

Can differences in autonomous selfing ability explain differences in range size among sister-taxa pairs of *Collinsia* (Plantaginaceae)? An extension of Baker's Law

April M. Randle, Jacob B. Snyder and Susan Kalisz

Department of Biological Sciences, University of Pittsburgh, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA

Summary

Author for correspondence:

April M. Randle

Tel: +1 412 624 4265

Email: apr8@pitt.edu

Received: 1 March 2009

Accepted: 27 May 2009

New Phytologist (2009) **183**: 618–629

doi: 10.1111/j.1469-8137.2009.02946.x

Key words: autonomous selfing, Baker's Law, *Collinsia*, elevational range, mating system.

- Species with greater selfing ability are predicted to be better adapted for colonizing new habitats (Baker's Law). Here, we tested an expansion of this hypothesis: that species proficient at autonomous selfing have larger range sizes than their less proficient sister taxa. We also tested competing hypotheses regarding seed production and niche breadth on range size.
- Floral traits affecting the proficiency of autonomous selfing were measured and seed production was calculated for six sister-taxa pairs in the clade *Collinsia*. We tested for the hypothesized effects of these variables on elevational distribution and range size.
- We found that species most proficient at selfing had significantly larger range sizes than their sister-taxa that were less proficient at selfing. Species proficient at autonomous selfing occupied a higher mean elevation than their sister taxa, but they did not differ in their total elevational range. Species with greater seed production did not have larger range sizes.
- Our results extend Baker's Law, suggesting that species proficient at autonomous selfing are better adapted to establish new populations and thus can more readily expand their range. Autonomous selfing ability may play a vital role in explaining variance in range size among other species.

Introduction

Why some plant species are narrowly distributed and others are widespread remains a fundamental question in the fields of ecology, evolution, biogeography and conservation biology (Brown *et al.*, 1996; Gaston, 1998; Holt & Keitt, 2005). Differences in the distribution of species have been attributed to a variety of factors including local and regional habitat conditions (e.g. geographic barriers, habitat availability and species interactions; reviewed in Brown *et al.*, 1996; Gaston, 1996); historical factors such as species age (Willis, 1922; Paul *et al.*, 2009); and species-level traits including dispersal and establishment (Böhning-Gaese *et al.*, 2006), fecundity (Lockwood *et al.*, 2005), niche breadth (McNaughton & Wolf, 1970; Brändle *et al.*, 2003), local abundance (Brown, 1984; Lawton, 1993), environmental or physiological tolerance (Brown *et al.*, 1996; Pither, 2002) and mating system (Henslow, 1879; Lowry & Lester, 2006). Of these possible influences on plant species distributions, mating system is of special interest

because it has long been held as a primary determinant of a species' success in establishing a breeding population in a novel location (e.g. Baker, 1955, 1967; Stebbins, 1957; Lloyd, 1980). Specifically, the ability to autonomously self-fertilize when mate availability is low has repeatedly been suggested as a key adaptive trait that increases the likelihood of successful colonization, establishment and population spread (e.g. Baker, 1955, 1967; Stebbins, 1957; Lloyd, 1980; Pannell & Barrett, 1998; Flinn, 2006). The ability to self-fertilize may also reduce the likelihood of extinction, if seed set can occur without mates or pollinators (Stebbins, 1950, 1957). If species that can autonomously self-fertilize are more likely to establish new breeding colonies and are less likely to become extinct after colonization, we hypothesize that they may also be expected to have larger range sizes than congeners of a similar age that are more outcrossing and less proficient at autonomous self-fertilization.

The relationship between range size and mating system was proposed over a century ago by Henslow (1879), who noted that most weedy plant species are self-fertilizing and that the

most widely distributed plants in Great Britain were also self-fertilizing. Thus, his general observations directly linked mating system with high colonization rates and large range size. This relationship remained mostly unaddressed until 1955, when Herbert Baker published a paper in *Evolution* entitled 'Self Compatibility and Establishment after Long-Distance Dispersal'. Baker proposed that a single propagule from a self-compatible (hermaphrodite) species was more likely to establish a viable population after long-distance dispersal than a self-incompatible (or dioecious) species, which would require at least two propagules to arrive at the same time and place. Baker noted that a high proportion of self-compatible species (or populations) were found in isolated locations (e.g. oceanic islands, isolated ponds; Baker, 1955; Longhurst, 1955). This pattern was strongly supported by Stebbins (1957 and references therein) and thought to be so general that Stebbins (1957) elevated it to the status of law (Baker's Law). Subsequent comparative studies showed a greater proportion of selfing species and greater propensity for selfing on islands compared with mainland sites and confirm these observations: Galapagos (McMullen, 1987), Hawaii (references in Baker, 1967 and Carr *et al.*, 1986), New Zealand (Webb & Kelly, 1993), the Juan Fernandez Islands (Anderson *et al.*, 2001; Bernardello *et al.*, 2001) and the Channel Islands (Schueller, 2004). In addition, shifts from dioecy to cosexuality (Cox, 1989; Sytsma & Smith, 1991; Pannell, 1997), and from heterostyly to homostyly (Barrett & Shore, 1987; Barrett *et al.*, 1989), were also noted after long-distance dispersal, which further suggests that traits which facilitate autonomous selfing can increase the probability of establishment after dispersal. However, selfing is not a requirement for successful range expansion (Abbott *et al.*, 2009).

