DISPERSAL SPECIAL FEATURE

Costs of persistence and the spread of competing seeders and sprouters

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Summary

1. Trade-offs between reproduction and persistence are thought to regulate life-history evolution and competitive interactions between plants. We examined how seeder (non-persistent semelparous) and sprouter (persistent iteroparous) life-history strategies compete in fire prone shrublands.
2. Our hypothesis was that a trade-off between persistence and colonization ability implies that seeders would be better colonizers than sprouters and would therefore stand to benefit from periods of rapid climate change, whereas sprouters are candidates for extinction in periods of shifting climates because of their relatively poor ability to colonize.
3. We developed an individual based simulation model that simulates lottery plant competition in a homogeneous spatial arena. We used an indirect method to estimate the fecundity and dispersal parameters needed by the model. Dispersal was described by a lognormal dispersal kernel.
4. We found that coexistence was possible in the system only for a restricted range of conditions. Moreover, the model when parameterized using our empirical estimates of demographic and dispersal rates, suggested that the sprouting strategies have a competitive advantage in the system we studied.
5. The migration capacities of the sprouter species were substantially lower than those of the seeder species. Our simulations suggested that, even though sprouters had a competitive advantage over seeders, interspecific competitive interactions did not slow the spread of seeder species, but did substantially hamper the spread of the slower spreading sprouter species.
6. *Synthesis.* We conclude that, in fire driven systems characterized by lottery recruitment, existing theories of colonization – persistence trade-offs do not completely describe interactions between persistent and non-persistent strategies. Moreover, our investigation of seeder – sprouter interactions suggests that sprouters, even though they might be competitively superior, will be more threatened by periods of rapid climate change because of their limited colonization ability.

Key-words: coexistence, dispersal, fire, iteroparous, life-history strategies, lottery models, plant migration, semelparous, shrublands, sprouting

Introduction

The trade-off between reproduction and persistence has intrigued life-history theorists for some time. Cole (1954) derived the result that a semelparous (non-persistent) strategy is superior to an iteroparous (persistent) strategy. This result was paradoxical, because most plant species are iteroparous. The paradox remained apparently un-resolved until Charnov & Schaffer (1973) demonstrated that including the empirical

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reality that the survival rates of adults are higher than those of seedlings allows one to understand why the iteroparous strategy is often superior to the semelparous strategy.

In fire driven shrublands, the Charnov–Schaffer model has been used to demonstrate that 'seeder' (semelparous) and 'sprouter' (iteroparous) strategies have equivalent fitness (Keeley 1977). While these studies have shown the equivalence of the fitness of seeder and sprouter populations, they ignore competition between sprouters and seeders and hence the conditions under which the two strategies can coexist. More recent work by Bulmer (1994) has elegantly shown, for

unstructured systems, the conditions under which the two strategies can coexist. Briefly, Bulmer shows that coexistence is possible when the inequality, $b_s > b_i / m_i$ holds, where b_i and b_s are the rates of offspring production of the iteroparous and semelparous strategies and m_i is the mortality rate of the iteroparous strategy. Should we apply this theory to the sprouter–seeder pair *Ceanothus spinosus* and *C. greggii* for which Keeley (1977) estimated $b_s = 1.41$ and $b_i = 0.37$, we would conclude that coexistence between these two species is only possible when $m_i > 0.26$. Keeley, in fact, assumed that the iteroparous strategy's mortality rates are close to zero, suggesting that the Bulmer model cannot explain coexistence in these systems.

Thus existing data and theory cannot adequately explain the coexistence of seeder and sprouter strategies in fire driven systems. This paper seeks to understand the conditions under which coexistence between seeders and sprouters is possible in these systems. We develop an individual-based spatial simulation model that allows us to simulate competitive interactions between seeders and sprouters in fire driven systems. Lotteries are regarded as the appropriate way to simulate recruitment dynamics in these fire driven systems (Lamont & Witkowski 1995; Laurie & Cowling 1995). Hence the model assumes that competition follows a weighted lottery, that is more fecund species recruit at higher rates. The model also assumes that sprouter individuals that survive fire by resprouting cannot be replaced by seedlings.

We use the model to interpret our own empirical estimates of the fecundity and dispersal ability of con-generic sprouting and non-sprouting species inhabiting the fynbos, South Africa. The parameters are derived from an inverse estimation method (Ribbens *et al.* 1994; Clark *et al.* 1999; Schurr *et al.* 2008). These data were used to parameterize the model, thereby testing whether the model can predict seeder–sprouter coexistence for a realistic combination of parameters.

