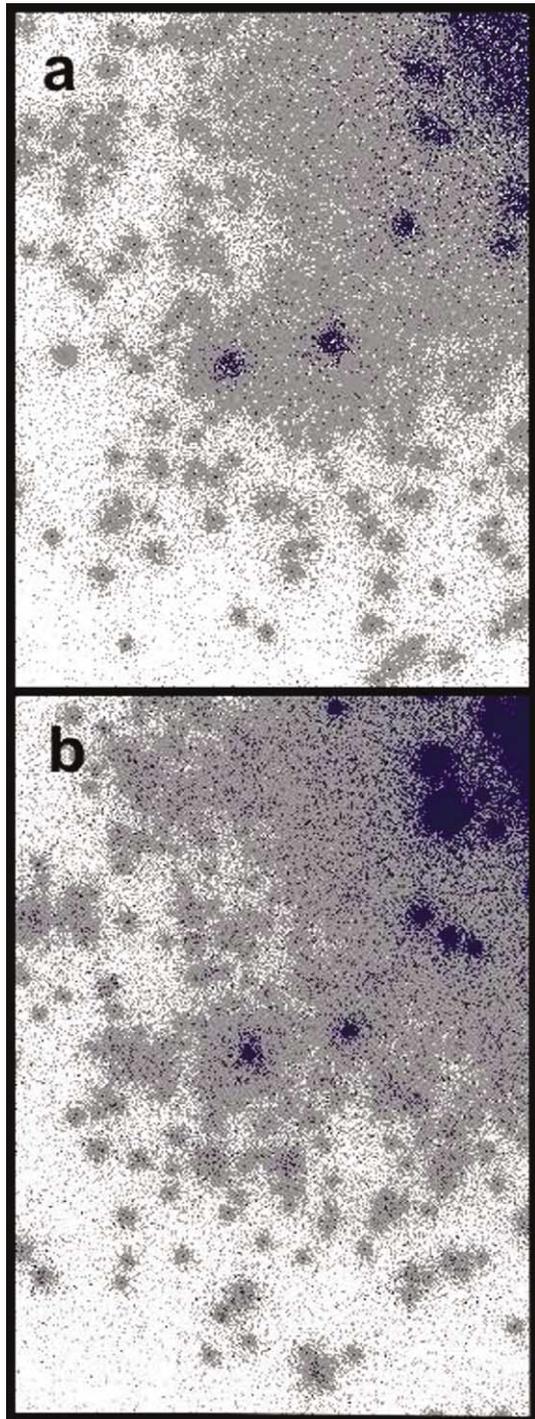
Figure 7. Snapshots showing part of the dispersal square area with L = 1024, and tm = 7, with LDD (α = 3.11), without (a) and with juvenile bank (b). Black dots correspond to reproductive individuals while the grey ones correspond to non-mature individuals, gaps are shown in white.

power laws are a byproduct of self-organising processes of populations and communities (Sutherland and Jacobs 1994, Pascual et al. 2002, Scanlon et al. 2007). Understanding the ability of a system to evolve to an organized state due to intrinsic mechanisms as self-organisation

(Mandelbrot 1982), we postulate that the LDD patterns we show, characterised by power laws and scale-free patterns, are robust indications of self-organisation arising from internal population mechanisms. For example, the P(s) scale-free pattern we found, showing the particular arrangement with two power laws separated by a break clearly depends only on the intrinsic dynamics of LDD dispersal and reproduction after dispersal. The existence of break-points in power laws has typically been interpreted as evidence for a change in the underlying processes (Krummel et al. 1987, Meltzer and Hastings 1992). However, in our system no such a change has occurred. Also, models of predator-prey systems analysing cluster size showed power laws separated by a break. As no change occurred in the underlying processes, authors attributed the scale-free patterns to self-organising processes (Sutherland and Jacobs 1994, Pascual et al. 2002).

