

Increased seed dispersal potential towards geographic range limits in a Pacific coast dune plant

Emily Darling, Karen E. Samis and Christopher G. Eckert

Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6

Summary

Author for correspondence:

Christopher Eckert

Tel: +1 613 533 6158

Fax: +1 613 533 6617

Email: chris.eckert@queensu.ca

Received: 20 August 2007

Accepted: 19 November 2007

• Dispersal may be favoured at geographic range edges by unstable population and metapopulation dynamics. However, dispersal may also evolve in response to geographic variation in other life-history traits, especially the mating system. Here, increased dispersal at range margins was tested for with a range-wide analysis of seed dispersal and mating system traits in *Abronia umbellata*, a plant endemic to Pacific coastal dunes of North America.

• Seeds disperse within winged anthocarps. Anthocarps from 34 populations varied widely in wing size (mass-corrected wing index). Wing index correlated negatively with threshold wind velocity for dispersal in wind tunnel tests, suggesting that wings facilitate tumbling over open sandy substrate. As predicted, wing index increased and threshold velocity decreased towards both range limits.

• Flower size, herkogamy and self-incompatibility declined towards range limits, indicating a shift to self-fertilization, and flower size and wing index correlated negatively. However, the increase in wing index towards range limits remained after statistically controlling flower size.

• These results are consistent with selection favouring dispersal at range margins. The evolutionary lability of dispersal across the range may affect the interaction between selection and gene flow in the establishment and maintenance of geographic range limits.

Key words: *Abronia umbellata*, dispersal, floral variation, geographic range limits, mating system variation, self-incompatibility.

New Phytologist (2008) **178**: 424–435

© The Authors (2008). Journal compilation © *New Phytologist* (2008)

doi: 10.1111/j.1469-8137.2007.02349.x

Introduction

Dispersal, the movement of individuals from where they were born to where they reproduce, is a central life-history trait with a wide variety of significant ecological and evolutionary consequences (Clobert *et al.*, 2001; Levin *et al.*, 2003; Kokko & López-Sepulcre, 2006). However, understanding the evolution of dispersal is complicated because it involves an array of fitness costs and benefits that may vary with spatial scale (Ronce *et al.*, 2001; Nathan, 2006). A good example of this involves the evolution of dispersal during the establishment of a species' geographic range (Holt, 2003). When the range is expanding, the rate of spread will be

determined by the distribution of individual dispersal distances (the dispersal kernel; Kinlan & Hastings, 2005), and individuals with higher dispersal abilities will tend to be found with greater frequency near the range margins (Thomas *et al.*, 2001; Travis & Dytham, 2002; Phillips *et al.*, 2006). Once the geographic distribution has stabilized, however, the pattern of geographic variation in selection on dispersal may change, depending on what limits the distribution.

If the range limit arises from a decline in habitat quality that reduces the fitness of individuals and, consequently, the growth rate of populations (Brown, 1984), then populations at the range limit may be demographic sinks, and dispersing individuals will tend to experience lower fitness. As a result,

dispersal may be selected against at range margins (Travis & Dytham, 1999; Holt, 2003). Conversely, populations at range margins may experience greater temporal variation in habitat quality (Nantel & Gagnon, 1999; Lönn & Prentice, 2002), which is generally expected to select for increased dispersal (reviewed in Travis & Dytham, 1999; Cadet *et al.*, 2003; Levin *et al.*, 2003). There is also growing evidence that, for a wide range of species, range limits are not coincident with or caused by declines in habitat quality (Sagarin & Gaines, 2002) and that populations at range limits are not demographic sinks (Carter & Prince, 1988; but see Griffith & Watson, 2006).

Alternatively, range limits may arise from geographic variation in metapopulation dynamics; resulting from reductions in how readily vacant habitat patches are colonized rather than a decline in the quality of the habitat patches themselves (Holt & Keitt, 2000; Holt *et al.*, 2005). It follows that the individuals sustaining metapopulations by colonizing vacant patches will tend to have greater dispersal ability at the range margins than towards the centre of the range. In other words, between-deme selection for dispersal (Olivieri *et al.*, 1995; Olivieri & Gouyon, 1997) increases towards geographic range margins. There is some empirical evidence that the individuals involved in patch colonization tend to bear alleles that cause higher than average dispersal (Hanski *et al.*, 2004). Moreover, within plant species, individuals in early successional habitats produce seed with a higher capacity for dispersal than those in later successional habitats (Olivieri *et al.*, 1983; Peroni, 1994; O'Connell & Eckert, 2001). However, these often-conflicting theoretical predictions have never been tested with range-wide surveys of traits that influence dispersal. Empirical patterns may, in turn, lead to clearer theoretical predictions given that dispersal is a key parameter in models for the evolution of range limits (Barton, 2001; Bridle & Vines, 2007).

Other life history traits may also evolve in response to geographical variation in population and metapopulation dynamics, and this may alter the intensity and scale of selection on dispersal (Cadet *et al.*, 2003). For example, wide-ranging plants sometimes exhibit a shift from outcrossing in central populations to self-fertilization at range margins (Eckert *et al.*, 2006). This is predicted by theory, under some conditions, because self-fertilization enhances the colonization of vacant habitat patches (Pannell & Barrett, 2000). The evolution of selfing may, in turn, affect selection on dispersal (Ravigné *et al.*, 2006), although theoretical predictions are, again, inconsistent. On one hand, selfed offspring that are closely related to their parent may be better adapted to the natal site than are more distantly related outcrossed progeny, and thus selfing generates selection for reduced dispersal (Schmitt & Gamble, 1990). On the other hand, increased relatedness between parents and offspring and among offspring may enhance kin-competition (Koelewijn, 2004) or rates of kin-to-kin parasite infection (Strauss & Karban, 1994),

thereby selecting for increased dispersal. Models for the joint evolution of pollen and seed dispersal also predict evolutionary interactions between traits. For example, reduced within- and between-deme pollen dispersal associated with a shift to selfing selects for and is selected for by increased seed dispersal, but the evolutionary outcome is strongly influenced by the relative cost of pollen vs. seed dispersal (Ravigné *et al.*, 2006). Accordingly, correlations between dispersal traits and the mating system are mixed. In some species with somatic mating system polymorphisms (i.e. where individuals produce two types of flowers), seeds from selfing flowers have higher dispersal potential than those from outcrossing flowers (Berg, 2000; Cheptou *et al.*, 2001). Yet in species with seed dispersal heteromorphisms, more highly dispersible seeds are usually outcrossed to a greater extent (Olivieri & Berger, 1985). However, very few studies have tested for differences in seed dispersal potential between closely related selfing vs outcrossing populations, so no empirical generalizations are possible.

Here, we test for correlated patterns of geographic variation in dispersal and mating system traits using range-wide surveys of phenotypic variation and functional analyses in *Abronia umbellata*, a plant endemic to Pacific coastal dunes of North America (Tillett, 1967). This species provides excellent opportunities to study geographical variation in life history. First, comprehensive range wide surveys are possible because: the species is a conspicuous member of the intensively studied Pacific coastal dune flora; it exhibits a roughly linear and continuous geographic distribution from northern Baja California, Mexico to southern Oregon, USA (Fig. 1); and numerous points of access to the narrow dune habitat enable surveys of the entire geographical range.