Finally, we explore the consequences of the trade-off between persistence ability and reproduction predicted by the model and observed in the data for the ability of species to spread. The expectation derived from previous theoretical and empirical work is that sprouting strategies have lower colonization ability and would therefore have slower migration rates (Bulmer 1994; Tilman 1994; Higgins & Cain 2002). Hence, the implication is that in periods of rapid climate change sprouting species may face higher extinction risk because they have a more limited capacity to adapt their distribution to changing climatic conditions.

Methods

STUDY SYSTEM

The study was conducted in the fynbos biome of the Cape Floristic Region, South Africa. We focus on native shrub species belonging to the *Protea* and *Leucadendron* genera (Proteaceae). The dynamics of the study system are strongly influenced by fire and recruitment is almost entirely limited to the post-fire phase. The study species are serotinous, that is seeds survive fire in cones and are released after fire. The contemporary record suggests that the mean fire return interval is 29 years (Polakow & Dunne 1999). The intensity of fynbos fires is such that all above-ground biomass is killed. The study species can be grouped into two distinct life-history strategies, *sprouters* and *seeders*. Sprouters are capable of resprouting after fire from below-ground root stocks, while seeders cannot resprout. Both strategies are capable of reproducing from seed after fire.

MODEL DESCRIPTION

We construct an individual based simulation model that is tailored towards simulating the study system. The model simulates individual plants that are located in homogeneous two-dimensional, continuous space. Time is discrete and we assume that a single time step represents the time between fires (*ca.* 29 years, Polakow & Dunne 1999). That is, it is assumed that all individuals are reproductively mature at the time a fire occurs. Plants are assumed to occupy patches, and plants within a patch are assumed to compete with each other. Specifically we assume that seed production of an individual of species z, S_z (where z indicates either the sprouter or the seeder species), in a time step is density dependent (N_R and N_S are the densities of the sprouter and seeder strategies in an individual's patch), but that individuals belonging to the two strategies are competitively equivalent,

$$S_z = \max\left[0, f_z\left(1 - \frac{N_R + N_S}{K}\right)\right].\qquad\text{eqn 1}$$

Here, K is the patch density at which seed production is zero and f_z is the seed production rate of species z. This description of density dependent processes is consistent with over-compensating density dependence, which has been reported in fynbos Proteaceae (Bond *et al.* 1995). The model allows patches to be asynchronous in density. In this model system, low density patches can recolonize high density patches that, according to eqn 1, produce no seeds. Note that because fractions of seeds cannot be dispersed, the number of seeds dispersed is taken as the integer part of $S_z + U$; where U is a uniform random number between 0 and 1. Individual seeds are dispersed assuming that the distances that seeds move can be described by a lognormal distribution. The lognormal has been found to be an adequate kernel for describing both local and long-distance dispersal (e.g. Greene *et al.* 2004; Wagner *et al.* 2004). We implemented dispersal by drawing dispersal distances from the lognormal distribution and direction from a uniform distribution. Hence we assume that dispersal is isotropic. We initially assume that seeders and sprouters have the same dispersal distances, although there may well be differences in the aerodynamic traits of seeds (F.M. Schurr, unpubl. data) and seed release heights (Bond & Midgley 2003) which would be expected to influence dispersal distances (Nathan *et al.* 2001; Schurr *et al.* 2005). We relax this assumption of equivalence in dispersal ability in a subsequent section of this paper. After dispersal, seeds recruit into the adult population following a weighted lottery for the occupancy of sites in a patch. The lottery recruitment process is simulated by calculating the probability that an individual seed recruits into a patch, which is defined as the number of unoccupied sites in the patch divided by the number of seeds in the patch. Since no seeders survive the fire, the number of unoccupied sites in a patch is determined by the survival rate of the sprouters (α) and the number of sprouters in the patch.

In summary, in the each iteration the model first simulates the seed production of each individual plant using eqn 1 and then disperses each individual seed using a distance drawn from a lognormal

distribution and a direction drawn from a uniform distribution. All seeder individuals are assumed to die, whereas a proportion (α) of the sprouter individuals survive; which individuals die and which survive is randomly assigned. The probability of a seed recruiting is then calculated as the ratio of un-occupied sites to seeds in a patch and this probability determines whether an individual seed recruits.

