

DISPERSAL SPECIAL FEATURE

Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges

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Summary

1. Invasive species usually exhibit different spatial population dynamics in their native and invaded range. This is often attributed to demographic differences, but may be due to differences in dispersal as well.

2. Regardless of how these dispersal and demographic differences from the native range arose, studying how they contributed to increases in population spread rates will increase our understanding of what has made these species invasive. Here we investigate which vital rates and dispersal parameters of the invasive thistle *Carduus nutans* drive the increases in spread rate in different invaded ranges compared to that in the native range in Eurasia.

3. We construct and analyse spatial integrodifference models that combine structured, local population models with mechanistic (WALD) models of seed dispersal by wind across a homogeneous landscape. Published and new demographic and dispersal data for single populations from the native (France) and invaded (Australia, New Zealand, Kansas and Pennsylvania) ranges were used for the parameterization.

4. We developed a variance decomposition method (c^* -LTRE) to analyse the contributions of the changes in the vital rates and dispersal parameters to the increases in the invasion wave speed (c^*) estimates for the different invaded ranges compared to that for the native range.

5. The c^* -LTRE analysis showed that the net contribution of the dispersal parameters to c^* increases varied among the populations from 51% (Australia), to 79% (Kansas), to 80% (New Zealand) and to 85% (Pennsylvanian experiment). Escape from natural enemies that reduce seed set by floral herbivory was important in all invaded ranges. Large positive contributions were also made by increases in rapid growth of seedlings and small rosettes, increases in flowering probabilities and potential seed production, as well as by increased plant height and lower falling velocities of the plumed seeds.

6. *Synthesis.* By incorporating a mechanistic dispersal model with a structured population model, and by linking this joint model to field data from several continents, we demonstrate the relative importance of dispersal and demography to invasion success. This approach can be used to analyse which aspects of an invader's life history have changed most importantly from the native range.

Key-words: fixed-factor life table response experiment (LTRE), integrodifference equations, matrix population models, musk or nodding thistle, native vs. invaded range, plant height, seed terminal velocity, vital rates, Wald analytical long-distance model, wind speed

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Introduction

There are many possible reasons why a species may become invasive after arrival in a new area outside its native range (Keane & Crawley 2002; Lee 2002; Shea & Chesson 2002; Müller-Schärer *et al.* 2004; Hierro *et al.* 2005). For instance, a species may perform better in the invaded range because it has escaped from natural enemies, because it has found an empty niche, or because it interacts differently with various components of the new ecosystem. In fact, multiple processes may be operating at the same time. However, irrespective of the underlying mechanisms that lead to invasiveness, such mechanisms will often result in either changed population dynamics, changed dispersal or both. By quantifying the changes in demographic and dispersal rates between native and invaded ranges, and the importance of these changes, it is possible to investigate which life-history changes are likely to have contributed most to the increase in invasiveness. The benefit of such an integrated, mechanistic approach over methodologies in which species traits are studied in isolation is that the impact of various demographic and dispersal parameters on the speed of invasion can be directly compared. This is also potentially of great applied value.

There are many studies that examine one invasive species in different invaded habitats within an invaded range (e.g. Shea & Kelly 1998; McEvoy & Coombs 1999; Parker 2000; Sheppard *et al.* 2002). Unfortunately, studies of a species' demography in both the native and the invaded ranges are relatively rare (Grigulis *et al.* 2001; Hinz & Schwarzaender 2004). Similarly, there are only a few studies that model spatial spread within an invaded range with both demography and dispersal included mechanistically (e.g. Neubert & Parker 2004; Buckley *et al.* 2005). Studies of invaded and native range dispersal are nearly non-existent; we are not aware of any. One species for which much is known about both demography and dispersal is *Carduus nutans* L. (Asteraceae), a monocarpic thistle of Eurasian origin that has invaded the Americas, New Zealand, Australia and Southern Africa. *Carduus nutans* therefore provides an excellent opportunity to study the relative importance of dispersal and demography for the increased spatial spread of an invasive species compared to the spatial dynamics in its native range (Kelly & McCallum 1995). Understanding what drives spatiotemporal dynamics is a crucial aspect of ecology in general (Schurr *et al.* 2007; Higgins *et al.* 2008), and invasive species in particular (Sakai *et al.* 2001).

Comparison of integrated dispersal–demography models across different parts of the global distribution requires a

modelling approach in which both aspects are modelled mechanistically. Mechanistic models have the advantage that model outcomes can be traced back to biologically meaningful parameters. However, mechanistic spread models in which native-invaded range comparisons can be decomposed into contributions from changes in the underlying parameters, have not yet been published, probably because the required data were lacking. Here we develop such methods for *C. nutans*, despite some potential deficiencies and possible confounding factors. We parameterize the mechanistic Wald Analytical Long-distance Dispersal (WALD) model (Katul *et al.* 2005; Skarpaas & Shea 2007) with plant, seed (achene) and wind data from the native and various invaded ranges. We use demographic data from previously published models from New Zealand (Shea & Kelly 1998), Australia (Shea *et al.* 2005) and France (Jongejans *et al.* 2006) combined with new data on dispersal attributes for these populations. Two new vital-rate based population matrix models are based on demographic data from Kansas (Lee 1977; Lee & Hamrick 1983) and from an experiment in Pennsylvania (K. Shea, unpubl. data). These mechanistic dispersal and demographic models are combined for each location using integrodifference equations (Neubert & Caswell 2000; Neubert & Parker 2004; Buckley *et al.* 2005; Jacquemyn *et al.* 2005; Lewis *et al.* 2006; Vellend *et al.* 2006). We then apply a fixed-factor life table response experiment (LTRE) technique (Horvitz *et al.* 1997; Caswell 2001; Caswell *et al.* 2003; Jongejans & de Kroon 2005) to analyse which underlying parameters cause differences in the invasion speeds in native-invaded range comparisons.

