

The effects of temporally variable dispersal and landscape structure on invasive species spread

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Abstract. Many invasive species are too widespread to realistically eradicate. For such species, a viable management strategy is to slow the rate of spread. However, to be effective, this will require detailed spread data and an understanding of the influence of environmental conditions and landscape structure on invasion rates. We used a time series of remotely sensed distribution maps and a spatial simulation model to study spread of the invasive *Lepidium latifolium* (perennial pepperweed) in California's Sacramento-San Joaquin River Delta. *L. latifolium* is a noxious weed and exhibited rapid, explosive spread. Annual infested area and empirical dispersal kernels were derived from the remotely sensed distributions in order to assess the influence of weather conditions on spread and to parameterize the simulation model. Spread rates and dispersal distances were highest for nascent infestations and in years with wet springs. Simulations revealed that spread rates were more strongly influenced by the length of long-distance dispersal than by temporal variation in its likelihood. It is thus important to capture long-distance dispersal and the conditions that facilitate spread when collecting data to parameterize spread models. Additionally, management actions performed in high-spread years, targeting long-distance recruits, can effectively contain infestations. Corridors were relatively unimportant to spread rates; their effectiveness at enhancing rate of spread was limited by the species' dispersal ability and the time needed to travel through the corridor. In contrast, habitat abundance and shape surrounding the introduction site strongly influenced invasion dynamics. Satellite patches invading large areas of invulnerable habitat present especially high risk.

Key words: corridors; habitat abundance; hyperspectral remote sensing; invasion rate; *Lepidium latifolium* (perennial pepperweed); regeneration niche; simulation model; spread rate.

INTRODUCTION

Charles Elton, author of the seminal work on biological invasions, termed invasions by exotic species "ecological explosions" (Elton 1958). Invasive species frequently exhibit explosive growth and spread in their new ranges; published rates of spread of invasive plants range from 2 to 370 m/yr, on average, with long-distance dispersal of up to 167 km/yr (Pyšek and Hulme 2005). Quantifying this spread, however, is nontrivial. Researchers generally recreate invasive species spread from floristic records (e.g., Pyšek and Prach 1995, Weber 1998, Mihulka and Pyšek 2001, Lavoie et al. 2007, Lelong et al. 2007, Shih and Finkelstein 2008) or county- to national-level inventories (e.g., Forcella 1985, Perrins et al. 1993, Smith et al. 2002, Evans and Gregoire 2007, Pyšek et al. 2008). These data suffer from collection biases, however, and cannot recreate all spread dynamics adequately as they are effectively

aspatial (due to coarse resolutions). The spatial scale at which spread analyses are performed is known to strongly influence estimated spread rates and invasion dynamics, with larger scales more heavily emphasizing long-distance dispersal (Pyšek and Hulme 2005). In contrast, detailed field studies can monitor local spread (e.g., Myers and Berube 1983, Nuzzo 1999, Frappier et al. 2003), but often fail to detect important long-distance dispersal events, due to the constrained temporal scale and spatial extent of observations. Estimated invasion speeds are thus highly sensitive to sampling effort (Skarpaas and Shea 2007) and are often orders of magnitude slower than observed (e.g., Andow et al. 1990).

Remote sensing technologies offer a valuable tool for characterizing invasive plant species spread. Image data are inherently spatial and provide 100% sampling at fine spatial resolution over a much greater extent than is feasible for field mapping. Remotely sensed distribution maps have been cited as one of the most accurate methods for estimating spread (Hastings et al. 2005). All remote sensing of invasive plant species spread to date has used aerial photography, typically analyzed by manual photointerpretation, due to the length and value of the photo record (Lonsdale 1993, Brown and Carter 1998, Higgins et al. 2001, Buckley et al. 2005,

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Müllerová et al. 2005, Maheu-Giroux and de Blois 2007, Browning et al. 2008). However, the limitations of photointerpretation restrict analyses to species that are broadly different from the invaded communities, for example, to shrub encroachment of deserts and grasslands (Brown and Carter 1998, Browning et al. 2008), pine invasions (Higgins et al. 2001, Buckley et al. 2005), and species with vivid floral displays (Müllerová et al. 2005). The number and variety of plant species that can be mapped and studied with remote sensing is expanded by hyperspectral instruments. These sensors record reflected electromagnetic radiation with many (>100 bands) narrow spectral bands, capturing subtle spectral features that may be used to map vegetation to the species level (e.g., Underwood et al. 2003, Lass et al. 2005).

While such observations can be used to characterize spread of invasive plants, modeling techniques are much more effective for understanding spread. Analytical and simulation models offer a tractable experimental setting to investigate the influence of demographic and dispersal (e.g., Shigesada et al. 1995, Kot et al. 1996, Neubert and Caswell 2000, Woolcock and Cousens 2000, Clark et al. 2001, Yamamura 2004, Buckley et al. 2005, Dwyer and Morris 2006, Nehrbaas et al. 2007, Skarpaas and Shea 2007, Jongejans et al. 2008a), and landscape (e.g., Bergelson et al. 1993, van Dorp et al. 1997, Collingham and Huntley 2000, King and With 2002, Söndgerath and Schröder 2002, Matlack and Monde 2004, With 2004, Nehrbaas et al. 2007, Sebert-Cuvillier et al. 2008) parameters on spread. These studies highlight that spread models are extremely sensitive to the input dispersal parameters, emphasizing that accurate predictions require high-quality dispersal observations, such as may be provided by remote sensing. Yet, to date, remote sensing has only rarely been used to parameterize (Lonsdale 1993, Buckley et al. 2005, Nehrbaas et al. 2007) and validate (Higgins et al. 2001) models of invasive plant spread.

Finally, observations often indicate temporal variation in spread (Liebhold et al. 1992) or dispersal, due to effects of weather conditions (Lonsdale 1993, Evans and Gregoire 2007, Browning et al. 2008), disturbance (Nuzzo 1999), and management practices (Brown and Carter 1998, Humston et al. 2005, Bullock et al. 2008, Marshall and Buckley 2008). However, surprisingly, the effect of temporal variation in dispersal on spread rates has almost never been explicitly studied (but see Neubert et al. 2000).

We mapped the invasive plant species *Lepidium latifolium* in a five-year time series of hyperspectral image data. The resultant distributions were used to characterize dispersal and spread and to relate temporal variation in spread to weather conditions. Dispersal observations were also used to parameterize a simple spatial model to assess the influence of temporal variation in dispersal and landscape structure on spread rates in a real landscape.

METHODS

Study species

Lepidium latifolium (perennial pepperweed; see Plate 1), native to Eurasia, is aggressively invading natural and anthropogenic landscapes throughout California. Although observed in nearly all biogeographic provinces and habitat types in California, it is primarily considered a wetland and riparian weed. *L. latifolium* has a high dispersal potential: it produces numerous small, wind- and water-dispersed seeds (up to 16 million seeds/ha; Young et al. 1997) and spreads vegetatively via perennial roots and root fragments (Francis and Warwick 2007). Eradication of *L. latifolium* is unlikely because of the limited effectiveness of many control strategies against its belowground structures (Young et al. 1998, Renz 2002), restrictions against herbicide use in the wetland systems it invades and where it frequently co-occurs with threatened and endangered species, and its already widespread distribution. However, slowing the spread of an invasive species is a viable management strategy and is often more cost-effective than attempting eradication (Sharov and Liebhold 1998). Understanding the influence of environmental and landscape characteristics on spread rates will allow managers to prioritize when and where to control populations, most effectively containing infestations of this noxious weed.