More recently, the generality of the link between colonization and mating system has been expanded. While Baker (1955, 1967) focuses on the benefits of selfing after long-distance dispersal, Pannell & Barrett (1998) argue that the premise of Baker's Law should apply at any dispersal distance, stating, '... solitary selfers will always be more successful than obligate outcrossers in founding new colonies' (Pannell & Barrett, 1998, p. 657). In fact, increased selfing ability in colonizing species has been noted in several studies (Henslow, 1879; Baker, 1974; Lloyd, 1980; Price & Jain, 1981; Kelly, 1996; Schueller, 2004; Flinn, 2006). The logical extension from the empirical and theoretical investigations described earlier is that species which are proficient at autonomous selfing should be better colonizers in general, and thus should have larger range sizes than species which are self-incompatible or otherwise poor autonomous selfers.

In contrast to the above prediction, autonomously selfing species are also predicted to have relatively smaller range sizes than outcrossing (nonselfing) species because of low genetic diversity and narrow niche-breadth (Lowry & Lester, 2006). Selfing species typically have lower levels of genetic diversity than outcrossing species (e.g. Hamrick & Godt, 1990), and

thus populations founded by selfed individuals are predicted to have lower genetic diversity than those founded by outcrossed individuals (e.g. Carlquist, 1966; Crawford *et al.*, 2008). Lack of genetic diversity may limit colonization of new habitats because of an inability to adapt to novel environments (Stebbins, 1957; Levin, 1968; McNaughton & Wolf, 1970; Hedrick *et al.*, 1976; Pound *et al.*, 2004), resulting in narrow niche-breadth and small range size (McNaughton & Wolf, 1970; Moldenke, 1975; Thompson *et al.*, 1999; Lowry & Lester, 2006). Few studies have examined the relationship between niche-breadth and range size in plants. In a comparison of 31 weedy plant species, those species with narrower-germination niche-requirements were shown to have smaller range sizes than those with broader-germination niche-requirements (Brändle *et al.*, 2003). However, similar studies examining germination niche-breadth and range size have found weak (Thompson *et al.*, 1999) or equivocal (Thompson & Ceriani, 2003) support. Lowry & Lester (2006) tested the predictions of the niche-breadth hypothesis in *Clarkia*, and in a pairwise analysis of sister-taxa found that outcrossing species had larger range sizes than primarily selfing species (Lowry & Lester, 2006). Clearly, the relationship among genetic diversity, niche-breadth and range size is not well resolved. However, if we assume that more selfing species do indeed have lower genetic diversity than more outcrossing species, it is reasonable to expect that this may have consequences for niche-width and range size.

Selfing species may also differ from outcrossing species in seed production (Primack, 1987). Selfing species are known to have higher seed set (reviewed in Burd, 1994) and lower pollen per ovule ratios (Cruden, 1977) than outcrossing species. However, selfing and outcrossing species may also differ in floral display size. Thus, it is not well understood if selfers or outcrossers produce more seeds in general. Differences in seed production may be important because seed production has been shown to be an important trait affecting range expansion (reviewed in Lockwood *et al.*, 2005; Colautti *et al.*, 2006).

Clearly, mating system and autonomous selfing ability have the potential to strongly influence range size; however, the direction of influence is difficult to predict given the contrasting predictions referred to earlier. In addition, because multiple factors are expected to influence the range size over the evolutionary history of a species, phylogenetically controlled comparisons are required to correctly assess the effect of mating system on range size. If species' niches are relatively constrained over evolutionary time (i.e. phylogenetic niche conservatism; Wiens & Graham, 2005), closely related species are more likely to occupy similar habitats and to overlap in traits than distantly related species (Harvey & Pagel, 1991). Thus, if sister species differ in range size, we can test for key traits that have led to those differences.

Flower size is often assumed to be diagnostic of a species' or population's mating system (Takebayashi & Morrell, 2001),

but this assumption is not often verified. Here, we quantify mating-system traits that are widely expected to influence autonomous selfing ability (flower size, herkogamy, dichogamy, stigmatic receptivity and autonomous seed-set) of sister-taxa pairs of *Collinsia* (Plantaginaceae) to determine the effects of mating system on range size. If increased ability for autonomous selfing results in greater colonization and establishment of populations or lower extinction rates, then we expect selfing species to have larger range sizes than outcrossing species. By contrast, if low genetic diversity limits population expansion, then we expect that selfing species will have smaller range sizes than outcrossing species. In this study, we quantify three dimensions of species' ranges: their total geographic extent of occurrence (Gaston, 2003; maximum spread across the landscape as measured by minimum convex polygons); their elevational range size (total elevational spread as a measure of niche-breadth); and their elevational mean. We contrasted these range size metrics between sister-taxa pairs that differed significantly in their autonomous selfing ability. Finally, we compared seed production between sister-taxa pairs.

Materials and Methods

Study system

Collinsia is an excellent model system for this study because all members of the genus share similar life history and pollination traits (annual, bee-pollinated, native herbs), occupy similar habitats and are not considered to be weedy or ruderal species (Neese, 1993; Armbruster *et al.*, 2002). Importantly, all species are self-compatible, but because of differences in floral size and development, are expected to differ widely in their ability to autonomously self-pollinate (Armbruster *et al.*, 2002). The genus *Collinsia* is a monophyletic group of plants comprising *c.* 22 species (B. G. Baldwin *et al.*, unpublished data) that are exclusively short-lived winter or spring annuals native to North America. A new robust molecular phylogeny for *Collinsia* (B. G. Baldwin *et al.*, in prep.) allows us to identify sister-taxa pairs for comparison. The center of diversity for *Collinsia* is central California, but many of the western species extend into Oregon, Washington and British Columbia. In addition, three *Collinsia* species occur in eastern North America: *Collinsia parviflora* extends north to British Columbia and Alaska and east to Michigan and Ontario, while *Collinsia verna* and *Collinsia violaceae* are found exclusively in the eastern and central parts of the USA, respectively.