Abronia umbellata is a prostrate, spreading, short-lived, herbaceous, perennial that produces umbellate inflorescences, each with about 14 uniovulate flowers that form indehiscent anthocarps. Anthocarps are accessory fruits that develop from the lower portion of the persistent perianth (Wilson, 1975), and bear 'wings' that have been hypothesized to facilitate wind dispersal (Wilson, 1976). Inflorescences are held approx. 5–10 cm above the substrate on erect stalks. However, as infructescences mature, these stalks bend downwards to lay the ripe fruits directly onto the substrate (often bare sand). Hence, primary dispersal distance is determined solely by the length of the stalk, and most movement occurs secondarily via wind. Long-distance seed dispersal may often involve more than one vector (Levin *et al.*, 2003). Although *A. umbellata* usually occurs well above the high tide line, wind may move *Abronia* anthocarps into the surf, especially during winter storms, where they may experience tertiary dispersal by water. Wings could facilitate water dispersal if they increase the time anthocarps remain afloat (Wilson, 1976). Previous taxonomic surveys of anthocarp wingedness revealed wide variation among species of *Abronia*. In *A. umbellata*, there is considerable variation in anthocarp wingedness at all levels (Wilson, 1974,

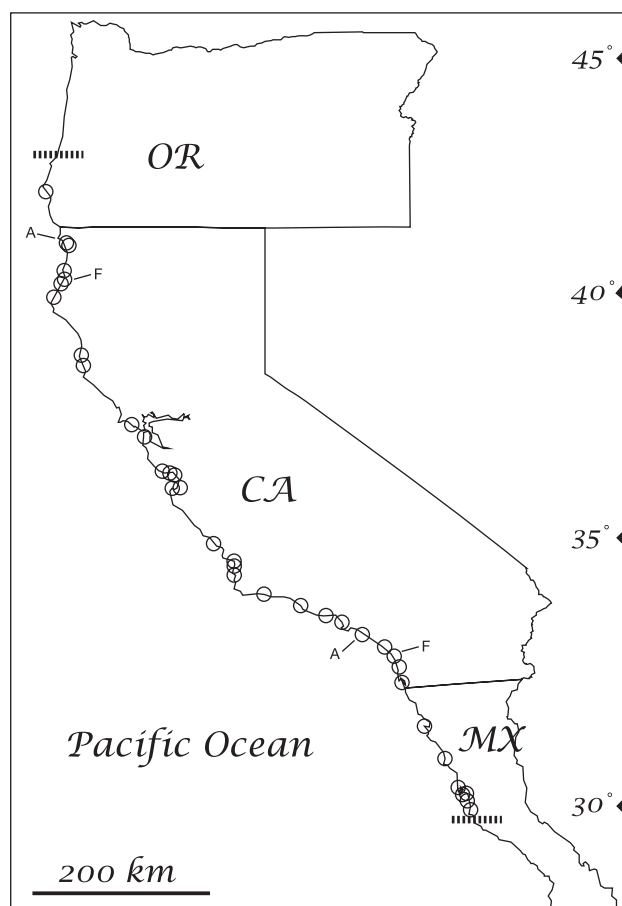


Fig. 1 Natural populations of *Abronia umbellata* sampled across the species' geographic range along Pacific coastal dunes of North America (OR, Oregon; CA, California; MX, Mexico). Points are population locations. Thick broken lines along the coast indicate the northern and southern geographical range limits determined by extensive population surveys and analyses of herbarium records (Samis & Eckert, 2007). Populations indicated with an 'A' were sampled for anthocarps only; those with an 'F' flowers only were sampled. Ticks at the right edge of the figure show latitude ($^{\circ}$ N).

1976): among anthocarps within an umbel, among individuals within populations and among populations, the last of which is the focus of this study.

There is also evidence of variation in the mating system across the geographic range of *A. umbellata* (Tillett 1967). From Baja California, Mexico, to around San Francisco, CA, USA, including several of the California Channel Islands, plants bear relatively large flowers that appear strongly self-sterile and are almost certainly highly outcrossing. Further north towards the range limit in southern Oregon, USA, plants bear much smaller flowers that are likely self-compatible and highly self-fertilizing. However, the pattern of variation in floral morphology and self-compatibility across the geographic range has not been quantified.

In this study, we survey variation in anthocarp traits of *A. umbellata* across the geographic range and perform

functional analyses of how anthocarp wings affect dispersal by wind and water to test the hypothesis that enhanced seed dispersal capacity is selected in geographically peripheral compared with central populations. We also quantify geographic variation in aspects of floral morphology and self-compatibility expected to influence the degree of self-fertilization, and determine whether there is any covariation between dispersal traits and the mating system, and whether an evolutionary change in the mating system may have affected the evolution of dispersal. Based on previous taxonomic work, we expect that the pattern of evolutionary differentiation in dispersal caused by geographic variation in population and metapopulation dynamics may be complicated by variation in the mating system towards the northern but not the southern range limit. For example, an increase in dispersal potential towards the northern limit could be caused by a shift to self-fertilization instead of or in addition to increased demographic instability, whereas increased dispersal towards the southern limit could only be attributed to enhanced demographic instability.

Materials and Methods

During the summers of 2002 and 2003, we sampled 36 populations of *A. umbellata* Lam. (Nyctaginaceae) along an 1800 km latitudinal transect from the southern range limit in Baja California, Mexico (30.05° N), to the northern range limit in southern Oregon, USA (42.74° N; Fig. 1; see the Supplementary Material, Table S1). Range limits were determined from intensive geographic surveys of site occupancy and analysis of location data from herbarium specimens collected over the last 150 yr (Samis & Eckert, 2007). In each of 34 of the 36 populations, a mature infructescence was sampled from each of 12 randomly chosen plants, packaged individually and dried at room temperature for several months. In each of 34 populations, including 32 sampled for infructescences, one fresh flower was collected from each of 10 randomly chosen plants and preserved in 70% ethanol.

Potential seed dispersal traits

Several morphological and wind-dispersal measurements were performed on one anthocarp from each of a random subsample of five infructescences per population. A pilot study indicated that anthocarps of *A. umbellata* vary in both the number and size of wings, although the latter varies to a much greater extent than the former. Almost two-thirds of all anthocarps have four wings. Hence, we used a measure of wingedness ('wing index') that integrates wing number and size. Wing index was calculated for each anthocarp by scoring the size of each wing on a subjective 1–5 scale (1, small; 5, large), and then summing these scores for all wings on the anthocarp. This index correlated strongly and positively with all other potential measures of wingedness (K. E. Samis and

C. G. Eckert, unpublished). All anthocarps were weighed to 0.001 mg. Not all anthocarps that develop contained filled seeds, however those with seeds tend to have larger wing index scores than those without (K. E. Samis and C. G. Eckert, unpublished). Accordingly, only anthocarps that contained filled seeds were used in our analyses (*c.* 5 per population, total = 164).

Measurement of wind-dispersal potential

The wing index of anthocarps correlated positively with their mass ($r = +0.34$, $P < 0.0001$), hence we used the residuals from a regression of wing index over anthocarp mass as a mass-corrected measure of anthocarp dispersal potential. The wind velocity required to start each anthocarp tumbling (threshold speed) was then measured. A lower threshold speed should indicate greater dispersal potential (Johnson & Fryer, 1992; Greene & Johnson, 1997). This measure is also likely to correlate strongly with alternative measures of dispersal such as distance moved away from a constant wind source (Wilson, 1976). Measurements were made using a Flotek 1440 wind tunnel (GDJ Inc., Mentor, OH, USA), which consists of a cylindrical steel body 400 cm long \times 30 cm diameter, with a 45-cm fan mounted at one end that blows air through a honeycomb flow straightener. Observations were made through a 90-cm long clear acrylic sidewall in the middle of the tunnel, controlled wind velocity with a variable transducer and measured it just above each anthocarp to 0.01 m s^{-1} with an air velocity transducer (TSI Inc., St Paul, MN, USA). Anthocarps were placed individually broadside to the airflow on sand paper, the velocity was gradually increased from 0.60 m s^{-1} to 4.10 m s^{-1} at a constant acceleration of 0.023 m s^{-2} , and the velocity at which each anthocarp entered the air stream and tumbled out of the observation area was recorded. Threshold velocity was measured twice for each anthocarp, changing the surface of the anthocarp that touched the substrate each time, and averaged across trials (correlation of threshold velocity between trials: $r = +0.81$, $P < 0.00001$). All measurements of anthocarp morphology and threshold velocity were made by a single observer, and were performed in a random order and blind to the population that each anthocarp came from.