Image data and analyses

Hyperspectral HyMap data were acquired of Bouldin Island (Fig. 1) in the Sacramento-San Joaquin River Delta on 8–9 July 2004, 7–8 July 2005, 21 and 26 June 2006, 23 and 26 June 2007, and 5–6 July 2008 by the HyVista Corporation ([available online](#)).² HyMap is an airborne imaging spectrometer that detects the entire optical range of reflected solar radiation (450–2500 nm) with 128 narrow spectral bands (each 15–20 nm wide) (Cocks et al. 1998). The aircraft was flown at an altitude of 1.5 km, resulting in pixels that are 3 m on a side. Image data were atmospherically corrected by the vendor and georegistered to within 1.0 pixel error with an orthorectification algorithm developed by Analytical Imaging and Geophysics (Boulder, Colorado, USA) and ground control points selected from 1-foot (30.5 cm) color orthophotos, 1-m USGS digital orthophoto quads, and USGS National Elevation Dataset digital elevation models.

Field data to train and validate image analyses were collected on 8 November 2005 ($n = 13$ *L. latifolium* patches, $n = 39$ other vegetation patches); 4 and 8–9 August 2006 ($n = 68$ *L. latifolium* patches, $n = 36$ other patches); and 22 and 30 August 2007 ($n = 92$ *L. latifolium* patches, $n = 68$ other patches). Data were geographic locations of patches of *L. latifolium* and co-occurring vegetation, and were collected with a GeoXT GPS unit (Trimble, Sunnyvale, California, USA). The

² (www.hyvista.com)

characteristics of the entire patch occurring at each point were recorded, including species identity (both dominant and co-occurring), percent cover, patch size, and patch orientation; photos were taken of all patches. All points were screened relative to each year's image data. Random samples of 3000 pseudo-absence points were created for each image date to supplement the field data. Pseudo-absence points were restricted from patches present in the field data, but were otherwise not screened for possible *L. latifolium* presence. The possibility of false negatives in the pseudo-absence set is acceptable given the low abundance of *L. latifolium* throughout the site.

L. latifolium was mapped from the hyperspectral data following the methods of Andrew and Ustin (2008). In short, this method uses an ensemble of decision trees to integrate the outputs of mixture-tuned matched filters (MTMF; Boardman et al. 1995), an advanced subpixel analysis, and spectral physiological indexes that are sensitive to specific vegetation conditions. MTMF models each pixel as a mixture of the target material (i.e., *L. latifolium*) and an unknown background material, solving for the proportional abundance of the target within each pixel as well as an estimate of the feasibility that it is present. This approach has proven to be flexible, accurate, and robust across a variety of environmental conditions (Andrew and Ustin 2008). It mapped *L. latifolium* successfully in each image date of Bouldin Island. To minimize biasing dispersal data with classification errors, *L. latifolium* maps were refined by requiring at least two years of consensus for a pixel to be classified as *L. latifolium*. Note that this correction is not appropriate for the 2008 classification as it would preclude detection of any new spread. Furthermore, pixels were assumed to include *L. latifolium* if it was mapped in that pixel at any earlier time step. This is a reasonable assumption because *L. latifolium* is a perennial species that is not undergoing any management on this island. The accuracy statistics for each year's distribution maps are given in Table 1.

Spread and dispersal observations

The spread of *L. latifolium* was assessed at three subsites on Bouldin Island (Fig. 1), two on the island bottom and one along the levee slope. The two island bottom sites differ primarily in soil texture (Soil Survey Geographic Database [SSURGO] for San Joaquin County, California, *available online*).³ The clayey bottom site (Fig. 1a) occurs on a Ryde-Peltier complex soil that is 31% clay, 35.4% sand, and 33.6% silt. The silty bottom site (Fig. 1c) has a Valdez silt loam, which is 22.5% clay, 7.2% sand, and 70.3% silt. The levee site (Fig. 1b) spans both of these soil types, and conditions seem to be defined much more strongly by the topography of the levee than by variation in the soils.

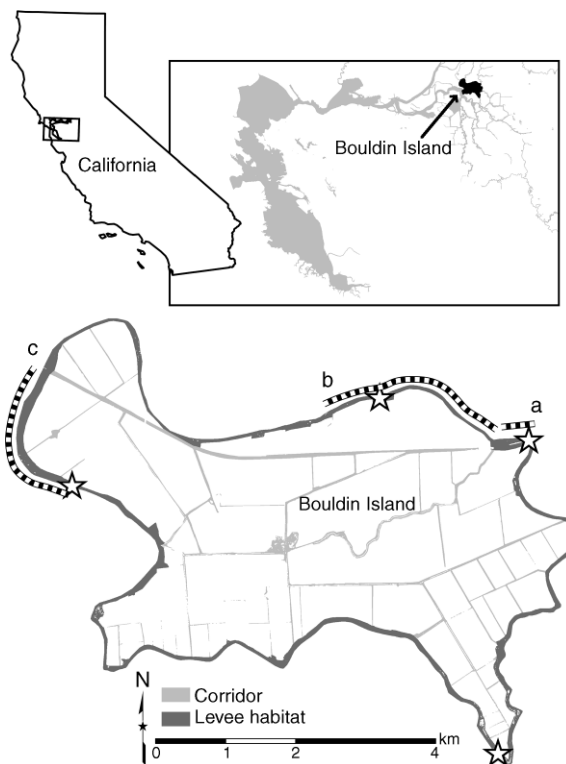


FIG. 1. Map showing the location of the Sacramento-San Joaquin River Delta, California, USA, with the enlargement showing waterways in gray and Bouldin Island in black. The detailed map of Bouldin Island has dashed bars paralleling the island that highlight the (a) clayey bottom, (b) levee, and (c) silty bottom subsites focused on for remotely sensed observations of the spread of invasive *Lepidium latifolium* (perennial pepperweed). Two shades of gray on the island map indicate suitable levee and corridor habitat for simulation experiments. Stars indicate introduction sites for simulation experiments.

These three sites encompass the most extensive infestations on this island. Area invaded was determined from the remotely sensed distribution maps for each year at each subsite.

Influence of weather conditions on spread.—Because the three subsites differed in total area, stage of invasion, and spread patterns observed, it was necessary to create standardized estimates of spread. To do so, invasion curves were fit to plots of area vs. time for each site. Linear, square root, log, and logit transformations were assessed, and the one with the best fit for each site was selected. The residuals between observed area and area predicted by the invasion curves were then tested against weather variables with simple linear regression. Weather data were obtained from the Lodi West CIMIS (California Irrigation Management Information System) station (*available online*).⁴ Variables tested included total water year (September–June) and spring-time (March–June) precipitation, growing degree days

³ (<http://soildatamart.nrcs.usda.gov>)

⁴ (www.cimis.water.ca.gov)



PLATE 1. *Lepidium latifolium* (perennial pepperweed) growing near Davis, California, USA. Photo credit: M. E. Andrew.

(1 January–31 May, base of 10°C), summed average temperature of winter and springtime months, number of frost days, average wind speeds, and number of windy days (>16 kph), with up to a three-year lag between weather observations and spread observations.

Estimation of empirical dispersal kernels.—Empirical dispersal kernels were constructed for each time step as the set of paired distances and directions from newly invaded pixels to the nearest source patch in the previous year's distribution map. Note that because the hyperspectral data detect only adult populations (as opposed to propagules), these estimates of dispersal actually include both dispersal (either vegetative or by seed) and establishment processes, and there may exist a lag between patch establishment and patch detection. Such lags can challenge the study and management of invasive species spread (Crooks 2005).

Simulation model

A simple spatial simulation model was constructed to assess the effects of the observed temporal variation in dispersal and of landscape structure on spread rates. This model tracked invaded grid cells, rather than individual organisms, over a 200-year run with a time step of one year. Every year, each occupied cell created five recruits to disperse, which corresponds to the maximum rate of exponential spread observed in the hyperspectral distribution maps. Each recruit was then

dispersed to a destination cell determined by randomly sampling a paired dispersal distance and direction from an empirical dispersal kernel derived from the remotely sensed distribution maps. Destination cells were updated as occupied if they were suitable habitat and if they had not been previously colonized. We assumed no loss of occupied cells and no temporal variation in the invasibility of destination cells. The number of cells occupied was output at the end of each time step, from which invasion curves were constructed and spread rates were estimated. The model was programmed and run in MATLAB (MathWorks, Natick, Massachusetts, USA). The simulation experiment tested the effects of dispersal kernel, corridors, and introduction site on invasion dynamics in a replicated ($n_i = 50$), fully-factorial framework. Each of these treatments are described in the following three subsections.