All species of *Collinsia* have zygomorphic flowers with a five-lobed calyx and a two-lipped corolla with a folded keel petal containing four stamens that develop sequentially. As in Kalisz *et al.* (1999), we define the developmental stage of a flower relative to the number of mature stamens exhibiting anther dehiscence (e.g. Stage 1 = one anther dehisced) in this study. Ovule number varies widely among species (ranging from 2 to 26 ovules per ovary, Armbruster *et al.*, 2002; S.

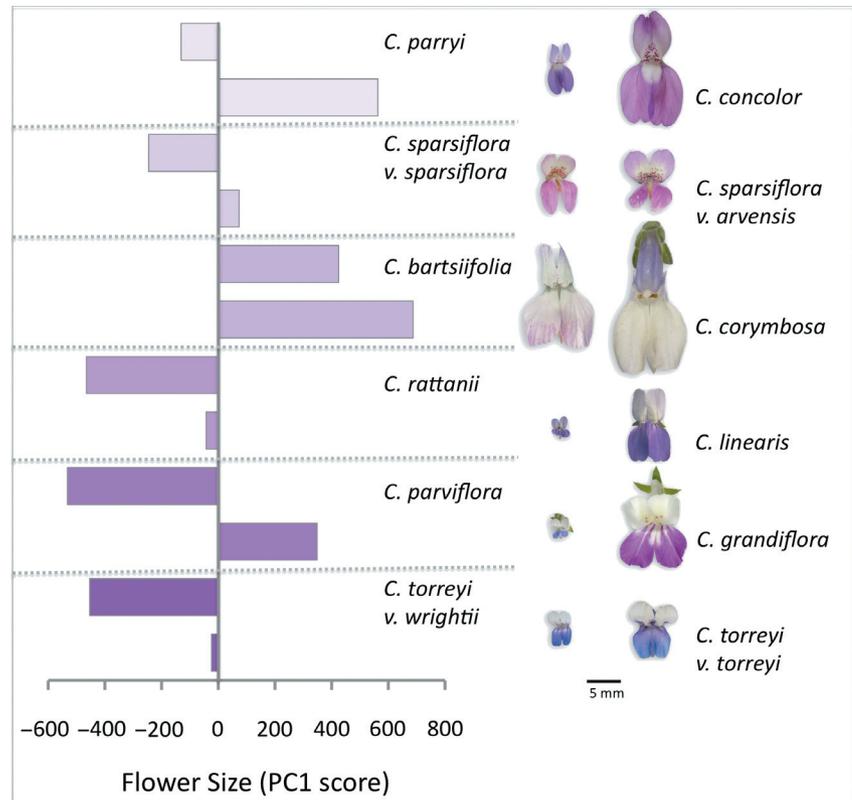
Kalisz & A. Randle, unpublished data) and can vary among populations within species (S. Kalisz & A. Randle, unpublished data). Flowers are borne in whorls, with display sizes ranging from *c.* 2 to 22 simultaneously open flowers in species across the genus. Bees are the primary visitors of all *Collinsia* species (Rust & Clement, 1977; Kalisz & Vogler, 2003; A. Randle, pers. obs.), even those considered highly selfing (A. Randle, unpublished data). Although all *Collinsia* species are self-compatible, proficiency at autonomous self-pollination varies among the taxa. *Collinsia* species have passively dispersed seeds, although some species are described as having winged seeds (Neese, 1993), including *Collinsia sparsiflora* (all varieties), *Collinsia tinctoria* and *Collinsia rattanii*. Differences in dispersal ability are not known among *Collinsia* species.

Selection of species pairs

We aimed to include sister-taxa pairs that were likely to differ in selfing ability. Because flower size is often used as a proxy for mating system (e.g. Grant, 1958; Jain, 1976; Takebayashi & Morrell, 2001), we selected sister taxa pairs within the genus *Collinsia* that differed significantly in flower size. To do this, we measured a suite of floral size and shape traits (three plants per population; one to three populations per species) across all *Collinsia* species. Flowers were collected from plants raised from field-collected seed under optimal conditions in the glasshouse facilities at the University of Pittsburgh. One mature flower from each plant was collected and preserved in 70% ethanol for up to 24 h before photographing. Lateral-view images of all flowers were made using a Hitachi KP-D50 digital camera affixed to a Nikon SMZ800 dissecting microscope. Images were captured using OPTIMUS 6.5 image-analysis software and stored for subsequent analysis. To describe the shape and size of flowers, we generated a shape-model template map in MATLAB, using the 'Point Model Editor' in the AAMToolbox (Hanna, 2006; Whibley *et al.*, 2006). For *Collinsia*, our template consisted of 76 points (8 primary points and 68 secondary points). These points were placed onto the scaled digital image of each flower at predefined intervals and locations to capture the shape and size information.