Measurement of water-dispersal potential

Whether anthocarp morphology might influence dispersal on seawater was tested using another set of anthocarps, randomly sampled, as above, from 33 of 34 study populations (*c.* six per population, total = 188). A single observer weighed and scored wing index for each anthocarp, as above, and placed them individually into 20 ml glass vials filled with 17.5 ml of artificial seawater created using 'Instant Ocean' (Aquarium Systems Inc., Mentor, OH, USA). Each vial was randomly positioned on a laboratory bench at *c.* 20°C, labelled so that

the observer was blind to population of origin. Vials were shaken every 12 h for 35 d and the number of days each anthocarp remained afloat (float time) recorded.

Floral traits related to the mating system

Flowers were dissected under a microscope and photographed with a Nikon Coolpix 4500 digital camera. IMAGEJ software (version 1.3, National Institute of Health, Washington, DC, USA) was used to measure (to 0.1 mm) the length of each flower (including the ovary) and the minimum distance between the stigma and the nearest anther (herkogamy). A single observer measured each image twice in random order and blind to the population of origin. The size of all floral organs (corolla width, floral tube length and width, style length and stamen length) correlated positively and strongly with flower length (all $P < 0.0001$), hence we used it as a general measure of flower size. Herkogamy was also analysed because it is widely expected to control self-pollination (for review see Herlihy & Eckert, 2007).

Our survey of floral morphology suggested potentially broader geographic variation in the mating system than expected. Hence, we evaluated the degree of self-compatibility using hand-pollination of 55 plants grown from seed under a common glasshouse environment representing 25 of the 34 populations (2–3 plants per population) for which floral traits had been measured. Plants were randomized across one glasshouse bench and all the flowers in an inflorescence (mean = 15) were either self-pollinated or cross-pollinated, without emasculation, using pollen from a single donor from the same or a nearby population (total $n = 2466$). Mature anthocarps were collected, dried for ≥ 5 d, and then classified as undeveloped or developed. Developed anthocarps were assumed to contain a filled seed, although this is not always the case. However, undeveloped anthocarps were too small ($\ll 4$ mm) to house a viable seed. The distribution of relative seed set after self- vs cross-pollination was strongly bimodal, with one mode centred on 0.012 (range = 0.000–0.143, classified as self-incompatible) and the other centred on 1.00 (range = 0.786–1.429, classified as self-compatible). Hence, the proportion of flowers forming developed anthocarps captured enough of the variation in seed set to accurately indicate the degree of self-compatibility.

Statistical analyses

One-way analysis of variance was used to test whether wing index, anthocarp mass, residual wing index, threshold velocity, float time, flower length and herkogamy varied among populations. Linear regression was used to test for associations between anthocarp traits and threshold velocity and between anthocarp and floral traits. Because 24% of anthocarps remained afloat after 35 d, we first tested whether anthocarp traits were associated with the probability of

remaining afloat using logistic regression, with significance evaluated using likelihood-ratio tests. Linear regression was then used to test whether anthocarp traits were associated with float time among those anthocarps that sank during the observation period.

To evaluate the prediction that dispersal traits increase towards range limits, population means were calculated for each variable that appeared to influence anthocarp dispersal and tested for second-order polynomial regressions of floral traits, anthocarp traits and threshold velocity over latitude (following Quinn & Keough, 2002). Quadratic terms were estimated using centred predictors (i.e. population values from which the grand mean has been subtracted) to eliminate collinearity between linear and squared terms. Whether a polynomial model fitted the data better than a linear model was evaluated using partial F -tests. R (version 1.16, R Development Core Team 2006) was used for all analyses. Statistical assumptions were met for all analyses: error residuals were normally distributed and independent of predicted values.

Results

Geographic variation in potential seed dispersal traits

Wing index varied widely among anthocarps (mean \pm 1 SD = 12.01 ± 4.08 , range = 3–24, CV = 34%) and exhibited significant heterogeneity among populations ($r^2 = 0.63$, $F_{33,130} = 6.8$, $P < 0.0001$, CV of population means = 27%). Mass also varied widely among anthocarps (9.71 ± 4.10 mg, range = 2.7–23.7 mg, CV = 42%) and populations ($r^2 = 0.36$, $F_{33,130} = 2.2$, $P = 0.0007$, CV = 26%). The threshold velocity for dispersal in the wind tunnel also varied widely among anthocarps (2.37 ± 0.74 m s⁻¹, range = 1.20–4.00 m s⁻¹, CV = 31%) and populations ($r^2 = 0.48$, $F_{33,130} = 3.6$, $P < 0.0001$, CV = 22%) and exhibited a significant and monotonic decrease with wing index ($F_{1,162} = 91.3$, $P < 0.0001$, standardized slope $\beta_{\text{std}} = -0.60$) and a significant but weaker increase with anthocarp mass ($F_{1,162} = 4.4$, $P = 0.036$, $\beta_{\text{std}} = +0.16$). Mass-corrected wing index (residuals from regressing wing index on mass) accounted for 49% of the variance in threshold speed (Fig. 2, $F_{1,162} = 153.6$, $P < 0.0001$, $\beta_{\text{std}} = -0.70$). An even stronger negative correlation was detected between mass-corrected wing index and threshold velocity among populations ($F_{1,32} = 70.1$, $P < 0.0001$, $\beta_{\text{std}} = -0.83$).

Of 188 anthocarps from 33 populations, 76.1% sank during 35 d of observation. Float time varied substantially among anthocarps (12.6 ± 5.9 d, range = 7–31 d, CV = 47%) and populations ($r^2 = 0.38$, $F_{32,110} = 2.1$, $P = 0.0024$, CV = 37%). Contrary to expectations, the probability of remaining afloat for > 35 d was negatively related to both wing index (logistic regression likelihood ratio $\chi^2 = 18.8$, df = 1, $P < 0.0001$, odds ratio = 0.87) and anthocarp mass ($\chi^2 = 22.3$, $P < 0.0001$, odds ratio = 0.86), but not mass-corrected wing index ($\chi^2 = 2.4$, $P = 0.12$). Of the anthocarps that sank, there was

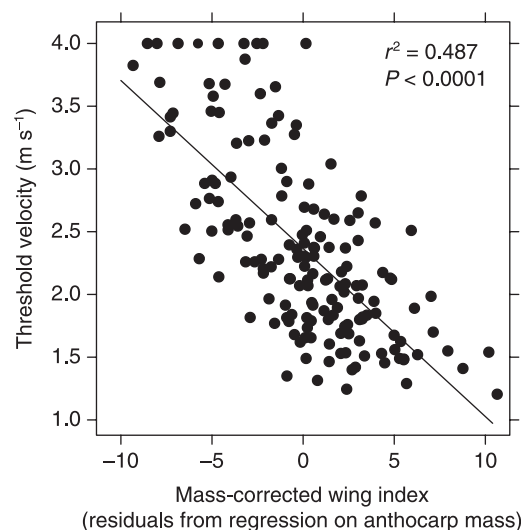


Fig. 2 Anthocarp wingedness increases dispersal potential of *Abronia umbellata* anthocarps. Dispersal potential was measured as, and should correlate negatively with, the threshold wind velocity for dispersal in a wind tunnel. Wingedness was measured as mass-corrected wing index calculated as the residuals of wing index regressed over anthocarp mass (see the Results section).

no relation between float time and wing index ($r^2 = 0.01$, $F_{1,141} = 1.8$, $P = 0.18$, $\beta_{\text{std}} = -0.11$), mass ($r^2 = 0.02$, $F_{1,141} = 3.5$, $P = 0.061$, $\beta_{\text{std}} = -0.16$) or mass-corrected wing index ($r^2 < 0.001$, $F_{1,141} = 0.03$, $P = 0.87$, $\beta_{\text{std}} = +0.01$).