Dispersal kernel.—Five dispersal kernel scenarios were tested: in the first four, the dispersal kernel was fixed and corresponded to one of the specific annual kernels from the time series of remotely sensed distributions. In the last case, temporal variation in dispersal was simulated by randomly choosing which kernel to sample at each year in the model run. When adequate data exist, it is preferable to sample observed dispersal data, as we chose to do here, rather than statistically fitted dispersal kernels because kernels with different tail shapes can yield similar fits, but wildly different spread behavior (Clark et al. 2001, Lewis et al. 2006).

Simulation landscapes—corridors.—We tested the influence of corridors on invasion dynamics because roadsides frequently provide habitat for invasive plant species (e.g., Spellerberg 1998, Gelbard and Belnap 2003, Pauchard and Alaback 2004, 2006, Hansen and Clevenger 2005, Lavoie et al. 2007, Lelong et al. 2007, Maheu-Giroux and de Blois 2007), including *L. latifolium*, prompting concern that roads and ditches connect distant habitats, allowing invasive species to become well distributed across large areas, and serving as propagule sources for the invasion of natural, interior communities (Lavoie et al. 2007, Lelong et al. 2007, Maheu-Giroux and de Blois 2007, Thiele et al. 2008). Four different simulation landscapes were tested. The first three were derived from the real Bouldin Island

TABLE 1. Accuracy statistics of the distribution maps of *Lepidium latifolium* (perennial pepperweed) classified from the hyperspectral image data of Bouldin Island, Sacramento-San Joaquin River Delta, California, USA.

Year	Omission error (%)	Commission error (%)	Overall accuracy (%)	Kappa
2004	16.1	1.9	91.5	0.829
2005	18.9	4.4	91.0	0.807
2006	41.2	13.0	75.2	0.502
2007	28.3	4.4	81.9	0.645
2008	9.3	6.9	92.0	0.840

Notes: Kappa is a measure of accuracy that corrects for chance agreement. Kappa >0.55 indicates good agreement; kappa >0.7 indicates very good agreement.

landscape (Fig. 1) and were designed to test the influence of connectivity by corridors on spread. For these landscapes, suitable habitat was designated as (1) full corridor trials, all nonagricultural lands, i.e., all levees, roadsides, and ditch-sides; (2) reduced corridor trials, all levees and a single pixel strip along roads and ditches; and (3) no corridor trials, only levees as suitable habitat. The simulation model output only the number of levee cells occupied at each time for the sake of comparability between all landscapes. The last simulated landscape was a homogeneous, square landscape with approximately the same number of cells as the total levee habitat on Bouldin Island. The real landscapes tested here are very different from the hypothetical landscapes generally used in spatially explicit models, which are often quite small and extremely simplified. Moreover, they are all extremely connected landscapes, even in the no corridor scenario, because the levee that uninterruptedly circles the island is the suitable habitat. The roadside and ditch-side corridors may therefore provide shortcuts rather than connectivity, *per se*, in addition to habitat.

The influence of corridors was tested with ANOVAs performed at every time step for a given dispersal kernel and introduction site to determine the times at which the invader in the full and reduced corridor landscapes infested a significantly greater area than that in the no corridor case. Nonparametric Wilcoxon tests were also performed and, in nearly all cases, differed by only one year from the ANOVA results.

Introduction sites.—The role of local landscape structure was tested with five sets of simulations initialized with different initial spatial distributions of *L. latifolium*: the observed 2004 distribution, or as a single occupied cell at one of the four sites designated by stars in Fig. 1. The homogeneous landscape was initialized with a single invaded cell in the center. Simulations initialized with the observed 2004 distribution produced unrealistically rapid spread rates, prompting us to investigate the establishment probability necessary to bring simulations in line with observations.

Habitat availability (%) and shape (the ratio of patch perimeter to the perimeter of a maximally compact patch of the same area) were determined for the local landscape within a 500 cell radius of each introduction site (Table 2). For these metrics, suitable habitat was considered to be the levee margin as well as road- and ditch-side corridors, when they were present in the simulation landscape. Metrics were calculated in Fragstats (*available online*).⁵ The relationship of clumpiness with spread rates was also assessed. Clumpiness is an index of contagion, which is known to influence spread through a landscape (Collingham and Huntley 2000). However, because all simulated landscapes were so highly connected, there was very little variation in this metric and it was not included in analyses.

⁵ <http://www.umass.edu/landeco/research/fragstats/fragstats.html>

TABLE 2. Landscape structure within 500 pixels of each introduction site, as characterized by the percentage of suitable habitat by area and the area-weighted mean shape index.

Landscape and introduction site	Habitat abundance (%)	Habitat shape (area-weighted mean)
Full corridors		
Clayey bottom	5.27	9.70
Silty bottom	6.78	10.03
Levee	5.36	6.79
Southeastern tip	3.83	15.70
Reduced corridors		
Clayey bottom	3.95	14.39
Silty bottom	5.18	16.44
Levee	3.42	7.76
Southeastern tip	3.56	20.19
No corridors		
Clayey bottom	3.37	5.70
Silty bottom	4.51	4.55
Levee	2.72	5.77
Southeastern tip	3.11	11.14

Note: Habitat shape was calculated as the ratio of patch perimeter to the perimeter of a maximally compact patch of the same area and integrated for the region surrounding each introduction site as the average shape of each habitat patch weighted by patch area.

Dispersal directionality.—One final set of simulations tested the influence of dispersal directionality on invasion rates by ignoring the direction component of the dispersal observations. This scenario randomly sampled dispersal distance from the empirical dispersal kernels but chose dispersal direction from a random uniform distribution. We tested this effect with all of the landscape scenarios (suitable habitat and corridors) and using each of the yearly dispersal kernels, but only for the clayey bottom introduction site (Fig. 1a).

Testing model effects.—The effects of dispersal kernel, corridors, and introduction site on invasion rates were tested with general linear models with the number of cells occupied (averaged over 50 model runs for each scenario) as the dependent variable and time, dispersal kernel, landscape, introduction site, and all interaction terms as the independent variables. A significant interaction with time indicates that a term has an effect on invasion rate. A separate test was performed between the model runs with the original and the adirectional dispersal kernels at the clayey bottom introduction site to determine the effect of dispersal directionality on spread rates.

Assessing the role of individual components of landscape structure.—Asymptotic invasion rates were calculated for each model run (i.e., any nonlinear portions of invasion curves due to early exponential growth or habitat saturation were excluded). To determine how habitat structure affects invasion rates, the following general linear models were performed: (1) invasion rate as a function of habitat abundance and dispersal, and (2) invasion rate as a function of habitat shape, landscape, and dispersal kernel. All statistical analyses