To analyze the floral variation among species, we conducted a principal components analysis (PCA) using the AAMToolbox (Hanna, 2006). Because we were interested in species-level comparisons, we used data from all available populations (one to three populations per species) in our analysis. The first three principal components (PC) described approx. 90% of the variation in floral shape and size across all taxa. PC1 corresponded to overall floral size, and accounted for 75% of the total variation among species. We used the PC1 scores of individual taxa to test for significant differences in floral size between sister taxa. In this study, sister taxa refers to both sister species or sister varieties, and thus we first tested for significant differences in floral size between the most closely related sister-taxa level in our phylogeny (e.g. variety). If flower sizes were not significantly

Fig. 1 Six sister-taxa pairs in the genus *Collinsia* that differ significantly in flower size, identified by principal component analysis (PCA). Principal component 1 (PC1) explains approx. 78% of the variation in flower size among all *Collinsia* species. Negative vs positive PC1 scores indicate species with smaller vs larger flowers than the genus average PC1 = 0, respectively. Note that species pairs are arranged by relative divergence times, with the *Collinsia torreyi* pair being the oldest taxon pair.



different between varieties, we pooled the varieties' data and compared flower size between sister species. Because sample sizes were generally small ($n = 3\text{--}9$ flowers per species), we used both an independent t -test and a Mann–Whitney U -test to compare flower size between sister taxa. The results did not differ between the two analyses. We found six pairs of sister taxa that differed significantly in flower size ($P < 0.05$): (1) *C. parryi* and *C. concolor*, (2) *C. sparsiflora* v. *sparsiflora* and *C. sparsiflora* v. *arvensis*, (3) *C. bartsifolia* (including v. *bartsifolia* and v. *dauidsonii*) and *C. corymbosa*, (4) *C. rattanii* and *C. linearis*, (5) *C. parviflora* and *C. grandiflora*, and (6) *C. torreyi* v. *wrightii* and *C. torreyi* v. *torreyi* (Fig. 1).

We compared floral traits among sister-taxa pairs that are known to correlate with species mating system, specifically the ability to autonomously self-pollinate. These traits included: stage of stigma–anther contact (S-AC); stage of stigma receptivity; autonomous fruit set; and proportion of floral life where the receptive stigma was in contact with the anthers. Species that are self-compatible can avoid self-pollination by spatial or temporal separation of male and female reproductive parts (herkogamy and dichogamy, respectively) or both. Highly selfing species, proficient at autonomous autogamy, reduce herkogamy and dichogamy early in floral development, whereas outcrossing species reduce herkogamy and dichogamy late in floral development or not at all (e.g. Lloyd, 1980; Lloyd, 1992; Bertin & Newnam, 1993; Schoen *et al.*, 1996; Kalisz *et al.*, 1999; Takebayashi & Morrell, 2001; Armbruster *et al.*,

2002; Kalisz & Vogler, 2003). In addition to mating-system traits, we also measured average seed production, mean elevation, elevational range size, and geographic range size of each species.

Stigma–anther contact

To determine the timing of S-AC, we scored the developmental stage of S-AC using one of two methods. First, *Collinsia* species of the focal sister-taxa were grown from field-collected seeds under optimal conditions in glasshouse facilities at the University of Pittsburgh. Stigma–anther contact was determined by depressing the lower petals of each sampled flower and noting the location of the stigma in relation to the position of the dehiscent anthers using either fresh or preserved flowers (two flowers in each stage on five plants per population from one to three populations per species ($n = 40\text{--}120$ flowers per species fresh sample; 20–40 flowers per species preserved samples). A subset of flowers never made S-AC during stages 1–4 and these flowers were given a score of 5. Second, in a subset of species (*C. concolor*, *C. grandiflora*, *C. linearis*, *C. rattanii*, *C. torreyi* v. *torreyi*) an additional measure of S-AC was made by scoring the presence/absence of pollen on stigmas at each developmental stage. One flower in each stage was collected from six individuals of each species listed above. To avoid accidental pollination, the two lateral petals were fastened to the sticky side of a Post-It Note™ (Kalisz *et al.*, 1999). This

allows the corolla to be depressed, the keel petal to be opened and the floral stage to be determined. Flowers still attached to the Post-It Note were placed under a dissecting microscope and the style was removed using a pair of fine dissecting scissors. The styles were mounted in a 1:1 solution of glycerol and 1% acetocarmine stain, and examined for the presence of pollen using a compound microscope ($\times 100$ magnification). We calculated the mean stage of S-AC for each individual plant (S-AC contact method) or population (pollen on stigma method). For the five species where both measures of S-AC were available, we pooled the data and compared the mean stage of S-AC between sister-taxa pairs.

Stigmatic receptivity

The stage of stigmatic receptivity is positively correlated with the stage when pollen tubes are first detected growing through the styles of *Collinsia* species (Armbruster *et al.*, 2002). The timing of stigmatic receptivity was determined by testing for stigmatic peroxidase activity (Kearns & Inouye, 1993; Kalisz *et al.*, 1999) across the four stages of flower development. Styles were excised from two fresh flowers in each stage from five plants per species (2 flowers \times 4 stages \times 5 plants = 40 flowers per species). Stigmas were examined for the presence of pollen and were only chosen if no pollen was present, as pollen on the stigma can result in false positives (Kearns & Inouye, 1993). Styles were placed on glass slides with 3% hydrogen peroxide and examined under a light microscope. If bubbling occurred within 2–3 min, the stigma was scored as receptive. Data were collected from plants grown in the glass-house facilities at the University of Pittsburgh under optimal conditions or from a natural population in the field (*C. concolor* only). The mean stage of stigmatic receptivity was calculated for each individual plant and a grand mean was calculated for the species.