Methods

LOCAL POPULATION MODEL

Population transition matrix models are commonly used to model species' demography (Caswell 2001). Matrix models have the advantage that they transparently represent a species' life cycle, and that various matrix properties, such as the dominant eigenvalue (λ , projected population growth rate), have a clear biological interpretation. Furthermore, the matrix elements can be explicitly written as functions of several vital rates such as survival (σ), growth (γ) of surviving plants and seed production (π) (Table 1). Properties of the matrix elements, for example the sensitivity of λ to changes in elements, can be transferred to these lower-level vital rates (Caswell 2001; Franco & Silvertown 2004). Therefore we use vital rate-based matrix models for *C. nutans* as presented by Jongejans *et al.* (2006), which were based on a four-stage classification by Shea & Kelly (1998):

$$\begin{pmatrix} \sigma_1 & \sigma_2\beta_2\pi_2\phi\nu & \sigma_3\beta_3\pi_3\phi\nu & \sigma_4\beta_4\pi_4\phi\nu \\ \varepsilon_1(1-\gamma_3-\gamma_4) & \sigma_2(1-\beta_2)(1-\gamma_{32}-\gamma_{42})+\sigma_2\beta_2\pi_2\phi\varepsilon(1-\gamma_3-\gamma_4) & \sigma_3(1-\beta_3)\rho_{23}+\sigma_3\beta_3\pi_3\phi\varepsilon(1-\gamma_3-\gamma_4) & \sigma_4(1-\beta_4)\rho_{24}+\sigma_4\beta_4\pi_4\phi\varepsilon(1-\gamma_3-\gamma_4) \\ \varepsilon_1\gamma_3 & \sigma_2(1-\beta_2)\gamma_{32}+\sigma_2\beta_2\pi_2\phi\varepsilon\gamma_3 & \sigma_3(1-\beta_3)(1-\rho_{23}-\gamma_{43})+\sigma_3\beta_3\pi_3\phi\varepsilon\gamma_3 & \sigma_4(1-\beta_4)\rho_{34}+\sigma_4\beta_4\pi_4\phi\varepsilon\gamma_3 \\ \varepsilon_1\gamma_4 & \sigma_2(1-\beta_2)\gamma_{42}+\sigma_2\beta_2\pi_2\phi\varepsilon\gamma_4 & \sigma_3(1-\beta_3)\gamma_{43}+\sigma_3\beta_3\pi_3\phi\varepsilon\gamma_4 & \sigma_4(1-\beta_4)(1-\rho_{24}-\rho_{34})+\sigma_4\beta_4\pi_4\phi\varepsilon\gamma_4 \end{pmatrix}$$

eqn 1

Table 1. Demographic vital rate and dispersal parameter estimates for each of the five populations

Country		Native range		Invaded ranges		
		France, La Cavalerie	Australia, Kybeyan	New Zealand, Midland	USA, Kansas, population A	USA, Pennsylvania, experiment
Stage class borders:						
	Between S and M (cm ²)	26.3	20.8	83.1	–	16.6
	Between M and L (cm ²)	60.7	43.4	175	–	841
Demographic parameters:						
	Survival of seed in SB	σ_1 0.2597	0.4430	0.0382	<i>0.2597</i>	<i>0.2597</i>
	Survival of S	σ_2 0.4831	0.0167	0.1164	0.2182	0.2619
	Survival of M	σ_3 0.8235	0.0818	0.6813	0.5633	0.6761
	Survival of L	σ_4 1.0000	0.4393	0.7532	0.7474	0.8971
	Growth of establishing seed to M	γ_3 0.0396	0.0841	0.0000	0.1627	0.2076
	Growth of establishing seed to L	γ_4 0.0099	0.0999	0.0000	0.0000	0.0911
	Growth of surviving, not-bolting S to M	γ_{32} 0.1256	0.1786	0.1065	<i>0.8028</i>	0.8028
	Growth of surviving, not-bolting S to L	γ_{42} 0.0205	0.6786	0.0651	<i>0.1268</i>	0.1268
	Retgression of surviving, not-bolting M to S	ρ_{23} 0.0000	0.0000	0.3333	<i>0.0000</i>	0.0000
	Growth of surviving, not-bolting M to L	γ_{43} 0.0000	0.8333	0.6667	<i>0.3824</i>	0.3824
	Retgression of surviving, not-bolting L to S	ρ_{24} 0.0000	0.1667	1.0000	<i>0.0000</i>	0.0000
	Retgression of surviving, not-bolting L to M	ρ_{34} 0.0000	0.3333	0.0000	<i>0.0000</i>	0.0000
	Bolting of surviving S	β_2 0.0250	0.1765	0.2620	0.0180	0.1932
	Bolting of surviving M	β_3 0.9286	0.5385	0.9516	0.3596	0.7143
	Bolting of surviving L	β_4 0.6000	0.9362	0.9828	1.0000	1.0000
	Potential seed production by S	π_2 62	125	2437	100	5443
	Potential seed production by M	π_3 65	349	2776	195	6150
	Potential seed production by L	π_4 93	1168	3576	1473	12446
	Potential seed escaping from floral herbivory	ϕ 0.0925	1.0000	1.0000	1.0000	0.8500
	New seed entering SB	ν 0.3235	0.4300	0.1570	0.2333	<i>0.2333</i>
	New seed establishing seedling	ε 0.1148	0.0194	0.0194	0.0300	0.2333
	Seed from SB establishing seedling	ε_1 0.1148	0.0048	0.1847	0.0300	0.2333
Dispersal parameters:						
	Geometric mean terminal falling velocity (m s ⁻¹)	F 0.9840	0.5716	0.4287	<i>0.5475</i>	0.5475
	SD of ln U	σ_F 0.2055	0.1774	0.1961	<i>0.3967</i>	0.3967
	Mean release height (mean plant height) (cm)	H 22	90	57	90	184
	Vegetation height (cm)	h 4	4	4	30	50
	Geometric mean wind speed (m s ⁻¹) at 10 m	U 3.7371	3.9570	3.5365	2.7332	1.7257
	SD of ln U	σ_U 0.6458	0.6064	0.7541	0.6522	0.7280
Response variables:						
	Projected population growth rate	λ 0.602	1.203	2.684	1.748	363
	Projected wave speed (m year ⁻¹)	c^* 0.5†	7	29	9	146

The stage classes of the matrix model (eqn 1) were: seeds in the seed bank (SB), small (S), medium-sized (M) and large (L) rosettes. Missing values (now the italicised numbers in the table) are dealt with as follows: falling velocity data and adult growth and retrogression rates in the Kansas column are estimated with the Pennsylvania data, the σ_1 estimations for USA population were based on the French data set, and ν was copied from Kansas to Pennsylvania. †French wave speed is calculated with $\phi = 1$.

See Table 1 for a definition of each vital rate. This matrix represents annual demographic transitions from the end of autumn of 1 year to the end of autumn a year later. The four stage classes are the same as in the published New Zealand, Australian and French matrix models of *C. nutans*: seeds in the SB, small rosettes (S) that have < 20% probability of surviving and flowering in the next year, medium-sized rosettes (M), and large rosette (L) that have > 80% chance of surviving and flowering next year. By defining the borders between the three stage classes by the chance of surviving and flowering in the following year (Shea & Kelly 1998), the boundary rosette sizes do differ from population to population. However, in matrix models it is important to group individuals that behave similarly (Caswell 2001) rather than to group individuals that look the same.