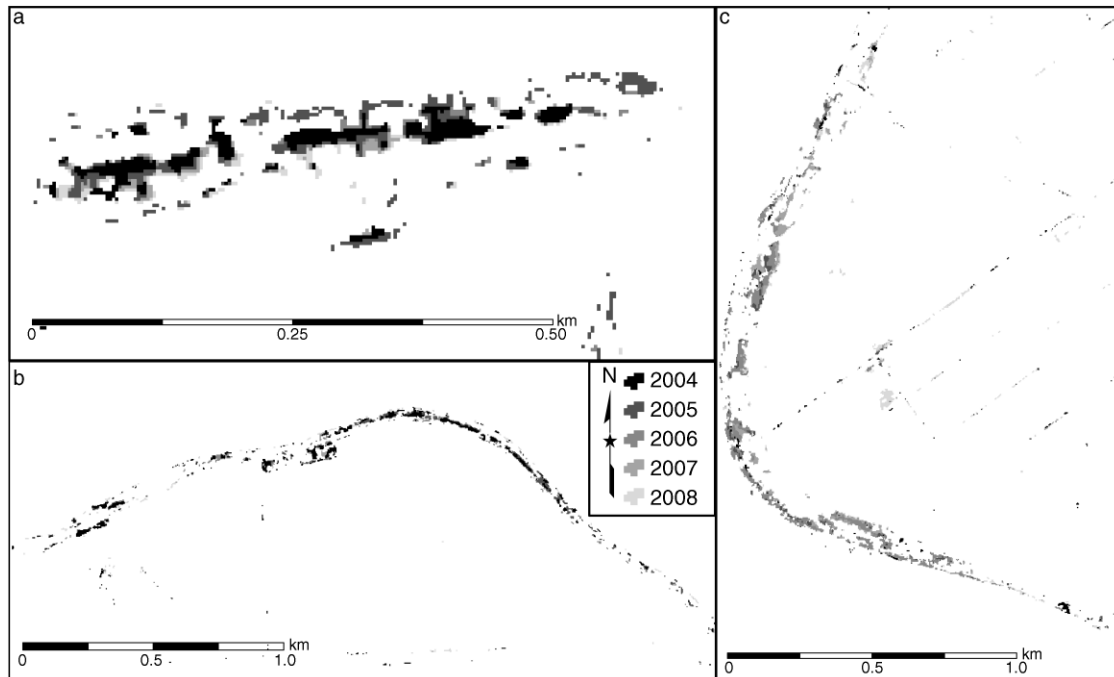


FIG. 2. Remotely sensed *L. latifolium* distributions over the five-year image series at the three Bouldin Island subsites: (a) clayey bottom, (b) levee, and (c) silty bottom.

were performed in JMP (SAS Institute, Cary, North Carolina, USA).

RESULTS

Remotely sensed observations

Yearly *L. latifolium* distributions as mapped from the hyperspectral imagery are shown in Fig. 2 for the clayey bottom (2a), levee (2b), and silty bottom (2c) subsites. At both the clayey bottom and levee subsites, the infestation was well established in 2004, the first year of the time series. Growth at these sites primarily occurred via creeping spread of existing patches, although some new patches were colonized, especially at the levee site and the levee portions of the clayey bottom site (the northern portion of this site). The infested area increased linearly at these sites, by 2000 m²/yr (clayey bottom, $R^2 = 0.872$, Fig. 3a) and 4000 m²/yr (levee, $R^2 = 0.910$, Fig. 3b).

Dispersal at the clayey bottom site averaged ~5 m, with maxima around 25 m (Table 3). However, dispersal distances were greater in the 2004–2005 time step (mean = 15 m, max = 78 m; Table 3), which is the year that the levee became extensively colonized. Dispersal was more variable at the levee site, with annual means around 10–20 m and maxima of over 100 m (Table 3).

L. latifolium was largely absent at the silty bottom subsite in 2004 (Fig. 2c), but its population exploded over the time series, especially in the 2005–2006 time step. At this site, *L. latifolium* spread logistically (with carrying capacity of 41 000 m² visually estimated as the

asymptote of the invasion curve; $R^2 = 0.997$), with very high annual rates of increase of 380–460% during the exponential phase of growth. Dispersal distances were extremely temporally variable at the silty bottom site, with means ranging from 5 to 50 m and maxima from 57 to over 200 m (Table 3). The years with exponential spread were also those with the farthest dispersal.

Dispersal observations from all three sites were pooled into the empirical dispersal kernels in Fig. 4. In all years, most recruits dispersed by just one to a few pixels (3 m each) from the parent patch. However, long-distance dispersal by >100 m occurred in the 2004–2005 and 2005–2006 time steps, and was relatively common in the former ($n = 34$, 1.9% of all observations; cf. $n = 5$, 0.2% of all observations in 2005–2006). Local dispersal tended to be adirectional; its apparent directionality in Fig. 5 results from the grid geometry. Long-distance dispersal was highly directional: source patches were most likely to be to the south and southwest of long-distance recruits (Fig. 5). This directionality may be an artifact of habitat shape (i.e., the silty bottom site has a southwest–northeast orientation), but it may be a very real function of the dispersal vectors. For example, the strong Delta breeze experienced at this site while *L. latifolium* is fruiting and senescing is expected to disperse seeds in this direction. Mechanistic dispersal models coupled with detailed vector data are the best way to characterize dispersal directionality and understand its influence on spread rates (Skarpaas and Shea 2007, Jongejans et al. 2008b); however, such data were not available to this study.

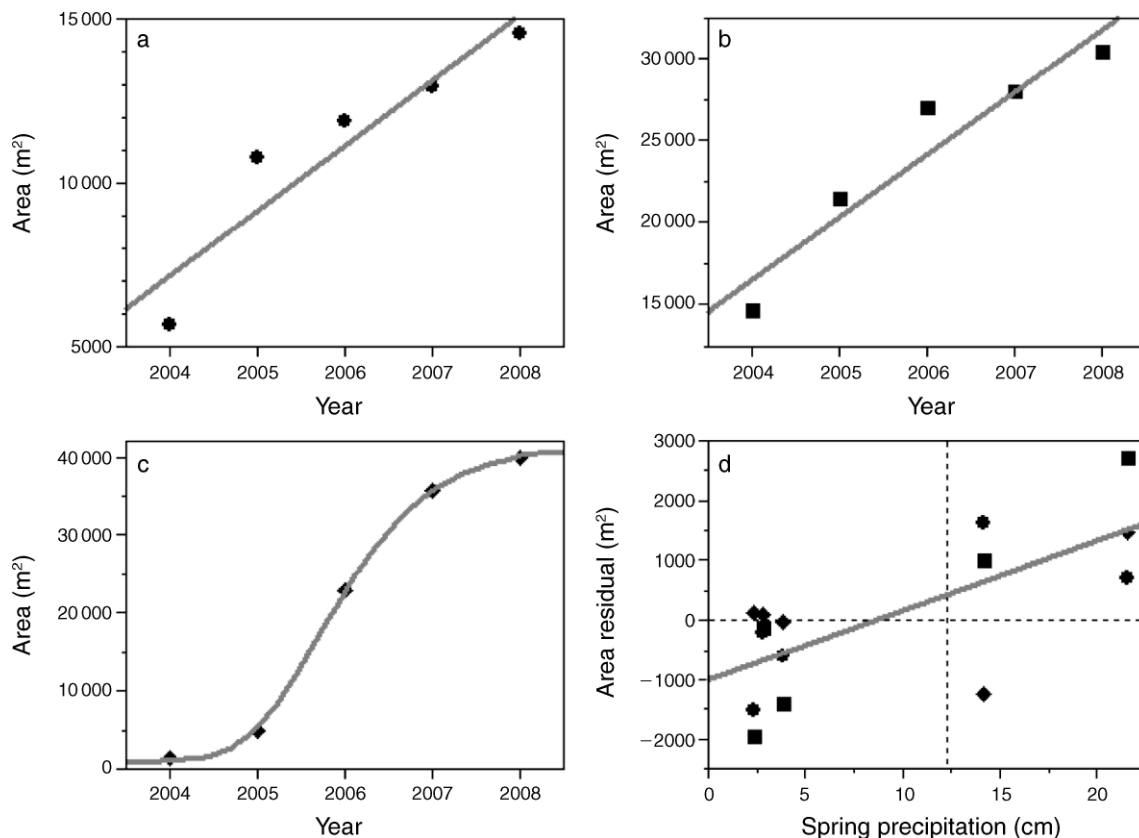


FIG. 3. *L. latifolium* invasion curves over five years, observed from remotely sensed distribution maps of the three Bouldin Island subsites: (a) clayey bottom, (b) levee, and (c) silty bottom. In panel (d) the residuals between observed area and area predicted by the lines fitted in panels (a)–(c) are plotted against springtime precipitation. Guidelines highlight expected spread (i.e., a residual of 0) and average springtime precipitation. Subsites are plotted with different symbols, which correspond to those in panels (a)–(c).