PARAMETER ESTIMATION

Data for six Proteaceae species were collected in the Silvermine Nature Reserve (Cape Peninsula, South Africa, 18.41′E, 34.08′S). *Leucadendron salignum* is a sprouter, whereas *L. laureolum* and *L. xanthoconus* are closely related seeders. *Protea cynaroides* is a sprouter and *P. repens* and *P. lepidocarpodendron* are closely related seeders.

For each species we indirectly estimated dispersal and fecundity parameters from data on the distribution of seed sources and seedlings using a procedure based on Ribbens *et al.* (1994) and Clark *et al.* (1999). Note that because we describe the distribution of seedlings, what we refer to as 'dispersal' actually includes post-dispersal processes and is therefore more correctly 'effective dispersal'. We assume that the seedling density in a plot can be described as,

$$\hat{s}_j(\mathbf{c}, \mathbf{N}, \mathbf{r}; \beta, K, \mu, \sigma) = \sum_{i=1}^{m} \beta c_i \max\left(0, 1 - \frac{N_i}{K}\right)$$
$$\frac{1}{(2\pi)^{1.5}\sigma r_{ij}^2}\exp\left[-\frac{(\ln r_{ij} - \mu)^2}{2\sigma^2}\right]. \qquad \text{eqn 2}$$

Here $\hat{s}_j(\mathbf{c}, \mathbf{N}, \mathbf{r}; \beta, K, \mu, \sigma)$ is the seedling density predicted in plot *j*, **c** is a vector of length *m* of the estimated cone number of each of *m* parent plants mapped, **N** is a vector of length *m* containing the number of con-specific adults (N_i) in a 10×10-m plot surrounding each parent plant, and **r** is a matrix containing the distances between the *i*th parent plant and the *j*th seedling plot. The parameters β, *K*, μ and σ are estimated from the data. β is the number of seedlings produced per cone, *K* is the con-specific plant density at which seedling production is zero (stands were essentially monospecific, so we ignore non-conspecific densities for parameter estimation) and μ and σ are the mean and variance of the log of dispersal distances as defined in Wagner *et al.*'s (2004) bivariate lognormal density function.

To estimate the parameters we calculate the likelihood of the observed number of seedlings per plot for a given vector of the parameters β, *K*, μ and σ. Following Clark *et al.* (1999) we assume that the errors are Poisson distributed and that the likelihood is the product of Poisson densities,

$$L(\mathbf{s}, \beta, K, \mu, \sigma) = \prod_n \text{Poisson}[\mathbf{s}, \hat{s}(\beta, K, \mu, \sigma)] \qquad \text{eqn 3}$$

where **s** is a vector of the observed seedling densities in *n* plots and **ŝ** is a vector of the expected seedling densities in the plots. Maximum likelihood estimates for the parameters β, *K*, μ and σ were obtained by minimizing the negative log likelihood using the Nelder Mead (Nelder & Mead 1965) algorithm as implemented by the R function *optim* (R Development Core Team 2006, version 2.4.1). The indirect method did in some cases converge to a local optimum. To ensure that a global optimum was found we started the parameter search with different initial parameter estimates.

Confidence intervals for the parameters were estimated using a Markov chain Monte-Carlo (MCMC) method. We use our own R implementation of the delayed rejection adaptive metropolis algorithm (DRAM, Haario *et al.* 2006) for running the MCMCs.

Table 1. Species specific Poisson (log link) regression models for cone number as a function of plant height (h) as reported by Flores (2001).

	Estimate	SE	z value	Pr(>|z|)
Leucadendron salignum (sprouter)				
(Intercept)	−3.61	0.17	−21.03	<0.001
Log (h)	1.93	0.04	50.19	<0.001
L. xanthoconus (seeder)				
(Intercept)	−3.92	0.16	−24.15	<0.001
Log (h)	1.82	0.03	55.27	<0.001
L. laureolum (seeder)				
(Intercept)	−6.84	0.29	−23.44	<0.001
Log (h)	2.19	0.06	37.97	<0.001
Protea cynaroides (sprouter)				
(Intercept)	−7.39	0.73	−10.12	<0.001
Log (h)	2.16	0.15	14.31	<0.001
P. lepidocarpodendron (seeder)				
(Intercept)	−9.76	0.32	−30.82	<0.001
Log (h)	2.71	0.06	44.91	<0.001
P. repens (seeder)				
(Intercept)	−10.64	0.21	−51.71	<0.001
Log (h)	2.92	0.04	76.88	<0.001