Autonomous selfing ability

The relative percentage of ovules fertilized provides the best measure of autonomous autogamy ability because it scales seed production to the total number of seeds possible. However, we found that for several species in our study, ovule number is highly variable among individuals within a population. Because we did not measure ovule number for each plant used in our study, and the mean value was not accurate, we used the ability of an unmanipulated flower to make a fruit as our estimate of autonomous autogamy proficiency. We marked the calyx or subtending leaf of three flowers on each plant using nontoxic fabric paint ($n = 3$ flowers per plant \times (6 to 12) plants per species = 18–36 flowers per species). Marked flowers were monitored after corolla abscission to determine if a fruit containing at least one seed was produced. We had sufficient data to estimate the autonomous autogamy for 10 of our 12 species.

Proportion of total floral life when autonomous selfing can occur

To determine the proportion of total floral life when autonomous selfing can occur, we first determined floral longevity for each species. Six plants from each of one to three populations per species were grown together in a Conviron PGW36 growth chamber under optimal conditions. On each plant, six flower buds were marked with a unique color of nontoxic fabric paint on the calyx or subtending leaf ($n = 6$ flowers \times 6 plants \times (1 to 3) populations per species) = 36–108 flowers per species). Flowers were checked daily at approx 09:00 and 15:00 h, and the stage of development (as already described) was noted for each flower at each time point until the corolla abscised. Because some stage transitions occurred rapidly, we did not always capture each stage for each individual flower using our sampling scheme. Thus, to calculate total floral longevity for each individual, we calculated the average duration of each stage across all flowers per individual. We took the grand mean of the duration of each stage across individuals for each species, and summed these values across each stage to obtain the mean total floral longevity per species. To determine the proportion of a flower's life in which autonomous selfing can occur, we determined the mean stage at which the stigma was receptive *and* the stigma and anthers were in contact (receptive S-AC) for each species. We then used the data on the proportion of time that each species spent in each developmental stage to calculate the total proportion of floral life in which a flower was able to autonomously self-pollinate.

Seed production

We estimated seed production for each species by multiplying the average seed number per fruit by the median daily floral display size for each species. Average optimal seed production per fruit was quantified using three flowers per plant, from 6 to 12 plants per species. Each flower was uniquely marked with nontoxic fabric paint on the calyx or subtending leaf. Anthers were removed from the immature marked flowers, and hand pollinations were conducted with outcrossed pollen three times during the time period when the stigmas were receptive. Fruits were collected, and the number of seeds per fruit was counted. The mean number of seeds per fruit was determined for each individual. Flowers that failed to make fruit (0 seeds) were excluded from the analysis, as they were probably the result of a lack of successful pollinations. Because of low germination of *C. torreyi* v. *wrightii* and *C. torreyi* v. *torreyi*, we used the published maximum seed number per fruit for these species (two seeds per fruit for both). The median daily floral display size was determined from open flowers counted from photographs of plants in the field found at the Calflora (www.calflora.org) and USDAPlants (plants.usda.gov) websites. The range for the number of open flowers was recorded, and we used this data to calculate the median floral display size. Seed production

for each species was calculated as the maximum outcrossed seed number multiplied by median daily floral display size.

Species collections and range-size projections

To determine the range size for each species, we searched and collated latitude and longitude data for each *Collinsia* species from 25 herbaria collections using data provided by the participants of the Consortium of California Herbaria (ucjeps.berkeley.edu/consortium/), biodiversity occurrence data accessed through the Global Biodiversity Information Facility Data Portal (www.gbif.net) on 2008-12-01, Oregon Flora Project (<http://www.oregonflora.org/atlas.php>) and BC E-Flora (Klinkenberg, 2008, <http://www.eflora.bc.ca/>). We converted all location data from these collections to the NAD 27 coordinate system and used ArcGIS (9.2) to create point shapefiles for each species. The shapefiles were then projected in North America Albers Equal Area Conical Projection in order to preserve accuracy for area. The number of points contained in each species' shapefile varied considerably (9–954, median 38). The points included were collected over a 126-yr period (1881–2007). Hawth's Tools extensions for ArcGIS 9 were used to create minimum convex polygons about the points. Polygons for each species were clipped where they extended over water. Bruce Baldwin, curator of the UC Berkeley Jepson Herbarium, validated all point location data used in our maps. For species with multiple varieties, we only used collections where the variety was identified. To calculate range size for each species, we used X Tools Pro (5.2) to calculate the square kilometers of each polygon.

Elevational range sizes

Elevation data for each species were extracted from the Worldclim altitude layer (www.worldclim.org; ~1 km² resolution) with Diva-GIS (Hijmans *et al.*, 2001) using our geo-referenced herbarium collection records (referred to earlier). We measured niche width as the elevational range (i.e. maximum–minimum elevation) occupied by small- and large-flowered sister taxa.

Statistical tests

Differences in means for sister taxa in the traits flower size, S-AC, stage of stigmatic receptivity, autonomous selfing ability and mean elevation were each compared with an independent *t*-test and, if sample sizes were small, with a Mann–Whitney *U*-test. In all cases, the results of these two tests did not differ and only results from the *t*-test were used. To test for the general pattern of differences across all species pairs, we conducted a combined probability test using a Z-transform (Whitlock, 2005) of the *P* values from the above *t*-tests. Differences between sister pairs in the 'proportion of total floral life when autonomous selfing can occur' was compared across sister-taxa pairs using a paired *t*-test. Elevational range and seed production were compared using Wilcoxon's signed-rank tests.