Conclusions

Comparing both dispersal modes, we found that simulated SDD spread using an exponential function generates a single circular patch with a well-defined invasion front showing a travelling-wave structure. The invasive spread is restricted to reproductive individuals occupying the outer zone of the circular patch, where density-dependent effects on growth rate are smaller than at the patch interior. As a consequence of this dispersal dynamics, spread is slower than spread generated by LDD. In contrast, the early and fast invasion of the entire habitat mediated by power law LDD not only involves a significantly greater invasion velocity, but also an entirely different habitat occupation. As dispersal of new individuals soon reaches very distant portions of the habitat as well as the vicinity of the original dispersal focus, new growing patches are generated while the main patch increases its own growth absorbing the closest patches. Population growth in LDD is not restricted to the periphery of the only one generated patch as in SDD, but it occurs at the same time at the inside of the main patch and the secondary patches. As a consequence of both dispersal and lower density dependence, growth of occupied area then is faster than with SDD.

SDD and LDD differ also regarding scale-free pattern generation. With SDD, fractal patterns appear only in the border of the invasion front in SDD when competitive interaction with residents is included. In contrast, LDD patterns show fractality both in the spatial set-up of patches as well as in patch borders. Moreover, values of border fractal dimension inform on the dispersal process in relation with habitat heterogeneity. The distribution of patch size is also scale-free, showing two power laws characteristic of small and large patch sizes directly arising from the dispersal and reproductive dynamics.

Ecological factors like habitat heterogeneity are relevant for dispersal, although their importance is greater for SDD, lowering the invasion velocity. Among the life history traits considered, adult mortality, the juvenile bank and mean dispersal distance are the most relevant for SDD. For LDD, changes in life history traits are not so relevant, causing minor changes in the values of the scale-free parameters.
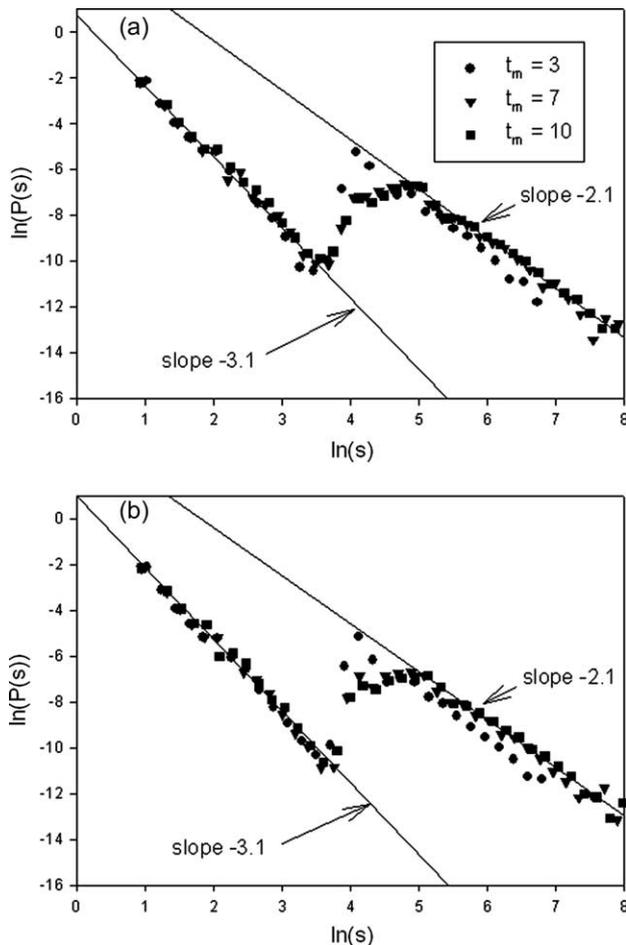
Figure 8. Log–log plot of the patch size distribution P(s) for L = 1024 at intermediate times, without (a) and with juvenile bank (b). α = 3.33. t_m = age of first reproduction.