As predicted, wing index and mass-corrected wing index both exhibited positive second-order polynomial regressions with latitude (Table 1, Fig. 3a). In both cases, linear terms were weak and not significant whereas quadratic terms were much stronger and highly significant. A polynomial model fitted the data better than a linear model for both variables (both $P < 0.0001$). In addition, threshold velocity exhibited a negative polynomial regression with latitude with a weak, positive linear term and a much stronger and negative quadratic term (Table 1, Fig. 3c). Again, the polynomial model fitted the data better than the linear model ($P < 0.0001$). Anthocarp mass exhibited only a weak and linear increase with latitude (Table 1, Fig. 3b), and adding a quadratic term to the model did not provide a better fit to the data ($P = 0.46$).

Geographic variation in floral traits

Flower length and herkogamy varied widely among individual flowers (length: mean \pm 1 SD = 32.7 ± 7.7 mm, range = 16.6–51.2, CV = 24%; herkogamy: 3.70 ± 2.75 mm, 0.00–11.41, 74%) and among populations (length: $r^2 = 0.86$, $F_{33,296} = 56.4$, $P < 0.0001$, CV of population means = 22%; herkogamy: $r^2 = 0.68$, $F_{33,296} = 19.1$, $P < 0.0001$, CV = 63%). The two traits correlated positively among flowers ($r = +0.82$, $n = 330$, $P < 0.0001$) and populations ($r = +0.95$, $n = 34$, $P < 0.0001$).

Table 1 Minimal adequate regression models of anthocarp traits related to seed dispersal and floral traits related to the mating system over latitude among 34 populations of *Abronia umbellata* across the species' geographic range

Response variable	Model	Linear term		Quadratic term	
	r^2	β_{std}	P	β_{std}	P
Anthocarp traits					
Wing index	0.49	−0.039	0.77	+0.718	< 0.0001
Mass-corrected wing index	0.58	−0.143	0.24	+0.790	< 0.0001
Anthocarp mass (mg)	0.11	+0.339	0.049	ns	ns
Threshold velocity (m s^{-1})	0.46	+0.316	0.027	−0.682	< 0.0001
Floral traits					
Flower length (mm)	0.75	−0.558	< 0.0001	−0.564	< 0.0001
Herkogamy (mm)	0.71	−0.509	< 0.0001	−0.582	< 0.0001

r^2 , The proportion variation in the response variable explained by the regression model; β_{std} , the standardized regression coefficients; P , statistical significance.

For all variables, except anthocarp mass, polynomial models (all $P < 0.0001$) fit the data better than linear models (comparison of linear vs polynomial models: all $P < 0.0001$).

For anthocarp mass, a linear regression was marginally significant ($P = 0.049$) but adding a quadratic term did not improve the fit to the data (ns, $P = 0.46$).

Plots of population means over latitude for residual wing index, anthocarp mass, threshold velocity and flower length are provided in Fig. 3.

Contrary to expectations from taxonomic work, geographic variation in flower size did not involve a simple contrast between large-flowered, outcrossing plants south of San Francisco Bay (*c.* 37.8°N) and small-flowered, selfing plants to the north. Instead, flower length and herkogamy were highest between 34°N and 36°N latitudes and declined significantly toward both the northern and southern range limits (Fig. 4). As a result, both floral variables exhibited negative second-order polynomial regressions with latitude (Table 1). The results of experimental crosses generally matched the floral measurements (Fig. 4). All 26 plants from nine small-flowered populations north of 37°N were self-compatible. Plants from five populations in Baja California (south of 32°N) exhibited variation in self-compatibility: four were self-compatible and three were self-incompatible. Of the 22 plants from 11 geographically central, large-flowered populations, 21 were self-incompatible.

Geographic covariation between dispersal traits and floral traits

Among the 32 populations for which both floral and anthocarp traits were measured, both floral traits correlated negatively with wing index (flower length: $r = -0.49$, $P = 0.0046$, Fig. 5a; herkogamy: $r = -0.53$, $P = 0.0017$) and mass-corrected wing index (flower length: $r = -0.45$, $P = 0.0099$; herkogamy: $r = -0.50$, $P = 0.0045$). However, neither floral trait correlated with threshold velocity (flower length: $r = +0.20$, $P = 0.26$; herkogamy: $r = +0.27$, $P = 0.13$) or anthocarp mass (flower length: $r = -0.24$, $P = 0.18$; herkogamy: $r = -0.26$, $P = 0.14$). Although variation in latitude and floral traits related to the mating system were confounded, residuals from a regression of wing index on flower length (i.e. the

variation in wing index not associated with variation in the mating system) exhibited a positive second-order polynomial regression on latitude (Table 2, Fig. 5b). Residual analysis of mass-corrected wing index yielded the same result (Table 2).

Discussion

The pattern of geographic variation in anthocarp traits related to dispersal is consistent with enhanced selection for dispersal at range margins. Populations of *A. umbellata* varied widely in anthocarp wingedness (wing index), and more highly winged anthocarps exhibited higher potential for wind-dispersal in wind tunnel tests. Wing index increased dramatically towards both northern and southern range limits, and correcting wing index for covariation with anthocarp mass to more closely reflect dispersal potential resulted in an even stronger polynomial relation with latitude. Anthocarp wings did not appear to enhance flotation on artificial seawater, a conclusion also reached by Wilson (1976) from a comparison among *Abronia* species.