The statistical method outlined in the previous paragraphs requires maps of seed sources and samples of seedling density in survey plots. We sampled populations where there was variance in the density of the seed sources and where the seed sources were isolated from neighbouring populations. We mapped the locations of seed sources and seedling plots using differential GPS surveying methods. The sampling was conducted approximately 10 months after a fire and the subsequent germination and establishment of seedlings. The height of the dead skeletons of the parent plants was recorded. To convert height into cones per plant, we used Poisson regression models of the relationships between plant height and cone number per plant for each species (Table 1, Flores 2001). The *Leucadendrons* are dioeceous and care was taken to map only female parent plants. Seedlings were counted in 5×5 m plots. A special effort was made to sample plots far away from sources so as to improve the estimates of the tails of the dispersal kernels.

SIMULATION EXPERIMENTS

In a first set of analyses, we perform a sensitivity analysis of the model. We use the concept of an invasion analysis (Turelli 1978) to examine the conditions under which coexistence was possible. Specifically, we initiated a simulation in a 500×500-m arena (regular grid of patches), where one strategy was common (2000 plants) and the other was rare (200 plants). If both strategies, when rare, could reciprocally invade the other strategy when it was common, coexistence is possible. The plants were randomly located in the arena and we assumed that the boundary of the arena was absorbing.

We ran simulations for a range of mortality rates of the sprouter and for a range of fecundity rates of the seeder and for cases when dispersal was global and local. For global dispersal we drew dispersal distances from a lognormal distribution with mean and variance that were large relative to the size of the arena (μ = 2 and σ = 2, eqn 2). For local dispersal we drew dispersal distances from a lognormal with parameters μ = −1, σ = 0.5. For these simulations we assume that the seed production rate of the sprouter is 0.5, that the size of a patch is 1×1 m and that *K* is 10. Each simulation was run for 50 iterations.

Table 2. Parameter estimates and negative log-likelihood (−ln *L*) for the inverse model described in eqn 2. The 95% CI, estimated using Markov chain Monte-Carlo methods, are listed in parentheses.

	Parameter estimates*				
Species	*f*	*K*	μ	σ	−ln *L*
Leucadendron salignum (sprouter)	48.53 (35.38–63.88)	6.68 (6.12–9.15)	2.49 (2.27–2.87)	0.69 (0.56–0.92)	204.79
L. xanthoconus (seeder)	207.08 (172.63–243.03)	22.66 (22.44–23.32)	3.94 (3.65–4.20)	1.17 (0.98–1.34)	772.95
L. laureolum (seeder)	54.93 (43.91–62.43)	38.52 (33.28–59.55)	3.63 (3.41–3.88)	1.29 (1.11–1.48)	1018.24
Protea cynaroides (sprouter)	20.15 (16.97–25.23)	6.61 (6.54–6.76)	1.72 (1.60–2.00)	0.82 (0.83–1.13)	487.61
P. lepidocarpodendron (seeder)	151.94 (114.35–186.24)	35.35 (33.20–42.90)	4.37 (4.03–4.83)	1.36 (1.10–1.66)	916.13
P. repens (seeder)	173.85 (135.39–234.71)	17.33 (10.42–43.52)	3.67 (3.48–3.86)	1.04 (0.92–1.26)	775.47

*f is the mean number of seedlings per plant of average size ($f = \beta \times \bar{c}$; where β is the number of seedlings per cone and $\bar{c}$ is the average number of cones per plant). K is per 100 m², μ and σ have units ln(meter). See eqns 1 and 2 for further details.
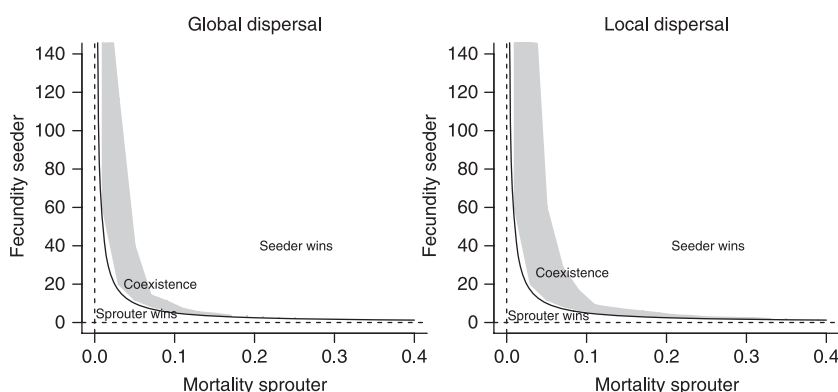

Fig. 1. The outcome of competitive interactions between seeders and sprouters as a function of the mortality rates of the sprouters and the fecundity (parameter f, eqn 1) of the seeders for the case of local dispersal and global dispersal. The solid line indicates the Bulmer (1994) boundary, above which coexistence is predicted. The fecundity parameter of the sprouter is set to 0.5 for these simulations.