Effects of weather conditions on L. latifolium spread

L. latifolium tended to spread more than expected (i.e., had positive area residuals) in years with wet springs ($R^2 = 0.504$, $P = 0.003$; Fig. 3d). This was the strongest relationship observed with weather data and was especially marked for the clayey bottom and levee subsites, which are more likely to be water limited than the silty bottom site due to the effects of topography and water-holding capacity on soil water availability. Area residuals also showed a negative relationship with summed monthly mean temperatures ($R^2 = 0.355$, $P = 0.019$). When allowing a lag between weather year and spread observations, there was a positive trend with total water year precipitation ($R^2 = 0.218$, $P = 0.079$) and a negative trend with number of frost days ($R^2 = 0.241$, $P = 0.063$) in year $t - 1$; a positive relationship with summed monthly mean temperatures ($R^2 = 0.415$, $P = 0.01$) and growing degree days ($R^2 = 0.218$, $P = 0.079$), and a negative relationship with number of windy days ($R^2 = 0.224$, $P = 0.075$) in year $t - 2$; and negative relationships with total precipitation ($R^2 = 0.346$, $P = 0.021$) and growing degree days ($R^2 = 0.343$, $P = 0.022$) in year $t - 3$.

TABLE 3. Observed spread and dispersal characteristics for each time step of image data for each Bouldin Island subsite.

Year and site	N (recruits)	Dispersal distance (m)		
		Mean	SD	Maximum
2004–2005				
Clayey bottom	570	15	18	78
Levee	754	8	8	43
Silty bottom	398	53	46	215
Total	1722	20.8	30.4	215
2005–2006				
Clayey bottom	120	5	5	25
Levee	613	17	19	123
Silty bottom	1979	16	15	123
Total	2712	15.7	16.0	123
2006–2007				
Clayey bottom	120	6	3	20
Levee	106	9	8	51
Silty bottom	1428	11	11	71
Total	1654	10.0	10.2	71
2007–2008				
Clayey bottom	178	5	4	31
Levee	280	14	11	57
Silty bottom	477	5	5	57
Total	935	7.8	8.1	57

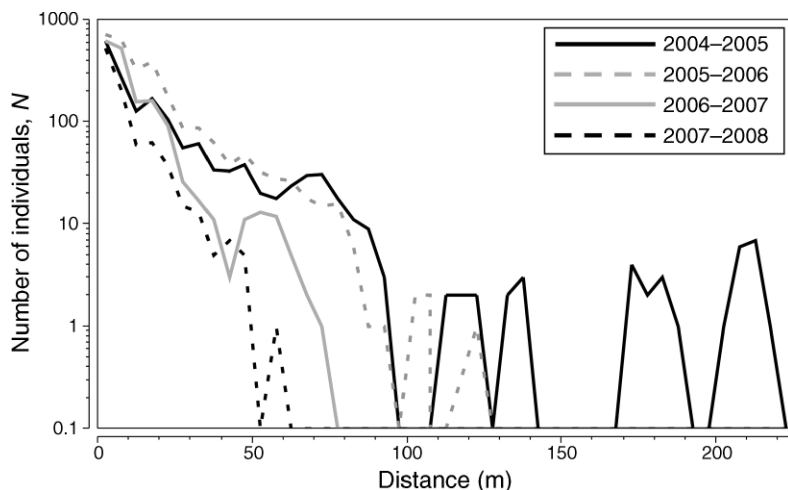


FIG. 4. Annual dispersal kernels for *L. latifolium* extracted from the time series of remotely sensed distributions. Note that the y-axis is a log scale.

Simulation model

The invasion curves for all simulated scenarios are plotted in Fig. 6 and the respective invasion rates are given in Table 4. All main effects (time, dispersal, landscape, introduction site) and all interaction terms were highly significant (Table 5), indicating that dispersal kernels and landscape structure, both local and overall, influence invasion rates and that their specific effects are highly context dependent.

Simulated spread rates.—When initialized with the 2004 distribution, *L. latifolium* very quickly saturated the available habitat (Fig. 6a). Simulated spread rates (Table 4) were an order of magnitude greater than those observed from the remotely sensed distribution maps (when considering the island-wide infestation, *L. latifolium* was observed to spread by 1917 pixels/yr in the time series of remotely sensed distribution maps). In 2004, 4313 pixels were occupied, which allowed large numbers of recruits to be generated, guaranteeing a number of long-distance dispersal events each year. Although the infestation in 2004 was concentrated on the northern half of the island, isolated patches occurred throughout the island, providing multiple foci for invasive spread and precluding any effects of landscape structure.

In response to the unrealistic simulations that resulted when the landscape was initialized with the observed 2004 distribution, we performed a set of model runs varying the establishment rate of new recruits. The simulated spread rates approximated observed invasion speeds at establishment probabilities ranging between 0.75% (when considering the asymptotic spread rate) and 2.5% (when considering the initial spread rate at times $t = [0, 4]$).

When simulations were initialized with a single invaded cell, spread was largely linear and much slower (Fig. 6, Table 4), giving spread rates on the order of

those observed at individual sites in the remotely sensed distributions. (Multiply by nine to convert from pixels and pixels/yr to m^2 and m^2/yr .)

Dispersal distance and directionality.—In general, the ranking of dispersal kernel scenarios by invasion rates paralleled the mean and maximum empirical dispersal distances. Randomly varying the dispersal kernel resulted in invasion curves and speeds that consistently grouped with the fastest dispersing scenarios, but increased variability. Deviations in the rankings of dispersal kernels by simulated spread, such as when the invasion was initiated at the clayey bottom site, were driven by the directionality of the long-distance dispersers and the local habitat configuration. These deviations were removed and the expected order restored when adirectional dispersal kernels were used (contrast Fig. 6b with Fig. 6f). Removing the directionality of the dispersal kernel dramatically increased invasion rates, indicating that spread was greatly constrained by directional dispersal.

Landscape structure.—The landscape structure of Bouldin Island limited invasion. Simulations in a homogeneous landscape gave extremely rapid spread (Fig. 6g, Table 4) and rapid saturation. As with the structured landscape, spread rates paralleled the mean and maximal dispersal distances of the specific dispersal kernels, and the variable dispersal kernel results were similar to those of the two fastest kernels.

Landscape structure: corridors.—The influence of corridors on invasion dynamics was highly context dependent, as shown by the significant higher order interactions involving this term (i.e., those between three or more model terms; Table 5). These can be explained by investigating the time to deviation in the invaded area between landscapes with corridors and the no corridor baseline (Table 4). A strong, positive effect of corridors on spread will cause rapid deviation from the no corridor scenario (i.e., the weed will soon spread to

occupy a greater area in a landscape with corridors than without). If corridors fail to enhance spread, the area occupied will never significantly differ between landscape types. Simulated deviation times depended on the dispersal kernel, corridor width, and the configuration of corridors around the introduction site. The full corridor landscape increased spread rates more than reduced corridors did, resulting in more likely and earlier times to deviation from the no corridor case. However, corridors only affected spread rates for simulations with the longest-ranging dispersal kernels (i.e., a time \times landscape \times dispersal interaction). For the other cases, *L. latifolium* could only very occasionally spread fast enough to reach the end of a corridor within the 200-year time frame and initiate spread from a new focus. The deviation times also reflect the availability of corridors to the introduction sites (i.e., a time \times landscape \times introduction site interaction).

Landscape structure: local habitat characteristics.—Local landscape structure also had strong impacts on spread, indicated by the introduction site \times time interaction (Table 5). Differences between introduction sites are explained in large part by habitat abundance surrounding the introduction site, in combination with the dispersal kernel ($R^2 = 0.845$; Fig. 7). Although invasion rate increased with increasing habitat availability for all dispersal scenarios, this effect was especially prominent with the fastest dispersal, showing that slow dispersers are less able to take advantage of higher habitat abundances.

Habitat shape also affected invasion rates (Table 6). As local patches became less compact, spread was generally reduced. However, this relationship was only observed for the weakest dispersal kernel (2007–2008) and the no corridor landscape, indicating that shape complexity reduces dispersal success only for local dispersal and in unconnected landscapes.