The pattern of geographic variation in floral traits related to the mating system was very similar to that for anthocarp morphology. As expected from previous taxonomic work (Tillett, 1967), plants in the core of the range bore relatively large, herkogamous, self-incompatible, obligately outcrossing flowers, whereas plants in populations north of San Francisco Bay bore much smaller, self-compatible flowers with negligible herkogamy that are almost certainly highly self-fertilizing. However, we also found evidence of a shift towards self-compatibility and smaller flower size in some of the populations at the southern range margin in Baja California that was not reported in previous taxonomic work. In addition,

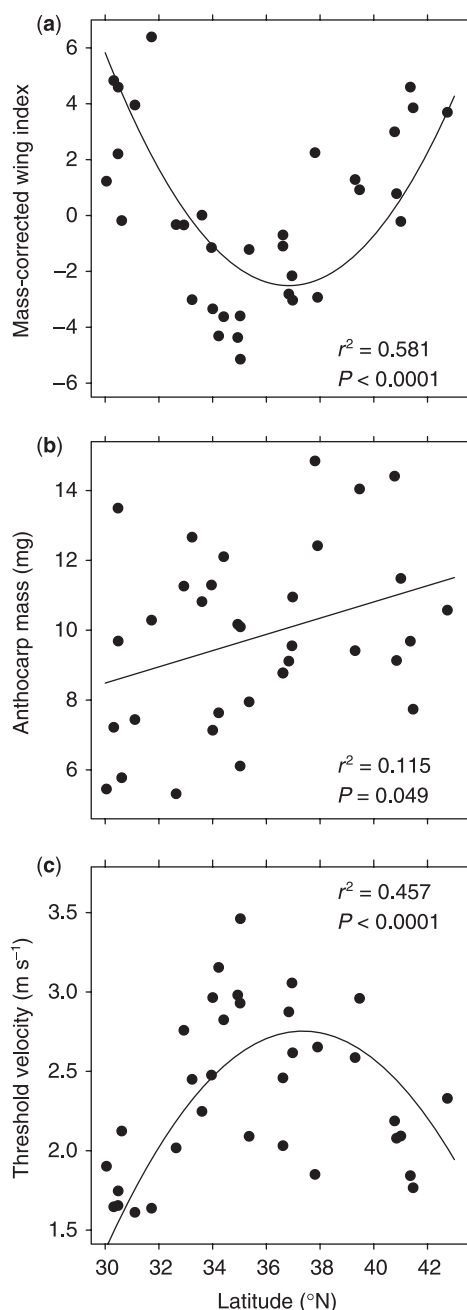


Fig. 3 Variation in (a) wingedness, (b) mass and (c) wind-dispersal potential of anthocarps sampled from 34 populations of *Abronia umbellata* across the full extent of the species' geographic range. Each point is a population mean. Best-fitting regression lines and associated r^2 and significance value (P) are shown for each variable. Full presentation of these analyses is provided in Table 1.

the correlation between flower size and self-compatibility among populations was looser than expected. Although small-flowered plants were consistently self-compatible, self-compatibility was also detected for plants from several large-flowered populations, both in Baja California and in north central California. Overall, *A. umbellata* appears to

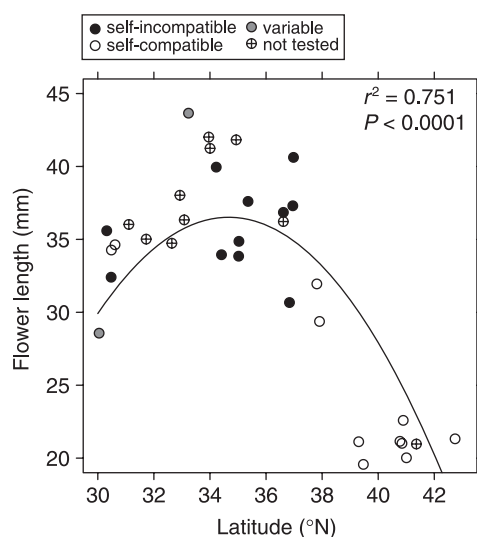


Fig. 4 Geographical variation in flower length among 34 populations of *Abronia umbellata* across the full extent of the species' range. Each point is a population mean. The best-fitting regression line and associated r^2 and significance value (P) are shown (see Table 1). Whether the plants from each population were self-incompatible or self-compatible, as determined by crosses in the glasshouse, is indicated with different symbols. Both incompatibility types were found in the two 'variable' populations.

exhibit considerable evolutionary lability in mating system, and our results hint that the loss of self-incompatibility may occur independently of reductions in flower size and herkogamy. A shift from outcrossing to selfing at range margins has occurred repeatedly within species and is often interpreted as a product of selection for reproductive assurance. A similar geographic trend in flower size and self-compatibility occurs towards both range margins in *Camissonia cheiranthifolia*, another short-lived endemic of Pacific coastal dunes that usually co-occurs with *A. umbellata* (Eckert *et al.*, 2006).

Coevolution or parallel evolution with the mating system?

The unexpected geographic covariation in seed dispersal and mating system traits complicates the interpretation that enhanced seed dispersal at the range limits is a direct evolutionary response to variation in population and metapopulation dynamics. Although theoretical predictions and empirical evidence concerning the effect of the mating system on dispersal evolution are inconsistent (see the Introduction), enhanced dispersal could be an adaptation to inbreeding in peripheral populations (Gandon & Michalakis, 2001; Ravigné *et al.*, 2006). However, our joint analysis of wing index and flower size suggests that dispersal traits exhibit a geographic trend that is at least statistically independent of geographic variation in floral traits that influence the mating system. The phenotypic correlation between the two

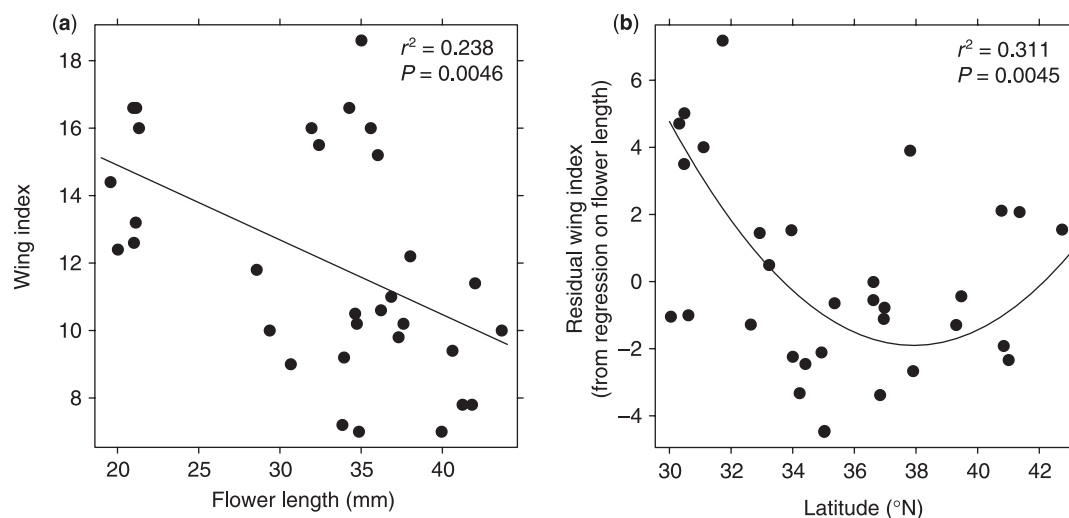


Fig. 5 Flower length (an indicator of the degree of outcrossing) correlates negatively with wing index (a seed dispersal trait) among 32 populations of *Abronia umbellata* sampled from across the geographic range (a). However, there is still a trend for highest wing index values in peripheral populations (b) even after covariation with the mating system is removed by taking the residuals from the regression illustrated in (a). The best-fitting regression lines and associated r^2 and significance values (P) are shown (see Table 2).

Table 2 Minimal adequate regression models of anthocarp dispersal traits over latitude after covariance between anthocarp traits and floral traits related to the mating system has been removed

Response variable	Model	Linear term		Quadratic term	
	r^2	β_{std}	P	β_{std}	P
Wing index	0.31	-0.382	0.022	+0.492	0.0037
Mass-corrected wing index	0.45	-0.487	0.0017	+0.571	0.00030

Data are from 32 populations of *Abronia umbellata* across the species' geographic range for which both anthocarp and floral traits were measured.

r^2 , The proportion variation in the response variable explained by the regression model;

β_{std} , the standardized regression coefficients; P , statistical significance.