In a second set of analyses, we repeated the analyses described in the previous paragraph, but used the empirical estimates of the fecundity and dispersal parameters (eqn 2). We ran simulations for *L. salignum* vs. *L. laureolum* and for *L. salignum* vs. *L. xanthoconus*. Similarly, we ran simulations for *P. cynaroides* vs. *P. repens* and for *P. cynaroides* vs. *P. lepidocarpodendron*. The average estimates of *K* for the *Leucadendrons* and *Proteas* were used to define the parameter *K* for these simulations (see Table 2). Hence we assume that the sprouters and seeders are competitively equivalent in the sense described by eqn 1. For the *Leucadendrons* we explicitly simulate the dioeceous habit by randomly assigning individuals a sex and by only allowing females to produce and disperse seeds. For these simulations the arena size was 500 × 500 m, patch size was 10 × 10 m and simulations were run for 50 iterations.

In a final set of simulations we examine the predicted spread rates of the study species when spreading alone and when spreading with a con-generic competitor. Each species was parameterized with the values listed in Table 2. The average estimates of *K* for the *Leucadendrons* and *Proteas* were used to define the parameter *K* and sprouter mortality rates were set to 0.05. These simulations used a 200 × 10 000-m arena and a 10 × 10-m patch size. The simulations were initiated with a row of plants at low density (one individual of each species per patch) on a short side of an empty arena. The mean distance the front (defined by the position of the furthest forward individual) moved in iterations 5–10 was used as an estimate of spread rate.

Results and discussion

SENSITIVITY ANALYSIS

The results of the sensitivity analysis suggest that three outcomes are possible – either the sprouter excludes the seeder, the seeder excludes the sprouter, or both species coexist. Which result is realized is determined by the mortality rate of the sprouter and the fecundity of the seeder (Fig. 1). This result holds for cases where dispersal is global and for cases where dispersal is local (Fig. 1).

The inequality derived by Bulmer (1994, solid line in Fig. 1) approximates the seeder fecundity below which sprouters dominate, but does not completely describe the outcome of competitive interactions in our model system. Specifically, the Bulmer inequality predicts coexistence at high seeder fecundity whereas our model predicts that seeders would exclude sprouters at high seeder fecundity. Coexistence models of the kind described by Bulmer (1994) appear not to be appropriate for describing coexistence between seeder and sprouter species in fire prone shrublands. For instance, Groeneveld *et al.* (2002) used a detailed rule-based simulation model to examine coexistence between sprouter and seeder species in the fire prone shrublands of Western Australia. They found that coexistence was only possible for a range of conditions more restrictive than those described by Bulmer (1994). In particular they report that variation in fire return intervals and differential species response to fire return interval were important for coexistence. Our result and those of Groeneveld *et al.* (2002) suggests that coexistence in fire driven seeder–sprouter systems is limited to a restricted range of conditions. Specifically, our results suggest that coexistence is most likely where the mortality rates of the sprouter are low (but not close to zero) and, to a lesser extent, where dispersal is restricted.
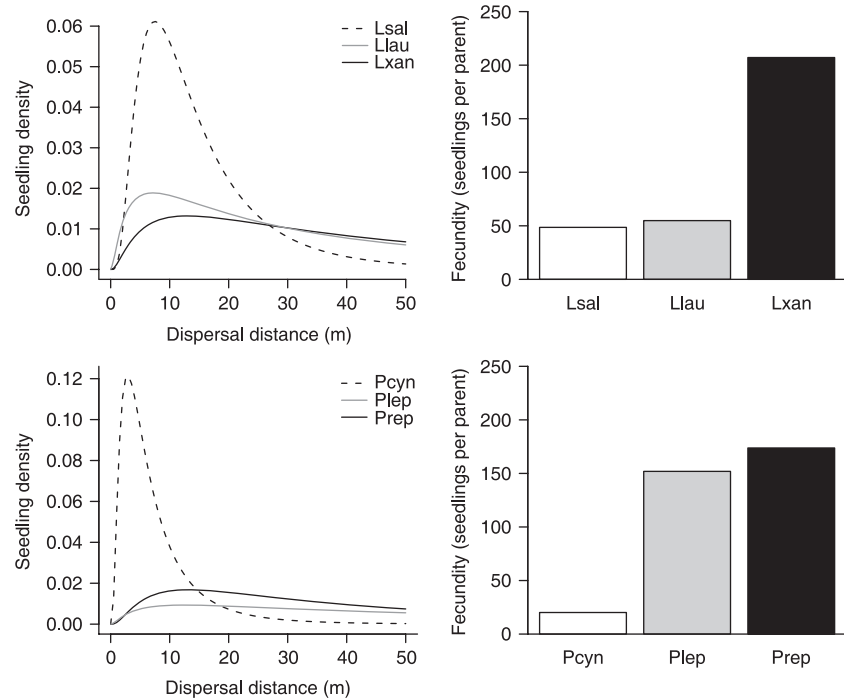
Fig. 2. The estimated dispersal kernels and fecundity (parameter *f*, eqn 1) for the study species as estimated using the inverse model described by eqn 2 ($f = \beta \times \bar{c}$; where β is the number of seedlings per cone and $\bar{c}$ is the average number of cones per plant). Table 2 lists the parameter estimates. The codes of the species names are the first letter of the genus name and the first three letters of the species names (see Table 1).