We have shown that while SDD is well modelled using moment-generating functions like the exponential decay, appropriately modelling LDD requires the use of 'fat-tailed' functions, like power law or Cauchy. This differs radically to the use of distribution functions allowing only short-distance dispersal (SDD), where the probability of dispersion far away (compared with the mean dispersal distance) to the initial focus is totally negligible. Our approach also radically differs from the 'stratified invasion' approaches, where there is a bimodal dispersion (Shigesada et al. 1995). We avoid difficulties in defining LDD (Nathan 2005) by simply using a power law distribution function for dispersal that allows for a continuous distribution from SDD to LDD, depending on the value of the α exponent.

In this paper we show novel theoretical differences between SDD and LDD in invasive systems (mechanisms of pattern formation, fractal and scaling properties, relevance of different life history traits and habitat variables) that correspond closely with field examples. The essential differences between SDD and LDD spatial patterns showed in this paper should be taken into account when dealing with species dispersal and habitat occupancy.

References

Becker, P. and Wong, M. 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* spp. (Meliaceae) in lowland dipterocarp rainforest. – Biotropica 17: 230–237.

Bolker, M. and Pacala, S. W. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. – Am. Nat. 153: 575–602.

Burgess, V. J. et al. 2006. Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of *Peraxilla tetrapetala* (Loranthaceae). – N. Z. J. Ecol. 30: 179–190.

Cannas, S. A. et al. 2003. Modelling biological invasions: species traits, species interactions and habitat heterogeneity. – Math. Biosci. 183: 93–110.

Cannas, S. A. et al. 2004. Plant spread dynamics and spatial patterns in forest ecology. – In: Gell-Mann, M. and Tsallis, C. (eds), Nonextensive entropy-interdisciplinary applications. Oxford Univ. Press, pp. 243–260.

Cannas, S. A. et al. 2006. Long range dispersal and spatial pattern formation in biological invasions. – Math. Biosci. 203: 155–170.

Clark, J. S. et al. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. – Am. Nat. 157: 537–554.

Filipe, J. A. N. and Maule, M. M. 2004. Effects of dispersal mechanisms on spatiotemporal development of epidemics. – J. Theor. Biol. 226: 125–141.

Gilbert, M. et al. 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. – Ecology 73: 459–468.

Higgins, S. I. and Richardson, D. M. 1996. A review of models of alien plant spread. – Ecol. Model. 87: 249–265.

Higgins, S. I. and Richardson, D. M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. – Am. Nat. 153: 464–475.

Kot, M. et al. 1996. Dispersal data and the spread of invading organisms. – Ecology 77: 2027–2042.

Krummel, J. R. et al. 1987. Landscape patterns in a disturbed environment. – Oikos 48: 321–384.

Levin, S. A. et al. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. – Annu. Rev. Ecol. Evol. Syst. 34: 575–604.

Mandelbrot, B. B. 1982. The fractal geometry of nature. – W. H. Freeman.

Marco, D. and Páez, S. 2000. Invasion of *Gleditsia triacanthos* in *Lithraea ternifolia* montane forests of central Argentina. – Environ. Manage. 26: 409–419.

Marco, D. E. et al. 2002. Species invasiveness in biological invasions: a modelling approach. – Biol. Invasions 4: 193–205.

Marco, D. E. et al. 2008. Comparable ecological dynamics underlie early cancer invasion and species dispersal, involving self-organizing processes. – J. Theor. Biol. 256: 65–75.

Meltzer, M. I. and Hastings, H. M. 1992. The use of fractals to assess the ecological impact of increased cattle population: case study from the Runde Communal Land, Zimbabwe. – J. Appl. Ecol. 29: 635–646.

Minogue, K. P. 1986. Disease gradients and the spread of disease. – In: Leonard, K. J. and Fry, W. E. (eds), Plant disease

epidemiology, population dynamics and management. Macmillan, pp. 285–310.

Mollison, D. 1977. Spatial contact models for ecological and epidemic spread. – J. R. Stat. Soc. B 39: 283–326.

Motta, R. et al. 2009. The rise and fall of the black locust (*Robinia pseudoacacia* L.) in the ''Siro Negri'' Forest Reserve (Lombardy, Italy): lessons learned and future uncertainties.. – Ann. For. Sci. 66: 410–420.