Results

Flower size and mating system

Flower size differed significantly for all six sister-taxa pairs (*C. sparsiflora* v. *sparsiflora* and *C. sparsiflora* v. *arvensis* ($t = 4.02$, $df = 7$, $P = 0.0051$), *C. parryi* and *C. concolor* ($t = 17.1$, $df = 4$, $P = 0.001$), *C. bartsiiifolia* and *C. corymbosa* ($t = 3.88$, $df = 13$, $P = 0.0019$), *C. rattanii* and *C. linearis* ($t = 18.4$, $df = 14$, $P = 0.0001$), *C. parviflora* and *C. grandiflora* ($t = 21.4$, $df = 9$, $P = 0.0001$) and *C. torreyi* v. *wrightii* and *C. torreyi* v. *torreyi* ($t = 13.7$, $df = 7$, $P = 0.001$), Fig. 1). To determine if flower size is a good proxy for mating system for these species, we compared a suite of traits known to correlate with autonomous autogamy ability. Overall, we found that relative to the large-flowered species, the small-flowered sister species had stigmatic receptivity at a significantly earlier stage ($Z = 2.96$, $n = 6$, $P = 0.002$; Fig. 2a) and had significantly earlier S-AC contact ($Z = 4.67$, $n = 6$, $P = 0.0001$; Fig. 2b). In four of six sister taxa pairs, small-flowered species spent a greater proportion of their floral life span with the receptive stigma in contact with anthers that were shedding pollen (Fig. 2c). However, in a paired *t*-test across all six pairs of sister-taxa, this difference was only marginally significant ($t = 2.23$, $df = 5$, $P = 0.08$). Our autonomous fruit-set data complement these floral developmental results. In three of the five sister-pairs where we were able to test for differences in autonomous fruit set, we found that small-flowered species had significantly higher fruit set than large-flowered species. When we looked across all five pairs, we found that, overall, small-flowered species were significantly better at autonomously selfing and producing fruit in the absence of pollinators than their large-flowered sister-taxa ($Z = 3.12$, $n = 5$, $P < 0.001$; Fig. 2d). Therefore, relative flower size of sister taxa is a good estimator of their relative autonomous selfing ability in *Collinsia*.

Flower size (mating system), geographic range size, seed production, occupation of marginal (high elevation) habitat and elevational niche-breadth

Collinsia species with greater seed production (propagule pressure) did not have larger range sizes than their sister-taxa with lower seed production. In 5 of 6 sister-taxa pair comparisons, large-flowered species produced more seeds per capita than small-flowered species, yet had smaller range sizes. Across all sister-taxa pairs, differences in seed production were not significant (Wilcoxon's sign rank: small mean = 14.12, large mean = 35.56; $W = 13$, $n = 6$, $P > 0.05$; Fig. 3).

The mean elevation of small flowered species was significantly greater than their large flowered sister-taxa ($Z = 6.26$, $n = 6$, $P = 0.0001$; Fig. 4). However, small and large flowered sister taxa did not differ significantly in the mean elevational

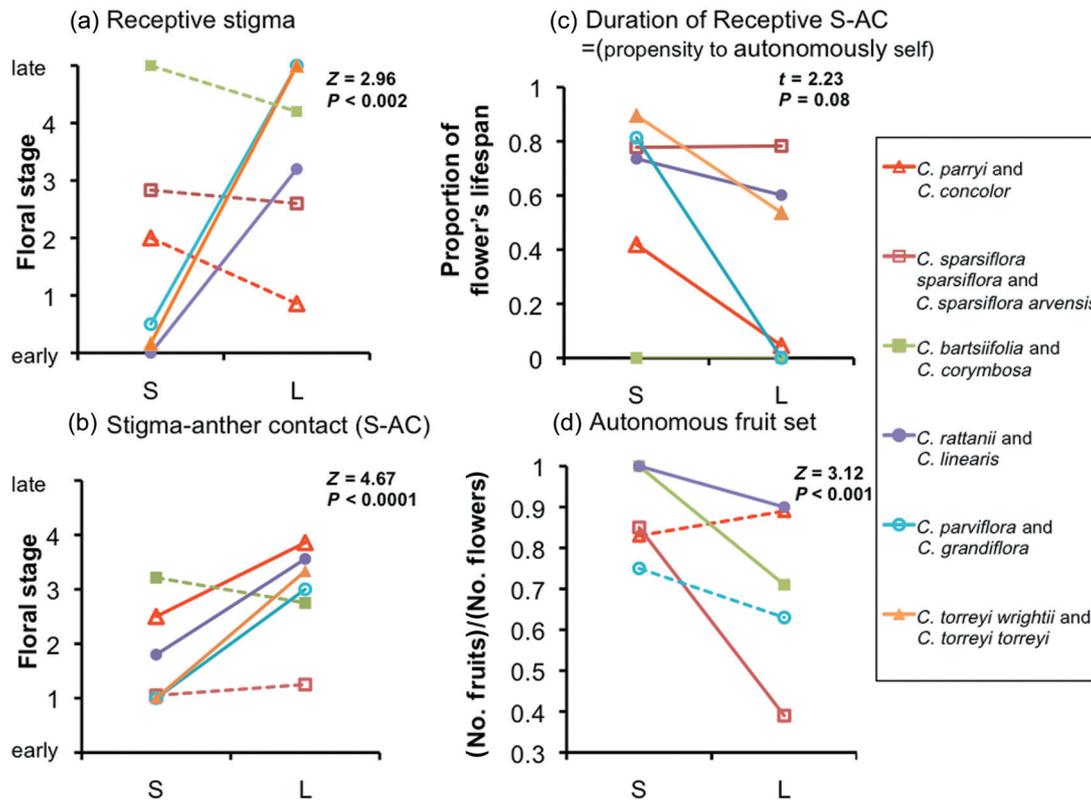


Fig. 2 Mean species values for small-flowered (S) and large-flowered (L) sister-taxa pairs. (a) Stigmatic receptivity, (b) stigma–anther contact (S-AC), (c) proportion of floral life span with receptive stigma in contact with dehiscent anthers (RS-AC) and (d) autonomous fruit set. Pairs connected by solid lines indicate significant differences between sister taxa in mean values; dotted lines indicate no significant difference between sister-taxa pairs. In (a, b), floral stage is the number of dehiscent anthers within a flower (see the text for details).