FIELD DATA

The field data illustrate that the sprouters produce lower numbers of seedlings per parent than the seeders (Table 2, Fig. 2). The estimated dispersal kernels show that dispersal is more restricted for the sprouters than for the seeders (Table 2, Fig. 2). These findings were true for both the *Protea* and *Leucadendron* comparisons, with the sprouter *P. cynaroides* having particularly restricted dispersal. Taken together the lower fecundity and more restricted dispersal of the sprouters mean that they have a lower potential of colonizing sites far away from the parent plant.

In our data collection we made a special effort to sample seedling densities far away from the seed sources. This, in combination with the known potential of proteaceous species for long-distance dispersal in the post-fire environment (Schurr *et al.* 2005), explains the relatively high dispersal distances reported (Table 2).

PARAMETERIZED MODEL

We parameterized the model with the dispersal kernel parameter estimates and the sprouter fecundity rates (Table 2). Analogous to the simulation experiment, we ran simulations using a range of sprouter mortality rates and seeder fecundity rates. These simulations illustrated qualitatively similar results to those yielded by the simulation experiment (compare Figs 1 and 3); namely there is a band of seeder fecundity and sprouter mortality parameter combinations for which coexistence is possible.

For the simulations of *L. salignum* vs. *L. xanthoconus* coexistence would be possible for the empirically estimated fecundity estimates, provided that *L. salignum* had a mortality rate of 0.27–0.40. For the *L. salignum* vs. *L. laureolum* combination, coexistence seems unlikely, primarily because our empirical estimates of seed production for *L. laureolum* are only marginally higher than those for *L. salignum.* For the *Protea* combinations, coexistence seems possible provided that the mortality rate of *P. cynaroides* is between 0.12 and 0.25 when facing *P. repens* and between 0.19 and 0.33 when facing *P. lepidocarpodendron.* These results lead one to ask what are sprouter mortality rates?

Studies in fire driven shrublands have often assumed that mortality rates of sprouters are so low as to be negligible (e.g. Keeley 1977; Bond & Van Wilgen 1996). Hence although we do not have data on mortality rates for our two sprouter study species, we anticipate that the mortality rates are lower than 0.20. Unpublished data of one of the authors for *L. salignum* suggest mortality rates of 0.1 (F.M. Schurr, unpubl. data). For mortality rates below 0.10, coexistence seems unlikely in our model system, as the seeders would require seedling production rates in excess of 200 seedlings per parent to coexist with sprouters that are producing 20–30 seedlings per parent. Fecundity rates of this magnitude were, in our study, only achieved by *P. repens.*