DEMOGRAPHY DATA

Population transition matrices were constructed for five populations: one in the native range (La Cavalerie, France), three in the invaded ranges (Kybeyan, Australia; Midland, New Zealand and Kansas, USA) and one experimental population in Pennsylvania, USA. The vital rates for each of these matrices were quantified with data from published and previously unpublished research.

French demography data were collected by Sheppard *et al.* (1989, 1994) from three populations near La Cavalerie (Département Aveyron) from 1987 to 1989. Jongejans *et al.* (2006) constructed matrix models for these populations. Here we use population three as representative of the population dynamics in the native range.

The study by Jongejans *et al.* (2006) used the same vital rate-based matrix model as in this paper (eqn 1) and the projected population growth rate of this declining population was therefore exactly the same ($\lambda = 0.602$). This site had low soil fertility and was grazed by sheep, and therefore had short thistles. *Carduus nutans* is rarely a problematic species in the intensively managed European grazing systems, where it occurs mainly with sheep which tend to be found on the lowest fertility land.

For the populations in the invaded ranges some parameters had to be estimated anew, even when matrix models had previously been published, since these matrix models did not build on exactly the same structure of vital rates. The dynamics of an Australian population near Kybeyan (New South Wales) were studied between 1988 and 1996. This population was previously modelled with an individual-based model (Shea *et al.* 2006) and with a matrix model (Shea *et al.* 2005). Here we estimated all vital rates for eqn 1 with the same Australian data as used for the Shea *et al.* (2005) matrix model, although a few vital rates were estimated in a different way than previously. Rather than assuming that all seedlings were small ($\gamma_3 = \gamma_4 = 0$) by definition, we acknowledged that a proportion of the seedlings grew into the medium ($\gamma_3 = 0.08$) or even the large stage class ($\gamma_4 = 0.10$) within their first season. We calculated flowering probabilities (β_2, β_3 and β_4) of surviving rosettes and seed production of flowering plants directly from the data on the surviving plants within each of the three separate stage classes, rather than by first fitting functions of plant size for these parameters as was done by Shea *et al.* (2005). Also, we corrected a construction error (in the way that raw data were averaged to generate matrix elements) in the earlier matrix model, which had artificially inflated some survival and growth rates.

A New Zealand *C. nutans* population near Midland was studied between 1985 and 1988 and has previously been modelled by Shea & Kelly (1998). Again we used the same data to construct the vital rates, while calculating mean flowering probabilities and seed production from the observed individuals within a certain stage class rather than by fitting functions. Analysis of the seedling sizes in this population showed that all seedlings stayed within the small class in their first autumn ($\gamma_3 = \gamma_4 = 0$; the border between the small and medium classes was at a larger rosette size in the New Zealand than in the Australian population).

For the Kansas population dynamics we used demographic data from Lee (1977) and Lee & Hamrick (1983). We modelled their population A, which was studied from 1975 to 1977. This population increased from a density of 4 to 44 plants m^{-2} over the 2 years studied. No population model has previously been constructed from these data, but many vital rates could be estimated from the summary life tables and additional information presented by these authors. However, since no detailed information was available on the relationship between rosette size and survival and growth in the next year, we used the Pennsylvanian (see below) distribution of the rosette survival rates over the stage classes (σ_2, σ_3 and σ_4) to rescale the overall Kansas rosette survival rate over the stage classes. We made the assumption that the three growth and the three retrogression (negative size growth) of the surviving plants in Kansas would be similar to those observed in the Pennsylvanian experiment. Since 36% of the Kansas seedlings that germinated soon after seed set (September) flowered in the next year compared to 3.5% of later germinating seedlings, we assumed that the September cohort (16% of all seedlings) had grown into the medium stage class by the end of the first autumn. Thus we were able to estimate $\gamma_3 = 0.16$ and $\gamma_4 = 0$. As with the Australian and New Zealand matrices, we assumed that escape from floral herbivores was 100% ($\phi = 1$) because no

floral herbivory was observed in these demographic studies since no biological control agents had been introduced to these invaded ranges at the time these demographic censuses took place.

To assess what population growth rates *C. nutans* can achieve under optimal conditions, we analysed preliminary data from a large field experiment in Pennsylvania (K. Shea, unpubl. data, 2002–05). The general outline of this experiment, in which the effect of different environmental and management factors on the performance of *C. nutans* plants was investigated, is presented in Shea & Chesson (2002). Here we use data on plants from two cohorts that were sown in late summer 2002 and 2003. Most of the resulting plants flowered or died by the following summer, but we also included the second and third year of the surviving plants in our analyses. We only used data from plants that were not mown and not fertilized. Half of the plots in the experiment were regularly weeded around the thistles as a 'no competition' treatment. Although 50.1% of the plants grew in plots without competition, differences in survival and growth rates resulted in 88.3% of the flowering plants being in competitor-free plots. Plants in half of the analysed plots were treated with insecticide once they bolted to exclude floral herbivores. In the other plots several musk thistle weevils (*Rhinocyllus conicus*) were added (according to their availability each year) to include the effect of this introduced bio-control agent. This experimental set-up allowed us to estimate seed production rates without floral herbivory (π_i) and the proportion of seeds that survived floral herbivory (ϕ) using a relationship between the number of weevils per plant in the experiment and the reduction in seed production as established by Sezen (2007).

DISPERSAL MODEL

Dispersal is often modelled by fitting one of a suite of probability density functions to dispersal distances (e.g. Bullock *et al.* 2006) or by developing mechanistic individual-based trajectory models (Nathan *et al.* 2002; Kuparinen 2006). Here we chose to use the recently developed WALD model (Katul *et al.* 2005) which has been shown to predict observed dispersal distances in *C. nutans* well (Skarpaas & Shea 2007). A big advantage of the WALD model is that it combines analytical and mechanistic properties. All parameters have clear interpretations: they are directly linked to characteristics of the species (seed release height and terminal velocity) and the environment (wind characteristics). The WALD model for hourly wind data (Katul *et al.* 2005) predicts an inverse Gaussian (Wald) distribution of dispersal distances r :

$$p(r) = \left(\frac{\xi'}{2\pi r^3} \right)^{\frac{1}{2}} \exp \left(- \frac{\xi'(r - \mu')^2}{2\mu'^2 r} \right) \quad \text{eqn 2}$$