DISCUSSION

Spread observations

L. latifolium exhibited very rapid spread rates, especially at the silty bottom subsite. Observed spread rates and dispersal distances were much greater than those previously reported, which are on the order of 1–3 m/yr (Blank and Young 1997, Young et al. 1997, Renz 2002, Orth et al. 2006). Such rapid spread underscores what a serious weed *L. latifolium* is. The silty bottom subsite illustrates that it can spread from small, isolated satellite patches to dominate a site within just a few years, although established infestations do continue to grow steadily (Figs. 2 and 3).

Temporal variation in spread and dispersal

L. latifolium spread was observed to be temporally variable, and the most explanatory factor was springtime precipitation in the year that spread was observed. Springtime precipitation is not likely to play a direct role

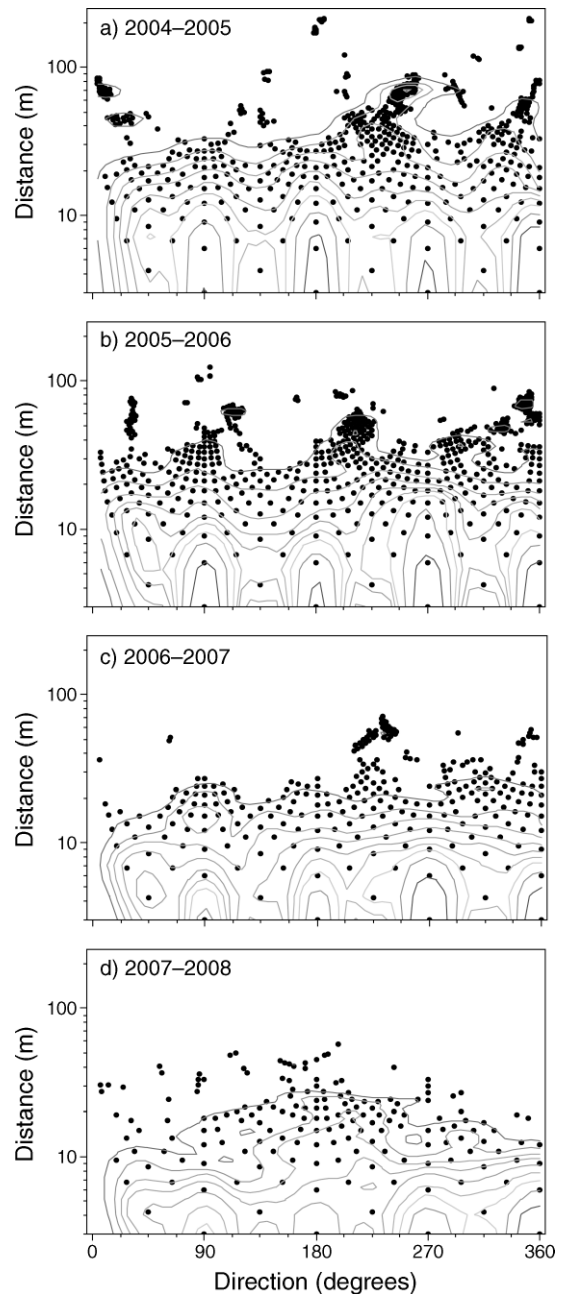


FIG. 5. Paired dispersal distance–direction observations for each time step, as extracted from the time series of remotely sensed distributions. Directions are estimated from the new patch to the nearest source patch. Contours represent 10% probability intervals. Note that the y -axes are log scales.

in *L. latifolium* dispersal, which is expected to occur in the summer and fall. The variation observed is therefore likely to be of effective dispersal, as mediated by establishment and survival, rather than dispersal alone. This points to the role of a regeneration niche (Grubb 1977) or a temporal storage effect (Melbourne et al. 2007) in *L. latifolium* spread. *L. latifolium* seedlings may be more competitive with increased springtime water

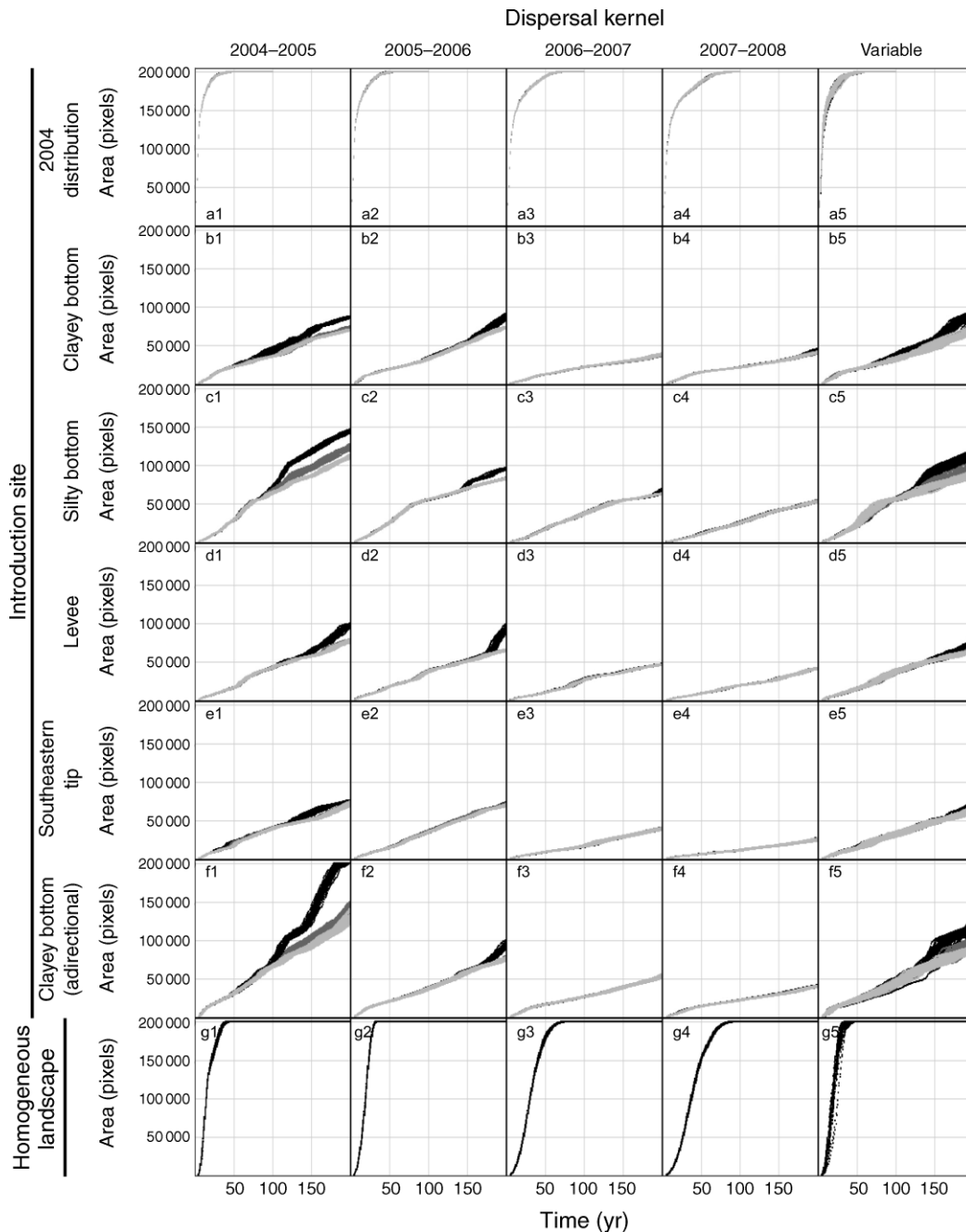


FIG. 6. Invasion curves from all simulation scenarios testing the effects of dispersal in columns, introduction site in rows, and landscape in shades of gray (full corridors, black; reduced corridors, medium gray; no corridors, light gray).

availability. Regeneration niches are likely to be most important for long-distance dispersal by seeds. In contrast, local vegetative spread by creeping rootstocks should be less subject to environmental conditions because the recruits can rely on belowground connections to established adults for competitive superiority and to withstand suboptimal environments. As a result, long-distance dispersal is temporally very variable, but local spread is relatively constant (Fig. 4).