Hence the fact that these species do coexist even though our model analysis suggests that sprouters should dominate needs explanation. Our data describes seedlings that established after the winter rains which followed a summer fire. Our analyses assume that these seedlings have the physiological capacity to survive the first summer (the warm, dry season) and establish into the adult class. One possibility that may favour coexistence is if the seedling mortality in the first summer after establishment is higher for sprouters than for seeders. For instance, Verdaguer & Ojeda (2002) report higher rates of allocation to below-ground resources in sprouter seedlings which may
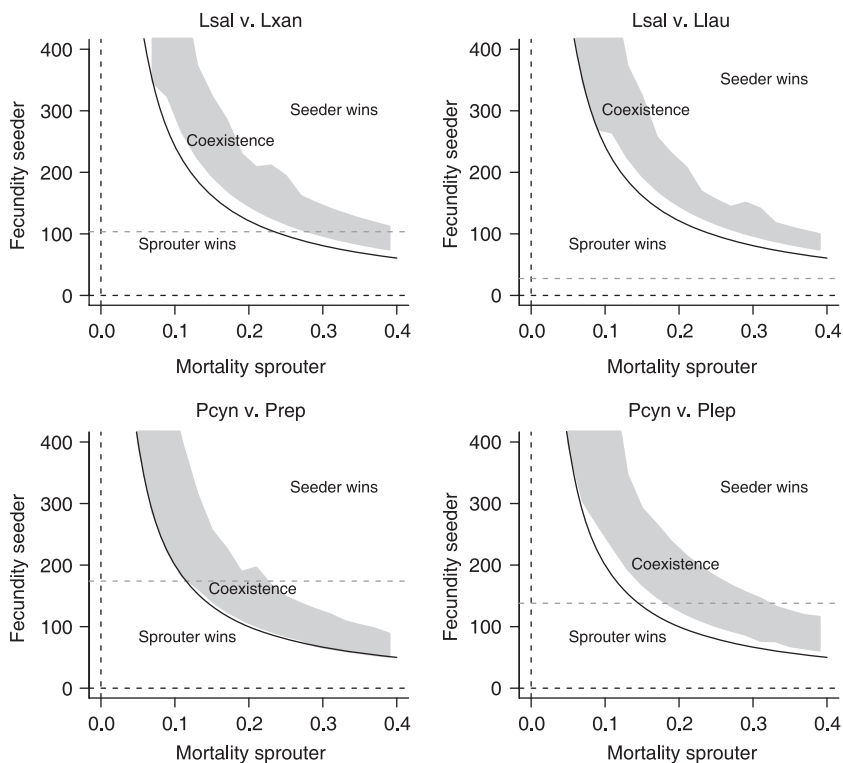
Fig. 3. The outcome of competitive interactions between seeders and sprouters as a function of the mortality rates of the sprouters and the fecundity (parameter *f*, eqn 1) of the seeders. Each competing species was parameterized using the dispersal kernel estimates listed in Table 2 and the fecundity rates of the sprouting species are set to the fecundity values listed in Table 2. The fecundity estimates for the seeder species are plotted as a dashed gray line. The solid line indicates the Bulmer (1994) boundary, above which coexistence is predicted. The codes of the species names are the first letter of the genus name and the first three letters of the species names (see Table 1).

reduce growth rates and possibly reduce the chances of recruitment into the reproductive class (Bond & Midgley 2003), although one could equally argue that the early investment in below-ground resources might favour the chances of surviving the first summer drought. It is therefore perhaps not surprising that Schwilk & Ackerly (2005) in a thorough investigation of the establishment phase in *Ceanothus* species found mixed evidence for differences in drought tolerance between seeders and sprouters.

Simulations that use the empirically estimated dispersal kernels (Fig. 3) produced qualitatively similar results to simulations where it was assumed that competing species had the same dispersal capacity (Fig. 1). One might have expected a locally dispersing species competing with a more widely dispersing species to fare better because they stand a higher chance of winning lotteries in their local environment. On the other hand such locally dispersing species would be exposed to higher levels of intra-specific competition than more widely dispersing species (Bolker & Pacala 1999). Hence it appears that differences in dispersal ability do not fundamentally influence the coexistence in the lottery system we examined.