The location parameter μ' (the mean) and the scale parameter ξ' are

$$\mu' = \frac{HU}{F} \quad \text{eqn 3}$$

$$\xi' = \left(\frac{H}{\sigma} \right)^2 \quad \text{eqn 4}$$

where H is seed release height, F is seed settling velocity, U is the hourly mean horizontal wind velocity between H and the ground, and σ is a turbulence parameter (Katul *et al.* 2005). To account for variability in terminal velocity and seasonal wind conditions, the WALD model was integrated (following Skarpaas & Shea 2007) to obtain the seasonal dispersal kernel

$$k(r) = \int \int p(F)p(U)p(r)dFdU \tag{eqn 5}$$

where $p(F)$ and $p(U)$ are the probability density function of F and U , respectively, and $p(r)$ is the WALD model (eqn 2). $k(r)$ gives the radial dispersal kernel in a 2D landscape. To estimate the rate of spread in one dimension x , we need to obtain the moment generating function for the dispersal kernel marginalized for x (Lewis *et al.* 2006; see Spread model section below). We estimated the empirical moment generating function by simulating a large number ($N = 10\,000$) of random dispersal distances r using $k(r)$ and random directions α using a uniform distribution ($0-2\pi$), and then calculate $x = r \cos(\alpha)$. The empirical moment generating function $M^E(s)$ is

$$M^E(w) = \frac{1}{N} \sum_{i=1}^N \exp(w x_i) \tag{eqn 6}$$

where w is an auxiliary variable (Lewis *et al.* 2006).

DISPERSAL DATA

The integrated WALD dispersal model required six parameters: terminal velocity (F), variance of F (σ_F), seed release height (H), vegetation height (h), wind speed (U) and variance of U (σ_U). The terminal velocity of seeds was measured in the laboratory within a c. 1 m tall, closed tube with still air. Twenty-nine flower heads (capitula) were collected from French populations near La Cavalerie in August 2005. One randomly chosen intact dispersal unit (i.e. pappus still attached to a seed) from each head was dropped through a tube to measure its terminal falling velocity. In Australia flower heads were collected in early March 2005. These heads were individually stored at room temperature before the terminal velocity of 30 random seeds (each from a different head) was measured in February 2007. In New Zealand 25 seeds were similarly collected in early April 2007 and measured in June 2007. In Pennsylvania 74 one- or two-year old seeds were measured. From Kansas no dispersal units were available to measure terminal velocities. Therefore we made the assumption that Kansas seeds had the same distribution of terminal velocities as the Pennsylvanian seeds as both populations are in the USA. Note that these terminal velocities were tested at or near the source population, while the French seeds were tested in the Netherlands. Similarly, as described above, some were tested while fairly fresh while others could not be tested for some time after collection. Because of these concerns, we have tested the effect of storage mode and head age on terminal velocity characteristics; we found no effects that would strongly impact this study (K. M. Marchetto, E. Jongejans, M. L. Jennis, E. M. Haner, C. T. Sullivan & K. Shea, unpubl. data).

As seed release height strongly impacts the resultant dispersal kernel, we required an estimate for the mean of the plant heights of flowering thistles in each of the populations. For most populations these measurements were available in the demography data sets (Table 1). Since plant height measurements were not available for the Kansas plants, we estimated H instead as the average of the two seed release heights (60 and 120 cm) that were used in a dispersal study described by Lee (1977). Vegetation heights were very low in the heavily grazed populations in France, Australia and New Zealand. The vegetation around the plots in the Pennsylvanian field experiment was about 50-cm tall, while the vegetation in Kansas was estimated to be c. 30-cm tall (Table 1).

Hourly wind speed measurements were obtained from the nearest available weather stations to each of the five areas. We used data from the main dispersal months in each location. The weather

stations, months and years for which hourly wind speeds were compiled were: Millau (France) June–July 2006, Bombala (Australia) December–February 1989–2007, Palmerston North (New Zealand) December–March 2003–07, Konza Prairie (Kansas) July–August 2002–06 and State College (Pennsylvania) July–August 1999–2006. Wind speed (U) at seed release height (H) was derived from the estimates of vegetation height (h) and wind speed data by numerically integrating over the logarithmic wind profile:

$$U = \frac{1}{H} \int_0^H \frac{u_*}{K} \log\left(\frac{z-d}{z_0}\right) dz \tag{eqn 7}$$

where u_* is the friction velocity, K is the von Karman constant (0.4), z is height above ground, and d and z_0 are surface roughness parameters (Stull 1988). Following Skarpaas & Shea (2007), we assumed $d = 0.7 h$ and $z_0 = 0.1 h$. The friction velocity u_* is given by

$$u_* = K U_m \left[\log\left(\frac{z_m - d}{z_0}\right) \right]^{-1} \tag{eqn 8}$$

where U_m is the mean wind speed at measurement height z_m (10 m). The instability parameter σ was estimated from the horizontal wind speed data using

$$\sigma = 2 A_w \sqrt{\frac{K(z-d)u_*}{C_0 U}} \tag{eqn 9}$$

where the constants $A_w = 1.3$ and $C_0 = 3.125$ (the Kolmogorov constant; for further details, see online appendix with Skarpaas & Shea 2007).

SPREAD MODEL: TRAVELLING WAVES

The framework of integrodifference equations has proven to be an elegant way to link demographic transition matrices with dispersal models (Neubert & Caswell 2000; Lewis *et al.* 2006). This framework allows for the calculation of a travelling wave speed, c^* , which can be interpreted as the speed with which a species invades a homogeneous landscape where the population dynamics as captured by the matrix model (**A**) and the dispersal kernel $k(r)$ apply everywhere. The link between demography (**A**) and dispersal ($k(r)$) is made in a new matrix **H**:

$$\mathbf{H} = \mathbf{M} \mathbf{O} \mathbf{A} \tag{eqn 10}$$

where **M** is a matrix of the same size as **A**, in which the elements contain the moment generating function of the dispersal kernel $k(r)$ marginalized in one dimension x (eqn 6), and **O** is the Hadamard product; this involves element by element multiplication rather than normal matrix multiplication (Neubert & Caswell 2000). However, the elements of **M** which correspond to transitions in **A** that do not involve dispersal (i.e. survival and growth) contain a 1 (see Appendix S1 in Supplementary Material for how we dealt with the nine matrix elements that contain both survival and seed production vital rates). The invasion speed c^* can then be calculated with the following formula (Lewis *et al.* 2006):

$$c^* = \min_{s>0} \left[\frac{1}{s} \ln(\rho_1(w)) \right] \tag{eqn 11}$$

In which ρ_1 is the dominant eigenvalue of **H**.