Nathan, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. – Divers. Distrib. 11: 125–130.

Neubert, M. G. and Caswell, H. 2000. Demography and dispersal: calculation sensitivity analysis of invasion speed for structured populations. – Ecology 81: 1613–1628.

Pascual, M. et al. 2002. Cluster size distributions: signatures of self-organization in spatial ecologies. – Phil. Trans. R. Soc. B 357: 657–666.

Peloquin, R. L. and Heibert, R. D. 1999. The effects of black locust *Robinia pseudoacacia* L. on species diversity and composition of black oak savanna/woodland communities. – Nat. Areas J. 19: 121–131.

Petit, R. et al. 1997. Chloroplast DNA footprints of postglacial recolonization by oaks. – Proc. Natl Acad. Sci. USA 94: 9996–10001.

Rejmánek, M. and Richardson, D. M. 1996. What attributes make some plant species more invasive? – Ecology 77: 1655–1661.

Rosindell, J. and Cornell, S. J. 2009. Species–area curves, neutral models and long distance dispersal. – Ecology 90: 1743–1750.

Scanlon, T. M. et al. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. – Nature 449: 209–211.

Schnabel, A. and Hamrick, J. L. 1995. Understanding the population genetic structure of *Gleditsia triacanthos* L.: the scale and pattern of pollen gene flow. – Evolution 49: 921–931.

Shaw, M. W. 1994. Modeling stochastic processes in plant pathology. – Annu. Rev. Phytopathol. 32: 523–544.

Shaw, M. W. 1995. Simulation of population expansion and spatial pattern when individual dispersal distributions do not decline exponentially with distance. – Proc. R. Soc. B 259: 243–248.

Shigesada, N. et al. 1995. Modeling stratified diffusion in biological invasions. – Am. Nat. 146: 229–251.

Silvertown, J. W. and Lovett Doust, J. 1993. Introduction to plant population biology. – Blackwell.

Silvertown, J. et al. 1992. Cellular automaton models of interspecific competition for space – the effect of pattern on process. – J. Ecol. 80: 527–534.

Silvertown, J. et al. 1993. Comparative plant demography: relative importance of life cycle components to the finite rate of increase in woody and herbaceous perennials. – J. Ecol. 81: 465–476.

Snyder, R. E. and Chesson, P. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. – Ecol. Lett. 6: 301–309.

Soons, M. B. and Ozinga, W. A. 2005. How important is long-distance seed dispersal for the regional survival of plant species? – Divers. Distrib. 11: 165–172.

Soubeyrand, S. et al. 2008. Modelling the spread in space and time of an airborne plant disease. – Appl. Stat. 57: 253–272.

Sutherland, B. R. and Jacobs, A. E. 1994. Self-organization and scaling in a lattice predator–prey model. – Complex Systems 8: 385–405.

Takasu, F. et al. 2000. Modeling the expansion of an introduced tree disease. – Biol. Invasions 2: 141–150.

Van den Bosch, F. and Metz, J. A. J. 1996. The velocity of spatial population expansion: an overview of the individual based approach. – Aspects Appl. Biol. 46: 231–238.

Viard, F. et al. 2006. Dispersal ability and invasion success of *Crepidula fornicata* in a single gulf: insights from genetic markers and larval-dispersal model. – Helgol. Mar. Res. 60: 144–152.

Westcott, D. A. and Graham, D. L. 2000. Patterns of movement and seed dispersal of a tropical frugivore. – Oecologia 122: 249–257.

Wingen, L. U. et al. 2007. The population genetic structure of clonal organisms generated by exponentially-bounded and fat-tailed dispersal. – Genetics 177: 435–448.

Xu, X. M. and Ridout, M. S. 1998. Effects of initial epidemic conditions, sporulation rate, and spore dispersal gradient on the spatio-temporal dynamics of plant disease epidemics. – Phytopathology 88: 1000–1012.

Zeng, Y. and Malason, G. P. 2006. Endogenous fractal dynamics at alpine treeline ecotones. – Geograph. Anal. 38: 271–287.