Response variables for analysis were the residuals from regressions of wing index and mass-corrected wing index over flower length (see Fig. 5a).

For both variables, second-order polynomial models (both $P < 0.005$) fit the data better than linear models (comparison of linear vs polynomial models: both $P < 0.003$).

Residualized wing index is plotted over latitude in Fig. 5b.

traits was weak compared with the latitudinal trend exhibited by both. For example, the reduction in flower size and self-incompatibility was much more pronounced towards the northern end of the range, whereas the increase in wing index was, if anything, greater towards the southern end. Moreover, the threshold wind velocity, which correlated strongly with wing index, did not correlate with flower size. Finally, after statistically controlling for the positive correlation between wing index and flower size, which effectively assumes that seed dispersal traits have responded directly to variation in the mating system, wing index still exhibited the predicted polynomial relation with latitude. All this suggests that invoking evolutionary interactions between dispersal and the mating system is not justified at this point. Even though the mating system and seed dispersal covary, this has likely arisen from independent evolutionary responses, possibly to the same ecological factors (e.g. demographic

instability). Next, we evaluate the assumptions that underlie this interpretation.

Does geographic variation in dispersal traits have a genetic basis?

Our study along with all studies of other species that have quantified variation in diaspore traits among populations examined anthocarps from natural populations, thus some of the phenotypic variation observed may have resulted from environmental rather than genetic variation among populations (Ronce *et al.*, 2005). Generally, the contribution of phenotypic plasticity to seed dispersal traits is not well understood (Olivieri & Berger, 1985; Donohue, 1999). Such is the case in *A. umbellata*. There is considerable phenotypic variation in morphology among *A. umbellata* anthocarps within individual umbels (C. G. Eckert and K. E. Samis, unpublished),

which may suggest a high degree of plasticity in anthocarp wingedness. However, we tentatively propose that the contribution of environmental variation to the among-population component of variation in anthocarp wingedness that we focused on in this study was probably small. First, it is difficult to conceive of an environmental factor that would produce more highly winged anthocarps at both ends of the range. It is possible that conditions in peripheral populations are less conducive to growth, survival and/or reproduction than in central populations, though it is likely the exact stresses differ between range margins (Vucetich & Waite, 2003; Samis & Eckert, 2007). However, this would reduce not increase most phenotypic traits. There was a weak geographic trend in anthocarp mass, but this involved an increase from south to north. Flower size was smaller at range margins, especially the northern margin, but anthocarp wingedness covaried negatively, not positively, with flower size.

The density of plants within populations, a possible indicator of environmental quality, varied widely across the range in *A. umbellata*, but was not lower towards range margins, and was not associated with measures of individual plant performance such as size or seed production (Samis & Eckert, 2007). The populations used in our pollination experiment maintained geographic variation in floral traits in a common environment, and there is no reason to expect a different result for anthocarps traits. Finally, even if geographic variation in environment influences anthocarp phenotype it does so in a way that produces an increase in wingedness towards both range margins. Hence, this kind of interaction between genes and environment, if it actually occurs, may still be interpreted as an evolved response.

Does variation in anthocarp wings affect dispersal under natural conditions?

There has been considerable scepticism over whether laboratory-based assays such as our wind tunnel tests reflect dispersal potential under natural conditions where wind patterns may be complex and strongly influenced by microtopography and vegetation structure (Greene & Johnson, 1990). It is even more problematic to extend laboratory-based tests to inferences of long-distance dispersal that might influence the evolution of dispersal traits at range margins (Nathan, 2006). For example, dispersal of *A. umbellata* anthocarps will be influenced by the extent to which open sand is interrupted by vegetation that entraps tumbling anthocarps. There is considerable geographic variation in the structure of dune vegetation, but there does not appear to be any consistent change in structure that occurs at both northern and southern range margins that would prevent greater wingedness from being manifested in longer dispersal distances under field conditions.

We must also address the possibility that other plant traits might potentially influence dispersal to a greater

extent than anthocarp wings under natural conditions. For example, wind dispersal of plumed seeds is strongly influenced by the height of the infructescence above the substrate (release height) as well as the wind velocity required to release the seed from the infructescence. However, our field observations and previous observations by Wilson (1976) suggest that the wings on *A. umbellata* anthocarps are the principal trait influencing seed dispersal by facilitating secondary 'tumble dispersal', which may be an effective dispersal mode in windy coastal environments (Schurr *et al.*, 2005). Infructescence height and the threshold velocity for release probably do not influence dispersal because, even though the inflorescences of *A. umbellata* are held *c.* 5–10 cm above the substrate during flowering, stalks bend downward during fruit development so that ripe infructescences are laid onto the sand. Anthocarps are then released directly onto the sand (Wilson, 1972; K. E. Samis and C. G. Eckert, pers. obs.). While conclusive evidence for the functional significance of anthocarp wings under natural conditions requires detailed analyses using field trials combined with assays of genetic and, possibly, isotope markers (Wang & Smith, 2002), we tentatively conclude from our observations that these wings play a significant role in seed dispersal and are targets of selection on dispersal distance.

Evidence of geographic variation in population and metapopulation dynamics favouring enhanced dispersal at range edges?

Demographic instability of populations is generally expected to be more pervasive towards geographical range limits (Carter & Prince, 1988; Nantel & Gagnon, 1999; Holt & Keitt, 2000; Lönn & Prentice, 2002) and this would seem to be implicated in dispersal evolution by our results. However, providing evidence for this mechanism is a formidable empirical challenge, especially because dispersal evolution may be potentially influenced by instability at a variety of temporal or spatial scales (Nathan, 2006). For example, coarse-scale, range-wide analyses of population density and productivity have not revealed much evidence for less abundant, smaller or less stable populations towards range margins in *A. umbellata* (Samis & Eckert, 2007). The occupancy of suitable sites, where sites are represented by whole-dune systems, was moderate across the range (55% of suitable sites occupied) and was not lower in geographically marginal than central regions, as might be expected from metapopulation models of range limits (Holt & Keitt, 2000). However, finer-scale demographic instability, at the level of patches within sites, might also select for enhanced dispersal. Ongoing monitoring of patch occupancy and productivity over longer time-scales and within a hierarchy of spatial scales will provide a better test of our interpretation. Genetic data

could also be informative because aspects of population genetic structure integrate the influences of variation in demography over the longer term. In many species, patterns of geographic variation in genetic structure are consistent with demographic instability and increased population turnover towards range margins (Lesica & Allendorf, 1995; Vucetich & Waite, 2003; Eckert *et al.*, in press). The one available population genetic analysis of *A. umbellata* included only populations within the northern range margin (McGlaughlin *et al.*, 2002). Our results suggest that larger-scale patterns of geographic variation in population genetic structure will likely be complicated by variation in the mating system.

Our interpretation thus far has assumed that the geographic range of *A. umbellata* is at equilibrium. An alternative scenario is that the range is shifting, which may also lead to selection for increased dispersal towards expanding and contracting range margins (Cwynar & MacDonald, 1987; Travis & Dytham, 2002; Parmesan, 2006). In general, very little is known about the phylogeography or historical biogeography of Pacific coastal dune plants, including *A. umbellata*. Like many other dune inhabitants, the species is entirely restricted to coastal dunes and has probably never expanded its range inland (Breckon & Barbour, 1974). McGlaughlin *et al.* (2002) suggested that the northern range margin of *A. umbellata* is contracting because of anthropogenic habitat disturbance, but this is not supported by a more detailed analysis of location data from 482 herbarium specimens compared with extensive field surveys of contemporary populations (Samis & Eckert, 2007). Of the specimens collected between 1850 and 2000, 15 were from 10 locations beyond the observed northern limit (see Fig. 1). Eight of these locations yielded only a single specimen collected only once, suggesting that these represent sporadic occurrences rather than evidence for range contraction. The two locations, in Washington and British Columbia from which the species was collected repeatedly are isolated by hundreds of kilometres beyond the northern limit. We attempted to test for range stability using a phylogeographic approach by sequencing several noncoding regions of the chloroplast genome from *A. umbellata* collected across the geographic range, but detected only a single haplotype, except for one variant plant collected on one of the Channel Islands. The available data, although not definitive at this time, suggest that the geographic range of *A. umbellata* has been relatively stable over historic times (Samis & Eckert, 2007).