However, the effect of springtime precipitation on spread is likely to be context dependent. For example, on Bouldin Island it was observed most strongly in the areas most likely to be water limited; at a brackish California marsh, *L. latifolium* spread also seemed to be driven by pulses of freshwater in wet years (Grewell 2008), but on a freshwater California floodplain, *L. latifolium* spread was reduced in wet years (Viers et al. 2008). Interestingly, at the latter site, there was

TABLE 4. Simulated invasion rates for all dispersal, landscape, and introduction site scenarios.

Introduction site and dispersal kernel	No corridors		Reduced corridors			Full corridors		
	Invasion rate (pixels/yr)		Invasion rate (pixels/yr)		t_{div} (yr)	Invasion rate (pixels/yr)		t_{div} (yr)
	Mean	SD	Mean	SD		Mean	SD	
2004 distribution								
2004–2005	22 125	122	22 144	102	†	22 182	101	†
2005–2006	21 581	117	21 599	107	†	21 660	87	†
2006–2007	18 835	107	18 880	96	†	18 924	99	†
2007–2008	16 047	98	16 057	96	†	16 100	97	†
Variable	19 969	1227	19 974	1132	†	19 911	1189	†
Clayey bottom								
2004–2005	348	3	359	6	56	445	6	50
2005–2006	353	6	354	6	†	396	9	92
2006–2007	178	3	178	3	†	178	3	†
2007–2008	181	4	181	4	†	184	4	186
Variable	328	13	330	15	†	427	19	70
Clayey bottom, adirectional‡								
2004–2005	625	15	702	16	75	1068	24	49
2005–2006	375	6	376	5	197	413	10	163
2006–2007	245	4	245	4	†	245	4	†
2007–2008	187	3	188	4	†	188	4	†
Variable	451	18	475	23	167	585	37	76
Silty bottom								
2004–2005	574	7	664	13	94	809	9	82
2005–2006	432	4	432	3	†	488	5	127
2006–2007	347	2	347	2	†	349	3	190
2007–2008	284	4	284	4	†	284	3	†
Variable	472	11	512	19	139	605	23	118
Levee								
2004–2005	388	5	393	6	116	479	11	108
2005–2006	336	4	338	4	†	386	12	105
2006–2007	249	2	249	2	†	249	3	†
2007–2008	201	4	201	4	†	200	4	†
Variable	343	8	345	8	194	368	14	140
Southeastern tip								
2004–2005	346	6	347	5	†§	391	6	22
2005–2006	373	4	374	4	†	374	4	189
2006–2007	199	5	198	4	†	197	4	†
2007–2008	118	4	118	3	†	120	3	124
Variable	322	11	323	8	†	335	11	150¶
Homogeneous landscape								
2004–2005	11 443	337						
2005–2006	7125	172						
2006–2007	5145	68						
2007–2008	3993	72						
Variable	8402	1222						

Note: The time at which full corridor and reduced corridor landscapes diverge from the no corridor case are also presented (t_{div}).

† Invasions in these landscapes never diverged from the no corridor situation over the course of the 200-year simulations.

‡ “Adirectional” refers to the set of simulations that sampled dispersal distance from the observed dispersal kernels but chose dispersal direction from a random uniform distribution. These trials were performed for the clayey bottom introduction site.

§ Deviates temporarily for years 38 and 44.

¶ Also deviates temporarily during years 36–79 and 101–112.

considerable spatial variation in spread rates, with greater spread at wetter sites (Hogle et al. 2006). It seems reasonable to generalize that at sites experiencing either water stress or osmotic stress, these conditions are ameliorated in wet years, enhancing spread. Conversely, wet years exacerbate flooding and the associated edaphic stresses (e.g., anoxia) at wet sites, reducing spread.

Surprisingly, simulations showed that invasion dynamics are little affected by temporal variation in

dispersal distances. This contradicts theoretical expectations from analytical models, which predict that temporal variation in either reproductive rate or dispersal will reduce spread rates to the geometric mean of the rates observed under the component constant conditions (Neubert et al. 2000). However, this is consistent with other model results that, although not allowing dispersal to vary temporally, have found that the distance of long-distance dispersers defines invasion

TABLE 5. Effect tests of the multiple regression models of the effects of landscape, dispersal, introduction site, and directionality of dispersal on invasion rates.

Source	df	Sum of squares	F	P
Test: area = $f(\text{time, landscape, dispersal, introduction site})$ (excluding adirectional, homogeneous landscape, and 2004 initial distribution)				
Time	1	4.59×10^{12}	800 369.2	<0.0001
Landscape	2	2.31×10^9	201.4721	<0.0001
Time \times landscape	2	1.54×10^{10}	1340.559	<0.0001
Dispersal	4	2.34×10^8	10.2038	<0.0001
Time \times dispersal	4	4.03×10^{11}	17 595.7	<0.0001
Landscape \times dispersal	8	1.78×10^9	38.9297	<0.0001
Time \times landscape \times dispersal	8	1.45×10^{10}	315.6009	<0.0001
Introduction site	3	2.73×10^9	158.8597	<0.0001
Time \times introduction site	3	2.12×10^{11}	12 343.77	<0.0001
Landscape \times introduction site	6	8.81×10^8	25.6163	<0.0001
Time \times landscape \times introduction site	6	5.15×10^9	149.6889	<0.0001
Dispersal \times introduction site	12	7.48×10^9	108.7964	<0.0001
Time \times dispersal \times introduction site	12	5.04×10^{10}	733.5275	<0.0001
Landscape \times dispersal \times introduction site	24	1.05×10^9	7.6195	<0.0001
Time \times landscape \times dispersal \times introduction site	24	6.57×10^9	47.7462	0.0001
Test: area = $f(\text{time, landscape, dispersal, directionality})$ (clayey bottom introduction site only)				
Time	1	2.63×10^{12}	286 441.1	<0.0001
Landscape	2	4.79×10^9	261.1836	<0.0001
Time \times landscape	2	2.91×10^{10}	1589.952	<0.0001
Dispersal	4	7.36×10^9	200.8469	<0.0001
Time \times dispersal	4	4.53×10^{11}	12 368.66	<0.0001
Landscape \times dispersal	8	5.93×10^9	80.9143	<0.0001
Time \times landscape \times dispersal	8	3.99×10^{10}	544.2578	<0.0001
Directional?	1	1.88×10^9	205.4034	<0.0001
Time \times directional?	1	8.56×10^{10}	9337.638	<0.0001
Landscape \times directional?	2	1.189×10^9	64.8382	<0.0001
Time \times landscape \times directional?	2	5.14×10^9	280.2085	<0.0001
Dispersal \times directional?	4	4.73×10^9	129.1065	<0.0001
Time \times dispersal \times directional?	4	1.14×10^{11}	3113.846	<0.0001
Landscape \times dispersal \times directional?	8	3.78×10^9	51.5732	<0.0001
Time \times landscape \times dispersal \times directional?	8	1.79×10^{10}	243.8471	<0.0001

Note: Invasion rates are indicated by the main effect of, and interactions with, the time term.

rates, which are remarkably insensitive to the frequency of long-distance dispersal (Neubert and Caswell 2000, Woolcock and Cousens 2000). Temporal variation in dispersal kernels changed the probability of long-distance dispersal, but not its distance and, consequently, not its overall effect.

Although temporal variation had relatively little effect on spread rates, the specific kernel used in the fixed kernel cases did have a strong effect, which has implications to monitoring and data collection. When forecasting spread rates from dispersal data, it is important that observations capture the long-distance dispersal and regeneration niche conditions of the species of interest. If not, dispersal and spread rates may be dramatically underestimated, undermining their usefulness.