DECOMPOSITION OF DIFFERENCES IN PROJECTED SPREAD RATES

In order to investigate which differences in dispersal and demography parameters contribute most to the differences in c^* among the invaded ranges, we need to assess how sensitive c^* is to small changes in each of the model parameters. We use the same analytical formulas that are used for the sensitivity of λ (Jacquemyn *et al.* 2005). Since we are interested in the vital rate level, we used the following formula for calculating c^* -sensitivity values of the vital rates (Caswell *et al.* 2003; Buckley *et al.* 2005):

$$\frac{\partial c^*}{\partial \tau_q} = \sum_{ij} \frac{m_{ij}(w^*)}{w^* p_1} \frac{\partial p_1}{\partial h_{ij}} \frac{\partial h_{ij}}{\partial \tau_q} \quad \text{eqn 12}$$

In which τ_q is the q^{th} vital rate, h_{ij} is the element of \mathbf{H} in row i and column j , and w^* is the value of the auxiliary variable w corresponding to c^* . As we integrated the WALD model numerically over the dispersal season (Skarpaas & Shea 2007), we calculated the sensitivity of c^* to each of the dispersal parameters numerically by introducing small perturbations in these parameters. We repeated these calculations 1000 times and used the medians of these runs to avoid potential outliers arising from the integrated WALD model.

We used the LTRE technique to decompose differences in c^* among the native ranges (see also Soons & Bullock 2008):

$$c^{*(k)} \equiv c^{*(N)} + \kappa^l \quad \text{eqn 13}$$

In which κ is the effect of the l^{th} invaded range compared to the $c^{*(N)}$ of the French population. However, since no c^* can be calculated for declining populations we changed one vital rate for the French population: we excluded floral herbivory ($\phi = 1$) which was the main factor causing λ to be low (0.602) (Jongejans *et al.* 2006). This also allows logical comparisons with the invaded sites, at which floral herbivores were absent when the demographic data were collected. Without floral herbivores, the French population was projected to be growing: $\lambda = 1.25$. The effect κ^l can then be estimated by the sum of the products of the demography and dispersal parameter (p_q) deviations and the c^* sensitivity (s) values of p_q :

$$\kappa^l = \sum_q (p_q^l - p_q^N) s_{p_q} \left| \frac{1}{2} (H^l + \bar{H}) \right. \quad \text{eqn 14}$$

Results

LOCAL POPULATION DYNAMICS

Table 1 shows all demography and dispersal parameter estimates for the native range population and the four invaded range populations. The projected population growth rate, λ , was above unity in the invaded ranges only, where it varied from 1.2 (Australia) to 2.7 (New Zealand). The high λ (1.7) of the Kansas population model still underestimates the observed 3.3-fold annual increase in population size in the 2 years studied. The λ of the matrix model constructed with data from the Pennsylvanian field experiment was the highest ever recorded (363). A decomposition of the differences in λ between each of the invaded ranges with the native range (Fig. 1) shows which differences in vital rates were particularly responsible for these high λ values. Under the favourable

conditions of the experiment (half of the plants grew in competitor-free plots) the life cycle loop of large plants that produce new large plants from seeds the year after caused *C. nutans* to behave like an annual (Fig. 1d). Notably high were the following components of this sexual reproduction pathway: seedling establishment ($\epsilon = 0.2333$), seedling growth to medium and large plant size in the autumn directly after they were produced as seeds ($\gamma_3 = 0.2076$ and $\gamma_4 = 0.0911$), and the seed production of medium and large plants ($\pi_3 = 6150$ and $\pi_4 = 12\,446$). Seed production and survival from floral herbivory (ϕ) was also importantly higher in the three naturalized populations in the invaded ranges compared to the native range (Fig. 1a–c). However, this was buffered by much lower seedling establishment rates than in the French population.

DISPERSAL AND SPREAD RATES

The median of the dispersal distances, $k(r)$, that were simulated with the French dispersal parameters was 0.27 m, while median distances were higher in the invaded ranges: 2.95 m in Australia, 1.82 m in New Zealand, 1.28 m in Kansas and 2.37 m in Pennsylvania. The tail of the dispersal kernels as quantified by the 99th percentile was 2.66 m for France, 37.5 m for Australia, 33.0 m for New Zealand, 19.5 m for Kansas and 36.3 m for Pennsylvania. Combining the population transition matrices and dispersal kernels resulted in invasion wave speed estimates of 0.5, 7, 29, 9 and 146 m year⁻¹ for these populations respectively (Table 1; the travelling wave speed of the French population was calculated with $\phi = 1$). Figure 2 illustrates these different invasion speeds. When we used the highest value for each of the vital rates and dispersal parameters from among the five study populations (but the lowest for F and h) in Table 1, the resulting 'maximal' invasion speed was 686 m year⁻¹.

SPREAD RATE DECOMPOSITION

The c^* -LTRE analysis (Fig. 3) shows that the naturalized populations in the invaded ranges have high spread rates for different reasons. However, they have in common that both dispersal and demography are important, albeit to different extents. Compared to the enhanced ($\phi = 1$) native range population, the Australian population wave speed was higher because the local population growth was higher due to higher seed production (π_j) and more rapid seedling (γ_4) and small rosette (γ_{42}) growth. However, these positive c^* -LTRE contributions were partly buffered by negative contributions caused by lower survival (σ_j) and establishment rates (ϵ). These negative contributions also buffered part of the positive contributions in the New Zealand-France comparison, which were mainly caused by higher seed production (π_2) and bolting probabilities (β_2) of small rosettes. In the Kansas-France comparison the only demographic parameters with major impact were seed production by large plants (positive effect) and establishment (negative effect). However, the increase in plant height (H) contributed most to the higher c^* of the Kansas population by increasing dispersal distances. Similar