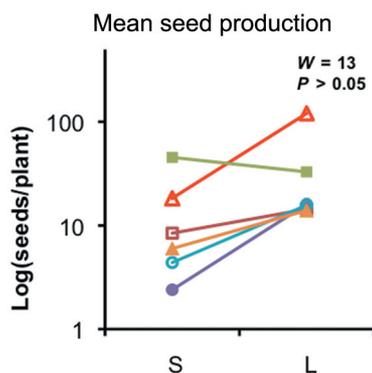


Fig. 3 Log of the mean seed production per plant in small (S) and large (L) sister-taxa pairs. Pairs connected by solid lines indicate significant differences between sister taxa in mean values; dotted lines indicate no significant difference between sister taxa. Species pair legend as in Fig. 2.

range size (e.g. elevational niche-breadth) (Wilcoxon's sign rank; $W = 7$, $n = 6$, $P = 0.2813$).

By contrast to the above results, mating system differences largely account for differences in range size in *Collinsia*. In all cases, small flowered species, which have significantly greater autonomous selfing ability, have significantly larger range

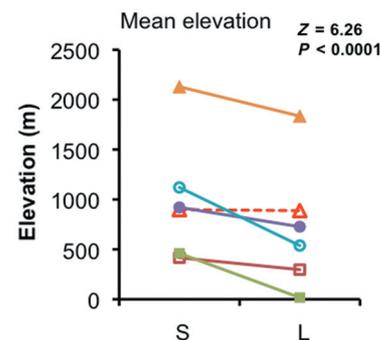


Fig. 4 Mean elevation of small (S) and large (L) sister-taxa pairs. Pairs connected by solid lines indicate significant differences between sister taxa in mean values; dotted lines indicate no significant difference between sister taxa. Species pair legend as in Fig. 2.

sizes than their large flowered sister-taxa (Wilcoxon's sign rank; $W = 21$, $n = 6$, $P < 0.030$; Fig. 5).

By contrast, seed production (propagule pressure) appears not to account for differences in range size. In five of six sister-taxa pair comparisons, large-flowered species produced more seeds per capita than small-flowered species; however, across all pairs, this difference was not significant (Wilcoxon's sign

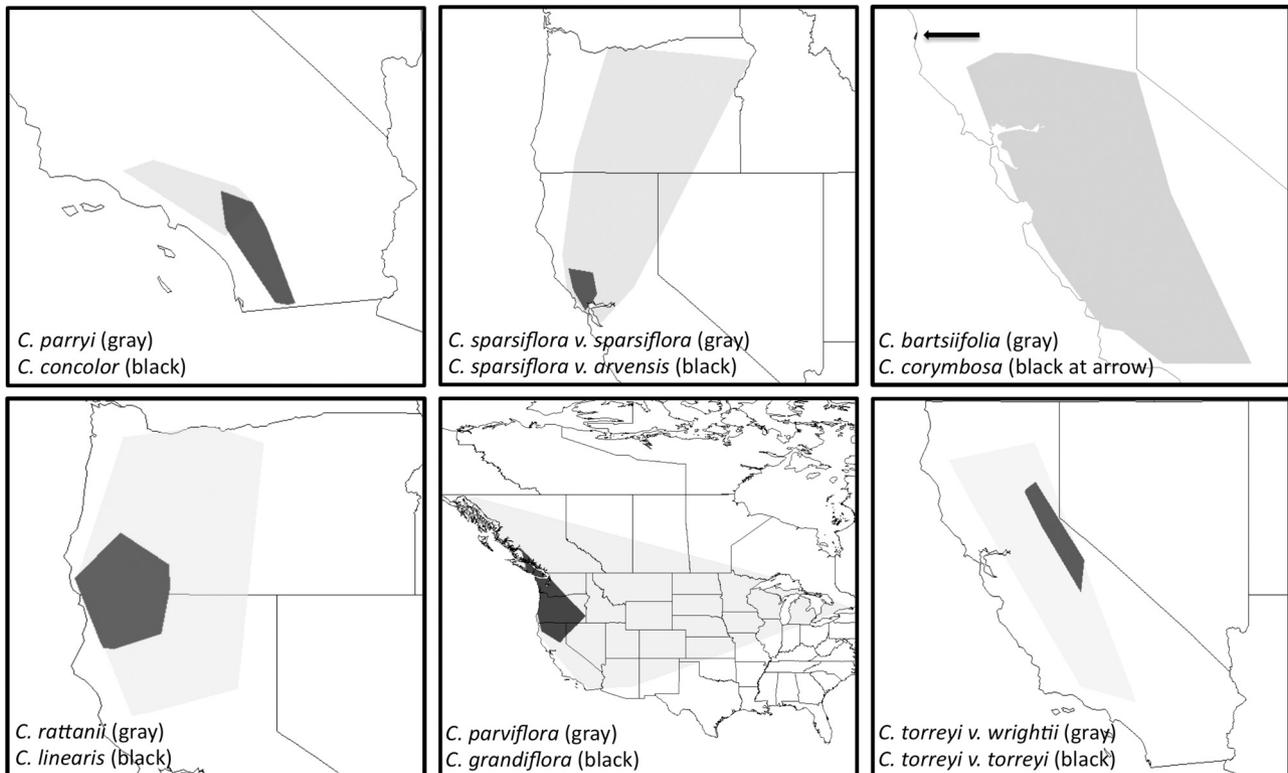


Fig. 5 Range maps for the six sister-taxa pairs in the genus *Collinsia* that differ significantly in flower size and autonomous selfing ability.