Landscape structure

Simulated invasion dynamics were affected by both connectivity of the entire landscape and, especially, the local landscape structure surrounding introduction sites. Of the parameters tested here, corridors were the weakest control on spread rates. The positive impact of corridors on spread was largely constrained by the organism's ability to take advantage of them, i.e., by

dispersal ability. This is interesting because corridors are often touted as being of greatest benefit to less vagile species (e.g., Söndgerath and Schröder 2002, Levey et al. 2005, but see van Dorp et al. 1997). Much work on corridors has used small model systems or small, simplified simulated landscapes, very unlike the long corridors of the real Bouldin Island landscape tested here. It could be that corridors are relatively ineffective at the scale of real landscapes, as demonstrated here for Bouldin Island. Alternatively, corridors may be most effective when they actively influence, direct, and enhance dispersal (Hoyle 2007), rather than simply provide habitat. Such mechanisms were not considered here and may be most relevant for the spread of animal species or animal-mediated dispersal of plants. Corridor width influenced the efficiency with which organisms traveled through them. With dispersal parameters that allowed for an effect of corridors, the full corridor landscape consistently had higher invasion rates and diverged from the no corridor case more quickly than the reduced corridor landscape was able to (Table 4), which agrees with the findings of van Dorp et al. (1997).

In contrast, local landscape structure had much stronger, more unequivocal effects on simulated invasion dynamics. Important local features include habitat

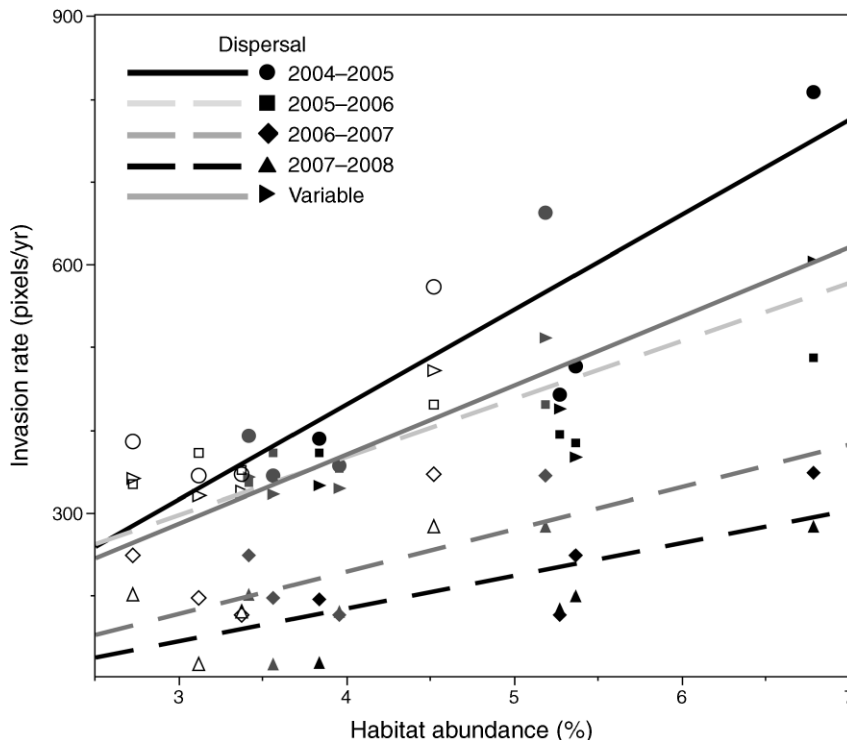


FIG. 7. Influence of habitat abundance (percentage of suitable habitat by area) within 500 pixels of the introduction site on invasion rate (pixels/yr). Points plotted are averages for each factorial combination of introduction site, dispersal kernel, and landscape type. Symbol shape represents dispersal kernels: 2004–2005 (circles), 2005–2006 (squares), 2006–2007 (diamonds), 2007–2008 (upright triangles), and variable (horizontal triangles). Landscape types are represented as: full corridors (black), reduced corridors (gray), and no corridors (open).

abundance, habitat shape, proximity to corridors, and habitat structure and connectivity relative to the dominant directionality of dispersal. Habitat abundance has been shown to be very important to spread dynamics and to mediate the effects of landscape structure on spread. Spread rates increase with increasing habitat availability; above a certain threshold of habitat abundance, landscape structure is unimportant (Collingham and Huntley 2000, King and With 2002, With 2002, Matlack and Monde 2004). Landscape structure was also found to be unimportant when the organism was initially relatively well distributed across the landscape.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Hyperspectral remote sensing was shown to be a valuable tool for mapping invasive species distributions and estimating spread characteristics. Remote sensing is much more efficient than ground-based mapping, and is more capable of monitoring over landscape scales and, thus, of capturing important long-distance dispersal events. Hyperspectral remote sensing, in particular, enables this research as many species, including *L. latifolium* at this site, are not detectable in aerial photography or multispectral satellite imagery. Moreover, coupled with simulation model

TABLE 6. Results of regression analyses of mean invasion rate (pixels/yr) on the area-weighted mean shape index for patches of available habitat within 500 pixels of the introduction site.

Landscape and dispersal	Intercept	Slope	R ²
Full corridors			
2004–2005	681	–14.22	0.079
2005–2006	442	–2.95	0.044
2006–2007	309	–6.17	0.090
2007–2008	310	–10.68	0.347
Variable	521	–8.30	0.066
Reduced corridors			
2004–2005	400	2.77	0.009
2005–2006	310	4.39	0.312
2006–2007	260	–1.14	0.006
2007–2008	251	–3.75	0.082
Variable	346	2.15	0.015
No corridors			
2004–2005	559	–21.35	0.337
2005–2006	393	–2.88	0.041
2006–2007	337	–13.85	0.294
2007–2008	333	–20.10	0.748
Variable	461	–13.94	0.333

Note: Landscape–dispersal combinations giving the strongest relationships are shown in bold.

outputs, these data provide valuable information on when and where to control invasive species in order to maximize management efficiency. These results are extremely valuable as they provide significantly more information than habitat suitability modeling analyses to identify invulnerable sites, for instance, which give no insight into when a species is likely to spread or which specific patches within a network of suitable habitat should be control priorities.

Both the invasion history and the landscape context of a patch are important controls on invasive species spread. Our observations and simulations showed that, within the invasion sequence, isolated satellite patches exhibit the fastest spread rates. This suggests that eradication should focus on nascent populations, lending support to established invasive species management theory and practice (e.g., Moody and Mack 1988). However, it is too simplistic to make management decisions on the basis of a satellite/mainland patch dichotomy. For example, established patches of *L. latifolium* did continue to spread steadily and, thus, should not be ignored. Additionally, the importance of landscape structure highlights that not all nascent patches are created equal. Rapid spread is facilitated when the invasion is initiated in large areas of suitable habitat, at sites near or within corridors connecting invulnerable habitat, and/or at sites where the configuration of invulnerable habitat aligns with the dominant directionality of long-distance dispersal.

Finally, strong temporal variation was observed in the dispersal and spread of *L. latifolium*, which were enhanced in wet years. Such variation is common in invasive species and is not surprising given the known importance of regeneration niches in general (Grubb 1977) and in invasions (e.g., the fluctuation resources theory of invasibility; Davis et al. 2000). However, spread models generally assume constant conditions; this study is one of the only tests of the effect of temporally varying dispersal on invasion dynamics. Surprisingly, we found that temporally varying dispersal did not substantially reduce invasion rates relative to constant, optimal conditions, and yielded much greater spread than constant, low-dispersal conditions. An effective strategy to reduce invasive species spread, containing infestations, is thus to eliminate the regeneration niche by performing intensive early detection and eradication in the years that facilitate spread and establishment. It is therefore extremely important to have high-quality, long-term monitoring, as may be provided by remote sensing, enabling researchers and managers to quantify long-distance dispersal and to identify the regeneration niche conditions that promote it.

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