In our spread simulations we estimate that the study species can move between 37 and 1600 m per generation (Fig. 4). In this system, generation time is equivalent to the fire return interval (Bond & Van Wilgen 1996) which has a mean of 29 years (Polakow & Dunne 1999), even though values as low as 6 years are not uncommon (Bond & Van Wilgen 1996). *Protea cynaroides* (a sprouter) has the slowest spread rate, whereas *P. lepidocarpodendron* has the fastest spread rate. In general the sprouting species spread considerably slower than the seeder species. We also found that the effect of the

competitor seeder species on the sprouter spread rates was proportional to the fecundity of the seeder species, whereas the spread rates of the seeders were unaffected by the presence of sprouters (Figs 2 and 4). Moorcroft *et al.* (2006) have also shown that spread rates are slower when competitors are present. However, Moorcroft *et al.* (2006) explored a situation where an invader invades an environment occupied by a competitor of equivalent competitive rank, whereas our simulations explore a situation where invaders of different competitive rank invade an unoccupied habitat. Hence, although our parameter estimates suggests that sprouters should dominate seeders (Fig. 3), we found that their poorer colonization ability ensured that they spread slower than the seeders (Fig. 4). Since our simulations examine two competing species invading an unoccupied environment, the rapid-spreading seeder species invades essentially unoccupied habitat and therefore achieves spread rates similar to those achieved when competitors are absent. Even though parameter estimates suggest that sprouters are superior competitors, they spread much slower and hence must invade habitat already occupied by the seeder, which retards their rate of spread.

Conclusions

A simplistic view of persistence-reproduction trade-offs is that more fecund species are better colonizers simply because they produce more seeds, and that the price for this high seed production is reduced persistence or ability to compete (Tilman 1994). Our study provides evidence for this trade-off. The persistent (sprouter) strategies had lower fecundity than
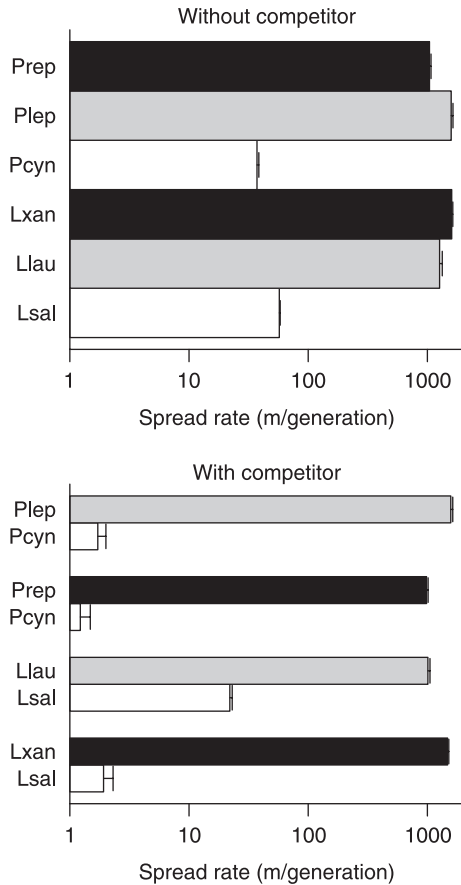
Fig. 4. Spread rates of the study species when spreading alone and with a congeneric competitor. The error bars represent standard errors of replicate simulations. The codes of the species names are the first letter of the genus name and the first three letters of the species names (see Table 1).

the non-persistent (seeder) strategies. Yet, our study system suggests an additional dimension to the colonization–competition debate that may be relevant in times of rapid climate change. It emphasises that colonization ability is not solely determined by seed production, but rather by the product of seed production and the dispersal kernel (Higgins & Cain 2002). Specifically, we found that the seeders were better colonizers not only because they produced more seeds but because they could disperse these seeds over greater distances.

An additional component of the trade-off is determined by the persistence ability of the adult life-stage. Individuals capable of persisting cannot be excluded by competitors for the simple reason that a seed cannot out-compete an established individual. Hence our sprouters are good competitors because of their ability to persist once established and because they have more restricted dispersal, which may increase their chances of winning lotteries in the parent neighbourhood. Our results therefore imply that there is selection pressure on sprouters to increase fire survival rates and on seeders to produce more seeds and to disperse these seeds more widely in the hope of finding unoccupied sites.

It is apparent that the sprouter species we investigated may battle to track climate change for two reasons. First, their capacity to spread into unoccupied habitat is lower than the capacity of con-generic seeders. Second, when invading unoccupied habitat in competition with con-generic seeders, they spread every more slowly. In comparison, the seeders spread at rates similar to those achieved in the absence of competitors. This is true, despite the fact that our empirical parameter estimates suggest that the seeders are weaker competitors. Hence, even though the competitive superiority of the sprouter strategies in lottery systems suggests that, if present, sprouters may dominate the communities that assemble in the wake of climate change, it seems unlikely that they will be on the playing field.

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