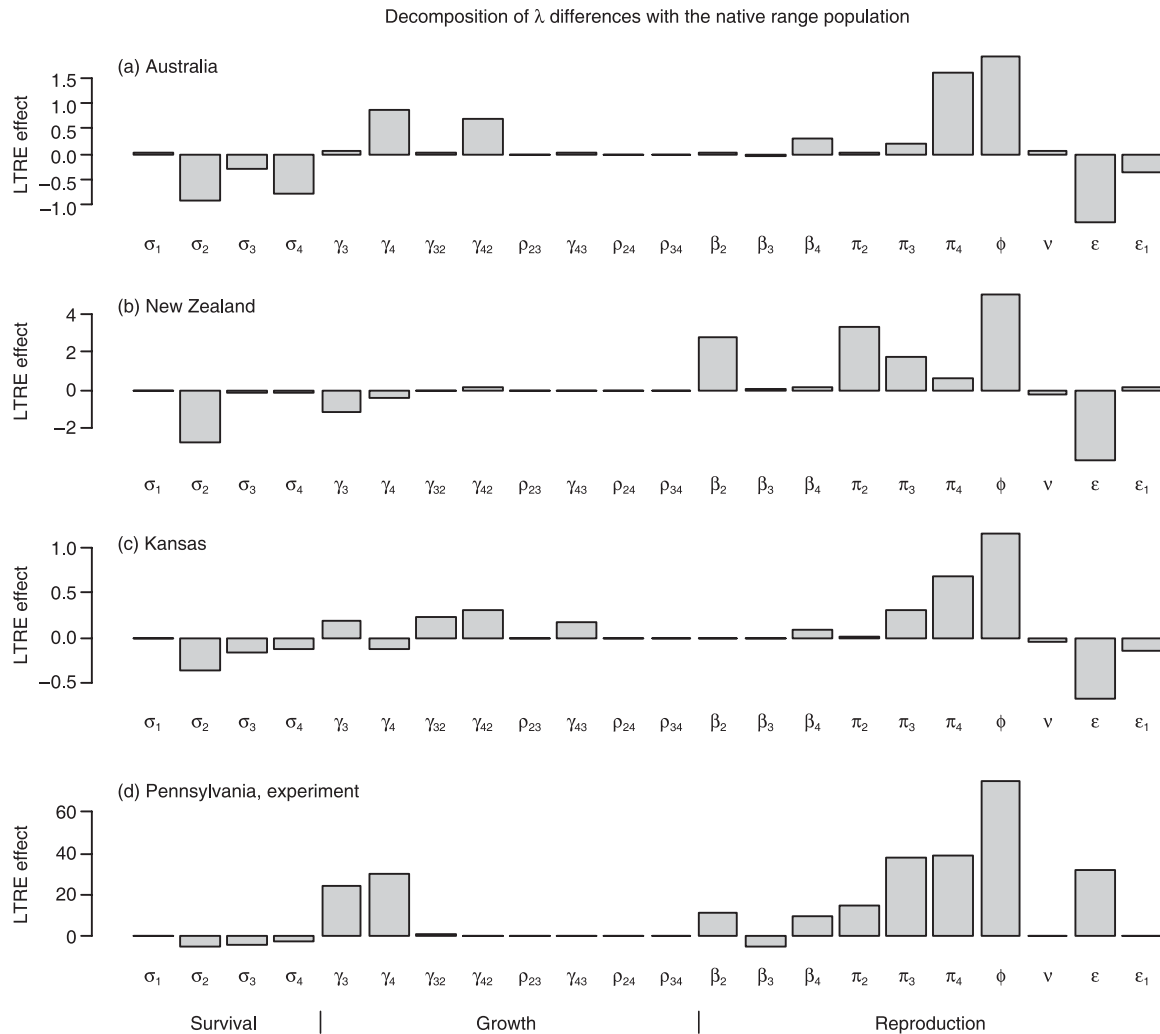


Fig. 1. Decomposition of the differences between the projected population growth rate (λ) of each of the invaded ranges and λ of the native range population, into contributions by the differences in the vital rates. See Table 1 for parameter definitions.

plant height increases were less important in Australia and New Zealand compared to changes in demographic vital rates, probably because these grazed sites had low vegetation heights and high wind speeds. The lower falling velocity (F) had the largest positive effect of the New Zealand dispersal parameters. The c^* -LTR vital rate contributions of the Pennsylvanian experimental population were overwhelmed by the magnitude of the contributions by dispersal parameters: H and F had very large positive contributions, while taller surrounding vegetation height (h) and the lower wind speed (U) had intermediate negative effects. Further comparisons between the invaded ranges are shown in Appendix S2 in the Supplementary Material.

Discussion

DISPERSAL AND DEMOGRAPHY CONTRIBUTIONS TO INCREASED SPREAD DIFFER AMONG INVADIED RANGES

The largest effect on the local population growth rate (λ) was the much higher seed escape from floral herbivores in all the

invaded ranges compared to the native range (see also Jongejans *et al.* 2006). Our mechanistic population spread model projected very different spread rates (c^*) among the invaded ranges. Apart from similar effects of escape from natural enemies, the spread rates differed for different reasons. Clear comparisons can be made in Fig. 3 between the contributions of the changes in the demography and dispersal parameters to the c^* increases of the invaded ranges compared to the native range: the net contribution of the dispersal parameters to c^* increases varied from 51% in the Australian population, 79% in the Kansas population, 80% in the New Zealand population to 85% in the Pennsylvanian experiment. The projected invasion speeds of the Australian and Kansas populations were similar (7–9 m year⁻¹): both had higher seed production than the plants in the native range population, but otherwise it was more rapid seedling growth in Australia and taller plant height in Kansas that contributed to the c^* increases. The New Zealand c^* was considerably higher (29 m year⁻¹), partly also because seed production was higher and plants taller than in the native range, but also due to lower falling velocities of the

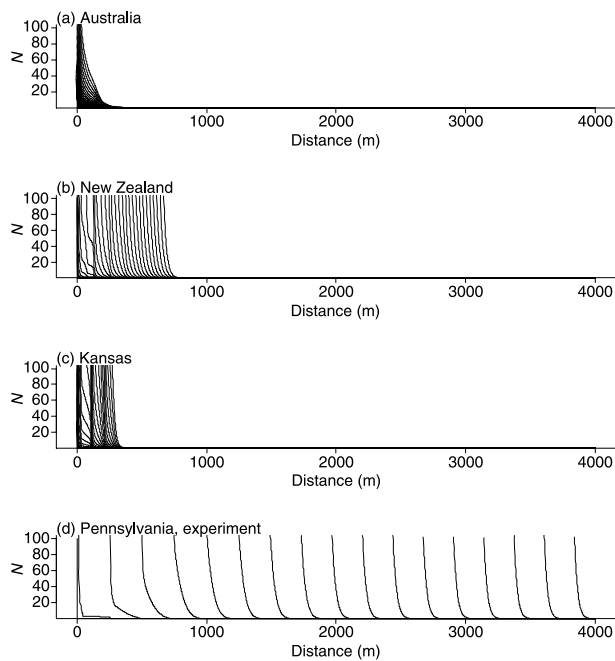


Fig. 2. Visualization of one realization of a travelling wave for each of the invaded-range populations with annual time steps over 30 years. The simulations were started with 100 seeds arriving at location 0. Note that the front of the wave converges to a constant shape and speed (Neubert & Caswell 2000), just as there are initial fluctuations followed by asymptotic convergence to constant population structure and growth rate in simulations with forward iterations of a single transition matrix.

seeds and because small plants had a higher chance of flowering when they survived.