Conclusions and implications

The results of this study are consistent with the hypothesis that geographic variation in population and/or metapopulation dynamics selects for enhanced dispersal towards geographic range limits. Although the underpinnings of this interpretation must be tested in greater detail, our review of the theoretical

literature on dispersal evolution has not yielded a more likely alternative explanation for the pattern observed. Moreover, our results concur with those from other studies demonstrating increased dispersal potential in habitats where episodes of colonization are more frequent or have occurred more recently. Previous analyses of intraspecific variation in dispersal traits have revealed enhanced dispersal potential in putatively younger than older plant populations (Olivieri *et al.*, 1983; Peroni 1994; Cody & Overton, 1996), or in habitats that appear more prone to disturbance (O'Connell & Eckert, 2001). There have been very few studies of large-scale geographic variation in dispersal traits, although increased dispersal potential has been documented in populations towards expanding margins associated with post-glacial range expansion by pine trees (Cwynar & MacDonald, 1987), range shifting in response to climate change by insects (Thomas *et al.*, 2001; Hughes *et al.*, 2003; Simmons & Thomas, 2004) and rapid spread during biological invasion by a toad (Phillips *et al.*, 2006).

Dispersal has long been viewed as a key life history trait with manifold influences on the ecology and evolution of species (Clobert *et al.*, 2001; Levin *et al.*, 2003). Hence, the extent to which dispersal is evolutionarily labile will affect how organisms respond to spatio-temporal variation in the environment, which might be of particular relevance to predicting the effects of anthropogenic changes to habitat (Travis & Dytham, 1999; Kokko & López-Sepulcre, 2006). For example, it has been suggested that an evolutionary shift towards enhanced dispersal at expanding range margins may allow species to better track changing climates (Hughes *et al.*, 2003; Parmesan, 2006). Dispersal is a key parameter in theoretical models that attempt to explain the stability of limits to species' niches and geographic ranges (Holt *et al.*, 2005), and populations at these limits are often the focus of conservation and other management efforts (Lesica & Allendorf, 1995).

Theoretical models suggest that geographic range limits arise because selection for traits that improve fitness in marginal populations is opposed by gene flow from larger, more productive geographically central populations (for a review see Bridle & Vines, 2007). These models generally do not allow for geographic variation in demographic instability (Barton, 2001) or the evolutionary shifts in life history traits that might arise consequently. Range limits are explained by assuming that dispersal behaviour is fixed and asymmetries in dispersal between populations across the range arise from simple mass action, with the number of immigrants and emigrants moving in and out of populations depending solely on population size. Our results suggest that, for species whose dispersal can be altered by evolutionary modification of morphological or behavioural traits, there is the potential for more complex evolutionary dynamics between selection and gene flow in the establishment and maintenance of geographic range limits.

Acknowledgements

We thank Kate Neville, Christine Grace, John Glew and Onno Oostensen for help in the laboratory, Emily Austen for help in the field, Troy Day for helpful suggestions and Kathleen Donohue, Susan Mazer, Pierre-Olivier Cheptou, Sonia Sultan, Jeffrey Lam and William Mi for comments on the manuscript. We also thank the Canada–US Fulbright Foundation for a Visiting Research Chair at University California Santa Barbara to CGE and the Natural Sciences and Engineering Research Council of Canada for scholarships to E.D. and K.E.S. and a Discovery Grant to C.G.E.

References

- Barton NH. 2001. Adaptation at the edge of a species' range. In: Silvertown J, Antonovics J, eds. *Integrating ecology and evolution in a spatial context*. Oxford, UK: Blackwell Science, 365–392.
- Berg H. 2000. Differential seed dispersal in *Oxalis acetosella*, a cleistogamous perennial herb. *Acta Oecologica* 21: 109–118.
- Breckon GJ, Barbour MG. 1974. Review of the North American Pacific coast beach vegetation. *Madroño* 22: 333–360.
- Bridle JR, Vines TH. 2007. Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology & Evolution* 22: 140–147.
- Brown JH. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124: 255–279.
- Cadet C, Ferriere R, Metz JAJ, van Baalen M. 2003. The evolution of dispersal under demographic stochasticity. *American Naturalist* 162: 427–441.
- Carter RN, Prince SD. 1988. Distribution limits from a demographic viewpoint. In: Davy AJ, Hutchings MJ, Watkinson AR, eds. *Plant population ecology. The 28th symposium of the British ecological society*. London, UK: Blackwell Scientific, 165–184.
- Cheptou PO, Lepart J, Escarre J. 2001. Differential outcrossing rates in dispersing and nondispersing achenes in the heterocarpic plant *Crepis sancta* (Asteraceae). *Evolutionary Ecology* 15: 1–13.
- Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. 2001. *Dispersal*. Oxford, UK: Oxford University Press.
- Cody ML, Overton JM. 1996. Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* 84: 53–61.
- Cwynar LC, MacDonald GM. 1987. Geographical variation of lodgepole pine in relation to population history. *American Naturalist* 129: 463–469.
- Donohue K. 1999. Seed dispersal as a maternally influenced character: mechanistic basis of maternal effects and selection on maternal characters in an annual plant. *American Naturalist* 154: 674–689.
- Eckert CG, Samis KE, Dart S. 2006. Reproductive assurance and the evolution of uniparental reproduction in flowering plants. In: Harder LD, Barrett SCH, eds. *The ecology and evolution of flowers*. Oxford, UK: Oxford University Press, 183–203.
- Eckert CG, Samis KE, Loughheed SC. (in press). Genetic variation across species' geographic ranges: the central-marginal hypothesis and beyond. *Molecular Ecology*.
- Gandon S, Michalakis Y. 2001. Multiple causes of the evolution of dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. *Dispersal*. Oxford, UK: Oxford University Press, 155–167.
- Greene DF, Johnson EA. 1990. The aerodynamics of plumed seeds. *Functional Ecology* 4: 117–125.
- Greene DF, Johnson EA. 1997. Secondary dispersal of tree seeds on snow. *Journal of Ecology* 85: 329–340.
- Griffith TM, Watson MA. 2006. Is evolution necessary for range expansion? Manipulating reproductive timing of a weedy annual transplanted beyond its range. *American Naturalist* 167: 153–164.
- Hanski I, Eralahti C, Kankare M, Ovaskainen O, Siren H. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7: 958–966.
- Herlihy CR, Eckert CG. 2007. Evolutionary analysis of a key floral trait in *Aquilegia canadensis* (Ranunculaceae): genetic variation in herkogamy and its effect on the mating system. *Evolution* 61: 1661–1674.
- Holt RD, Keitt TH. 2000. Alternative causes for range limits: a metapopulation perspective. *Ecology Letters* 3: 41–47.
- Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML. 2005. Theoretical models of species' borders: single species approaches. *Oikos* 108: 18–27.
- Holt RD. 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* 5: 159–178.
- Hughes CL, Hill JK, Dytham C. 2003. Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceedings of the Royal Society of London Series B* 270: S147–S150.
- Johnson EA, Fryer GI. 1992. Physical characterization of seed microsites – movement on the ground. *Journal of Ecology* 80: 823–836.
- Kinlan BP, Hastings A. 2005. Rates of population spread and geographic expansion. What exotic species tell us. In: Sax DF, Stachowicz JJ, Gaines SD, eds. *Species invasions. Insights into ecology, evolution and biogeography*. Sunderland, MA, USA: Sinauer Associates, 381–419.
- Koelewijn HP. 2004. Sibling competition, size variation and frequency-dependent outcrossing advantage in *Plantago coronopus*. *Evolutionary Ecology* 18: 51–74.
- Kokko H, López-Sepulcre A. 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313: 789–791.
- Lesica P, Allendorf FW. 1995. When are peripheral populations valuable for conservation? *Conservation Biology* 9: 753–760.
- Levin SA, Muller-Landau HC, Nathan R, Chave J. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology Evolution and Systematics* 34: 575–604.
- Lönn M, Prentice HC. 2002. Gene diversity and demographic turnover in central and peripheral populations of the perennial herb *Gypsophila fastigiata*. *Oikos* 99: 489–498.
- McGlaughlin M, Karoly K, Kaye T. 2002. Genetic variation and its relationship to population size in reintroduced populations of pink sand verbenas, *Abronia umbellata* subsp. *breviflora* (Nyctaginaceae). *Conservation Genetics* 3: 411–420.
- Nantel P, Gagnon D. 1999. Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica*. *Journal of Ecology* 87: 748–760.
- Nathan R. 2006. Long-distance dispersal of plants. *Science* 313: 786–788.
- O'Connell LM, Eckert CG. 2001. Differentiation in reproductive strategy between sexual and asexual populations of *Antennaria parlinii* (Asteraceae). *Evolutionary Ecology Research* 3: 311–330.
- Olivieri I, Berger A. 1985. Seed dimorphism and dispersal: physiological, genetic and demographical aspects. In: Jacquard P, Heim G, Antonovics J, eds. *Genetic differentiation and dispersal in plants*. Berlin, Germany: Springer-Verlag, 413–429.
- Olivieri I, Gouyon P-H. 1997. Evolution of migration rate and other traits. In: Hanski IA, Gilpin MA, eds. *Metapopulation biology. Ecology, genetics and evolution*. San Diego, CA, USA: Academic Press, 293–323.
- Olivieri I, Michalakis Y, Gouyon P-H. 1995. Metapopulation genetics and the evolution of dispersal. *American Naturalist* 146: 202–228.
- Olivieri I, Swan M, Gouyon P-H. 1983. Reproductive systems and colonizing strategy of two species of *Carduus* (Compositae). *Oecologia* 60: 114–117.
- Pannell JR, Barrett SCH. 2000. Effects of populations size and metapopulation dynamics on a mating-system polymorphism. *Theoretical Population Biology* 59: 145–155.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37: 637–669.