Most remarkable is the decomposition of the very large increase in c^* of the experimental population in Pennsylvania compared to the native range dynamics. The c^* -LTRE analysis shows that this increase is overwhelmingly due to changed dispersal conditions, namely taller plants (which in turn probably resulted from the absence of competition in half of the experimental plots) and increased dispersal capacity of the seeds, despite lower wind speeds and taller vegetation. These high-magnitude contributions of dispersal parameters, however, do not mean that the changes in the demographic vital rates were not important for the increase in c^* . On the contrary, the fact that the plants in the experiment behaved essentially like annuals in an exploding population caused c^* to become especially sensitive to changes in the dispersal parameters, leading to very large c^* -LTRE contributions by the dispersal parameters. This illustrates how strongly demography and dispersal contributions depend on each other. Just as the λ -sensitivity values of all vital rates change when the value of one vital rate is altered, so do all c^* -sensitivity values of all vital rates and dispersal parameters change when one or more of these parameters change.

Our study of *C. nutans* shows how comparisons between very different types of parameters (demography and dispersal) can be combined analytically in a spatial and mechanistic population model. This has the advantage of allowing the

comparison of the influence of these parameters with a single measure, their impact on c^* . The relative magnitude and direction of the c^* -LTRE values also present a powerful and standardized method for comparison among populations, species and studies (cf. Silvertown *et al.* 1993; Franco & Silvertown 2004). Although we had to calculate c^* -sensitivity values for the dispersal parameter numerically due to the numerical method of our season-integrated WALD model, analytical derivations would be possible for the sensitivity values of parameters of functional forms of dispersal kernels (e.g. exponential) that are directly used in spread rate calculations.

FUTURE IMPROVEMENTS AND APPLICATIONS OF MECHANISTIC DECOMPOSITION ANALYSES OF CHANGES IN INVASION SPREAD

The classification of the stages is a notorious weak-spot of matrix models: different classifications (e.g. different stage borders or different number of stages) can lead to different results and interpretations (Enright *et al.* 1995; Ramula & Lehtilä 2005). We distinguished small, medium and large plants as separate stage classes based on the combined survival and flowering probabilities. Thus, plants that behave similarly are grouped together and compared among populations, instead of using fixed plant size borders for all populations. However, this had the consequence that seedlings were more likely to grow into the medium or large stage classes within months of germinating in populations in which the stage border sizes were smaller (e.g. Australia; Table 1). Such consequences of how stage classes are defined seem inevitable, and have led to the development of integral projection models that combine the analytical advantages of matrix models with continuous state variables (Easterling *et al.* 2000; Ellner & Rees 2006; Rees *et al.* 2006). Therefore, we plan to incorporate size as a continuous variable in wave speed calculations in future studies of *C. nutans* (E. Jongejans, K. Shea, O. Skarpaas, D. Kelly & S.P. Ellner, unpubl. data).

In our approach we implicitly assumed that space was homogeneous. This is, of course, a critical and false assumption; landscape and vegetation structure can strongly affect both demography and dispersal (e.g. Pouden *et al.* 2008). Including spatial heterogeneity will therefore be a very promising future direction in invasion biology research. Still, the current analysis generates important insight into which demographic and dispersal parameters can cause major differences between populations in their local and spatial population dynamics. For instance, seed release height and terminal velocity turn out to be as important for the spread rate of naturalized populations in the invaded ranges as previously identified vital rates, such as seed production, seedling establishment and rapid seedling growth. Unfortunately, the projected spread rates based on wind dispersal are not the whole story; other mechanisms also move this species over larger distances. For example, *C. nutans* reached New Zealand, and from there invaded Australia, as a contaminant of agricultural seed (Popay & Medd 1995). Human-mediated transport is also strongly implicated in North America. In