- Peroni PA. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. *American Journal of Botany* **81**: 1428–1434.
- Phillips BL, Brown GP, Webb JK, Shine R. 2006. Invasion and the evolution of speed in toads. *Nature* **439**: 803–803.
- Quinn GP, Keough MJ. 2002. *Experimental design and data analysis for biologists*. Cambridge, UK: Cambridge University Press.
- R Development Core Team. 2006. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org>
- Ravigné V, Olivieri I, González-Martínez SC, Rousset F. 2006. Selective interactions between short-distance pollen and seed dispersal in self-compatible species. *Evolution* **60**: 2257–2271.
- Ronce O, Brachet S, Olivieri I, Gouyon PH, Clobert J. 2005. Plastic changes in seed dispersal along ecological succession: theoretical predictions from an evolutionary model. *Journal of Ecology* **93**: 431–440.
- Ronce O, Olivieri I, Clobert J, Danchin E. 2001. Perspective on the study of dispersal evolution. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, eds. *Dispersal*. Oxford, UK: Oxford University Press, 341–357.
- Sagarin RD, Gaines SD. 2002. The 'abundant centre' distribution: to what extent is it a biological rule? *Ecology Letters* **5**: 137–147.
- Samis KE, Eckert CG. 2007. Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology* **88**: 1747–1758.
- Schmitt J, Gamble SE. 1990. The effect of distance from the parental site on offspring performance and inbreeding depression in *Impatiens capensis*: a test of the local adaptation hypothesis. *Evolution* **44**: 2022–2030.
- Schurr FM, Bond WJ, Midgley GF, Higgins SI. 2005. A mechanistic model for secondary seed dispersal by wind and its experimental validation. *Journal of Ecology* **93**: 1017–1028.
- Simmons AD, Thomas CD. 2004. Changes in dispersal during species' range expansions. *American Naturalist* **164**: 378–395.
- Strauss SY, Karban R. 1994. The significance of outcrossing in an intimate plant–herbivore relationship. 1. Does outcrossing provide an escape from herbivores adapted to the parent plant. *Evolution* **48**: 454–464.
- Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, Conradt L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–581.
- Tillett SS. 1967. Maritime species of *Abronia* (Nyctaginaceae). *Brittonia* **19**: 299–327.
- Travis MJM, Dytham C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London, Series B* **266**: 723–728.
- Travis MJM, Dytham C. 2002. Dispersal evolution during invasions. *Evolutionary Ecology Research* **4**: 1119–1129.
- Vucetich JA, Waite TA. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. *Conservation Genetics* **4**: 639–645.
- Wang BC, Smith TB. 2002. Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**: 379–385.
- Wilson RC. 1972. *Abronia*: I. Distribution, ecology and habit of nine species of *Abronia* found in California. *Aliso* **7**: 421–437.
- Wilson RC. 1974. *Abronia*: II. Anthocarp polymorphism and anatomy for nine species of *Abronia* found in California. *Aliso* **8**: 113–128.
- Wilson RC. 1975. *Abronia*: III. Pericarp and seed coat anatomy and its ecological implications for nine species of *Abronia*. *Aliso* **8**: 289–299.
- Wilson RC. 1976. *Abronia*: IV. Anthocarp dispersibility and its ecological significance for nine species of *Abronia*. *Aliso* **8**: 493–506.

Supplementary Material

The following supplementary material is available for this article online:

Table S1 Locations of the populations of *Abronia umbellata* sampled across the species' geographic range for this study

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-8137.2007.02349.x>

(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the journal at *New Phytologist* Central Office.



About New Phytologist

- *New Phytologist* is owned by a non-profit-making **charitable trust** dedicated to the promotion of plant science, facilitating projects from symposia to open access for our Tansley reviews. Complete information is available at www.newphytologist.org.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as-ready' via *OnlineEarly* – our average submission to decision time is just 28 days. Online-only colour is **free**, and essential print colour costs will be met if necessary. We also provide 25 offprints as well as a PDF for each article.
- For online summaries and ToC alerts, go to the website and click on 'Journal online'. You can take out a **personal subscription** to the journal for a fraction of the institutional price. Rates start at £135 in Europe/\$251 in the USA & Canada for the online edition (click on 'Subscribe' at the website).
- If you have any questions, do get in touch with Central Office (newphytol@lancaster.ac.uk; tel +44 1524 594691) or, for a local contact in North America, the US Office (newphytol@ornl.gov; tel +1 865 576 5261).