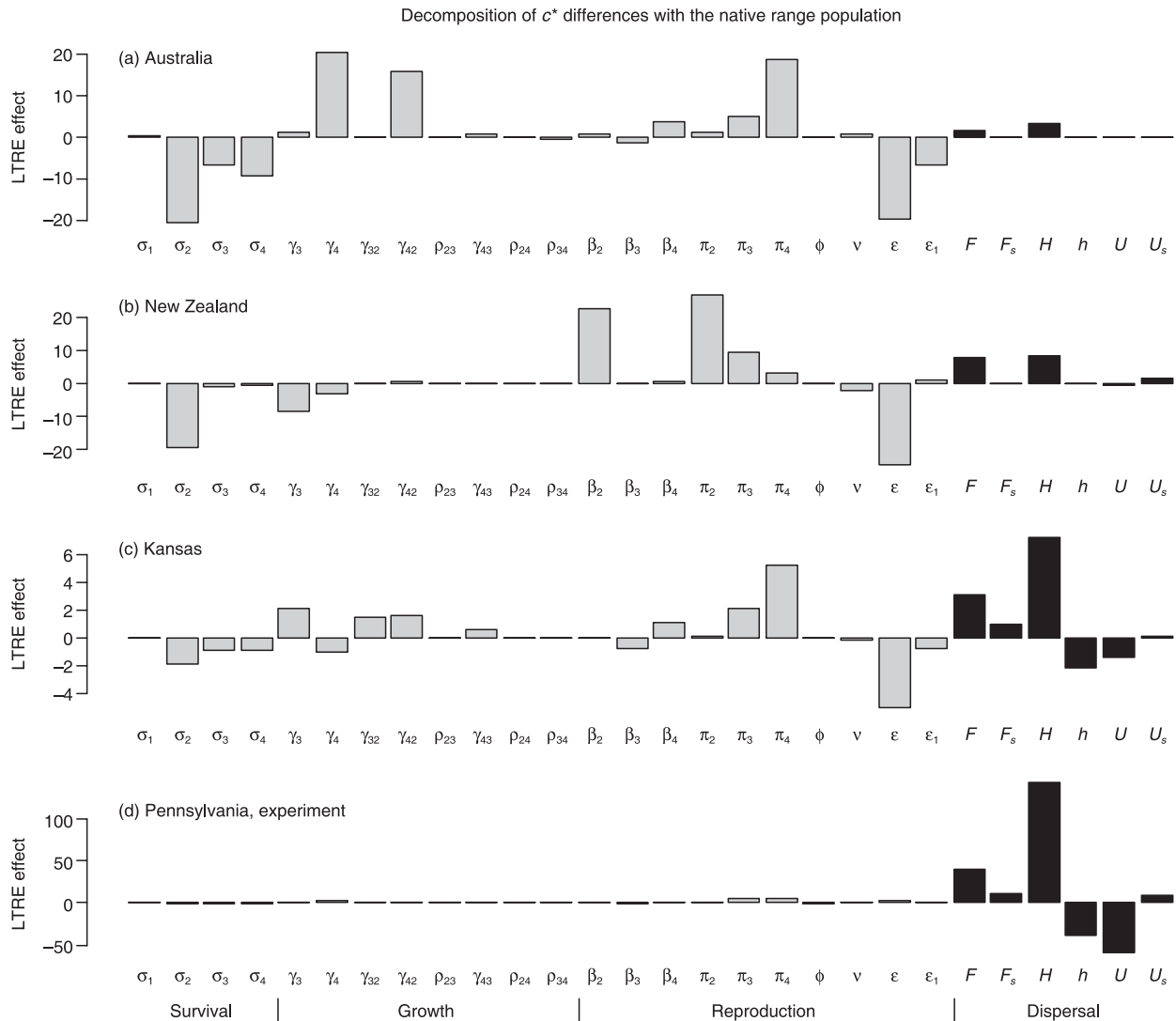


Fig. 3. Decomposition of the differences between the projected invasion speed (c^*) of each of the invaded ranges and c^* of the native range population, into contributions by the differences in the vital rates (grey) and dispersal parameters (black). See Table 1 for parameter definitions and eqn 14 for the calculation of the plotted values. Note that the contributions of ϕ (seed survival from floral herbivory) are artificially small because the native range ϕ was set to 1 to allow for native range c^* computation.

the USA, *C. nutans* was first recorded near Harrisburg, Pennsylvania, in about 1853 (Desrochers *et al.* 1988), and populations now span the entire width of the continent (Allen & Shea 2006). The wind-dispersal based projected spread rates, even for the experimental population, are not sufficient to explain this rapid spread of *C. nutans* across North America.

However, wind dispersal is likely to be a key driver of spread at smaller scales, for example, along roadsides and across adjoining farms. It is at these smaller scales also that our models can contribute to management improvements and generate more detailed insight than simply that invasions are stopped when all populations are declining ($\lambda < 1$) and/or dispersal is entirely blocked. In particular, they will allow us to tailor management efforts specifically to the reduction of local abundance, or to the reduction of spread, as desired (Jongejans *et al.* 2008). Sometimes these efforts may coincide, but strategies that most strongly reduce local population

growth rates may not be the same as those that best limit spatial spread (Shea 2004). Similarly, it is important to note that biological control agents (e.g. the weevil *R. conicus* and gall fly *Urophora solstitialis* on *C. nutans*) that damage seeds but have no effect on local plant density may be valuable for reducing the rate of spread (Kelly & McCallum 1995) as they not only destroy seeds, but can also disrupt dispersal mechanisms of remaining viable seeds.

An important caveat in this case study (as with many other international studies) is, of course, the extremely poor to no replication of populations in different countries. Furthermore, some Kansas data were unobtainable and we extrapolated from the Pennsylvanian experiment; these parameters were relatively unimportant to our conclusions (their sensitivity values were low). Ideally many populations in the native range and in each of the invaded ranges would have been used for statistical analyses of the differences between the ranges.

Such a multi-population approach for native-invaded range comparisons has already been used in studies that focus on, for instance, seed size (Buckley *et al.* 2003), plant size (Jakobs *et al.* 2004) and genetic variation (Lavergne & Molofsky 2007). However, multiple demographic and dispersal studies on the same species in different parts of the native and invaded ranges are very time-consuming and logistically challenging and are therefore relatively rare; clearly there is a great need for more such studies. In this case, we are already fortunate that *C. nutans* has been studied so widely, and that we have been able to synthesize these diverse studies here. One or two extra populations have been monitored in France, Australia, New Zealand and Kansas, but these populations are either close to the ones included in our comparison or the accompanying data sets are smaller. Including these few extra populations would therefore probably not have changed the outcome of our analyses much and certainly would not have met the requirements for statistical analyses. However, a hierarchical c^* -LTRE decomposition approach would allow for the quantification of the main effects of invaded or native ranges, and of the effects of deviations of individual populations within ranges. Such an approach will be very useful in future studies that include many populations with both dispersal and demography data.

Another important aspect to be aware of is that the studied populations were likely to be in different invasion phases. Populations of short-lived and well-dispersed plants like *C. nutans* are likely to show a rapid increase in population size after seeds arrive in a suitable, yet-uncolonised habitat (Jongejans *et al.* 2007), while after a number of years the population size stabilizes or declines depending on factors such as interspecific competition, natural or introduced enemies and other forms of management (van der Meijden *et al.* 1992). It should therefore be noted that the New Zealand and Kansas populations represent the growing phase of a population's life history, while the Australian study was a relatively well-established population and the French population was in decline after a flush of larger flowering plants in the year prior to sampling started. The explosive dynamics of the experimental population in Pennsylvania, on the other hand, showed what *C. nutans* is capable of when invading highly favourable habitats. The reported plant heights and seed production levels are certainly not unrealistic since such large plants can be found in overgrazed pastures, on unmanaged farms or on construction sites (E. Jongejans, unpubl. data 2005). At this time, it is unclear whether the effects of population phase (growing, stable or declining) and of range (native or various invaded) are additive or whether they interact. It will be very interesting to see if this can be assessed within the c^* -LTRE framework, but it is yet not possible with the currently available data sets for this or any other species.

Conclusions

Our results clearly show that the same species may invade for different reasons in different locations. This is attributable to

either demographic or dispersal-related parameters, or both, in different invaded ranges, which in turn is most likely due to differences in the population ecology of the species in each novel environment (Shea & Chesson 2002). Our approach also allows their relative contributions to be assessed quantitatively. Even though there are drawbacks to the present study, such comparisons of not only demography but also of dispersal and spread will be critical to understanding and managing invasive species in an increasingly disturbed world, and the present study lays out both the agenda and appropriate methods for such critical work. In order to understand the factors that promote spread and invasiveness of non-native species, we must extend our focus to include dispersal as well as demography.

Acknowledgements

We are grateful to Janet M. Clegg (formerly Lee) and James L. Hamrick for providing useful information and for trying to locate 30-year-old demographic data. We thank Jim Cullen for initiating the demographic study in France, and Anthony Swirepek and Mick Neave for collecting the flower heads in Australia. We thank Ran Nathan and two anonymous referees for their constructive comments. This research was partly funded by the National Science Foundation (grants DEB-0315860 and DEB-0614065) and USDA-CSREES (Biology of Weedy and Invasive Plants) NRI grant 2002-35320-12289. The field work in New Zealand was funded by Landcare Research under the Outsmarting Weeds programme, FRST contract C10X0318.

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Received 2 August 2007; accepted 19 February 2008

Handling Editor: Ran Nathan

Supplementary material

The following supplementary material is available for this article:

Appendix S1 Disentangling survival and reproduction rates from matrix elements.

Appendix S2 c^* -LTRE analyses with the mean of the populations in the invaded ranges as a reference.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2008.01367.x>

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