rank: small mean = 14.12, large mean = 35.56; $W = 13$, $n = 6$, $P > 0.05$; Fig. 3). This result suggests that in most, but not all, *Collinsia*, large-flowered taxa exert greater propagule pressure than their small-flowered sister taxa, but across all species, there is no significant difference in seed production.

The mean elevation of small-flowered species was significantly greater than their large-flowered sister taxa ($Z = 6.26$, $n = 6$, $P = 0.0001$; Fig. 4). However, small-flowered and large-flowered sister taxa did not differ significantly in the mean elevation range size (e.g. elevational niche-width) (Wilcoxon's sign rank; $W = 7$, $n = 6$, $P = 0.2813$).

Discussion

Our analysis of range size for *Collinsia* sister taxa supports the hypothesis that species which are more proficient at autonomous self-pollination have larger range sizes than their less proficient sister taxa. In all six sister-pair comparisons, species with traits associated with proficient autonomous self-fertilization had larger range sizes. To our knowledge, our analysis is only the second phylogenetically controlled test of the effects of mating system on range size. Surprisingly, our results contrast with those of Lowry & Lester (2006), who, in a pairwise comparison of *Clarkia* sister-taxa, concluded that outcrossing species have larger range sizes than selfing species. It is unclear why *Collinsia* and *Clarkia* would differ in this regard. Both genera are annual plants that occur in similar regions of North America (Lewis,

1993; Neese, 1993). *Clarkia* differs from *Collinsia* in the number of polyploid species in the genus, but these species were removed from their sister-pair analysis. Also, the *Clarkia* phylogeny was not as well resolved as the *Collinsia* phylogeny, containing many polytomies, which may have influenced their results. Also, polyploidy selfers in *Clarkia* are widespread (Lowry & Lester, 2006), whereas diploid selfers tend to be at the range margins of the genus (Gerber & Moeller, 2006). This distribution pattern may influence the range size of *Clarkia* species. Finally, many factors influence range size (Brown *et al.*, 1996; Gaston, 1996), and the benefits of selfing to colonization may play a relatively smaller role in *Clarkia*. As Pannell & Barrett's (1998) model suggests, if *Clarkia* species are common across the landscape, or if they have a seed bank, or if they experience relatively high inbreeding depression (Holtsford, 1996), the benefits of selfing (e.g. reproduction assurance) may not be realized. Our results for *Collinsia* extend Baker's Law (Baker, 1955; Stebbins, 1957) beyond the comparison of self-compatible and self-incompatible species to include a wider spectrum of the mating system.

Despite the fact that many studies find seed number or propagule pressure to be important in colonizing species (e.g. Lockwood *et al.*, 2005; Colautti *et al.*, 2006) we did not find that species with greater propagule pressure achieved larger range sizes. In our analysis, all five of the six sister taxa with low autonomous selfing ability had greater seed production than their sister-taxa, yet all had smaller range-sizes.

Our results also did not support what Lowry & Lester (2006) termed the Niche-breadth hypothesis. In contrast to their predictions, highly selfing species (with purportedly low genetic diversity) had larger range sizes than their outcrossing sister taxa. In addition, we found no difference between sister taxa in elevational range size (i.e. magnitude of elevational range occupied), which we used as a proxy for one dimension of niche breadth. Our data suggest that species with higher autonomous selfing ability did not suffer narrower niche-breadth or reduced range size as a result of low genetic diversity caused by the mating system. The autonomous selfing species may lack genetic variation, but may maintain beneficial gene complexes that confer an advantage for colonizing new habitat, which are not broken up by sexual reproduction (Stebbins, 1957). Alternatively, although the proficient autonomous selfers have a higher propensity for selfing in the absence of mates or pollinators, they are not strictly selfing in the long run, so they may not differ substantially in genetic diversity from their sister taxa. Supporting this idea, S. Kalisz (unpublished data) found that in some populations of the smallest-flowered *Collinsia* species, outcrossing rates calculated for wild-produced progeny arrays estimated using microsatellite markers can reach as high as 40–82%. These surprisingly high outcrossing rates suggest that the ability to autonomously self may buy time for the establishment of dense populations that are attractive to pollinators despite their small flower size. This idea is supported by observations of pollinators regularly visiting the small-flowered species *C. parviflora* and *C. rattanii* in the field (A. Randle, unpublished data).

We compared the mean elevation range between sister-taxa pairs to determine if small-flowered, highly selfing-species were more likely to inhabit high elevation sites than their large-flowered sister-taxa. Because all *Collinsia* species are annuals, with short life cycles and some level of self-compatibility, all *Collinsia* species should be relatively good at colonizing open, unsaturated, or temporary habitats with few mates or pollinators (Lloyd, 1980). However, those that are most proficient at selfing should be best at moving into these sites. High elevation sites have been shown to have a lower abundance of pollinators (Kalin-Arroyo *et al.*, 1985; Malo & Baonza, 2002), and may represent harsher environments than low elevation sites. Stressful environments, especially those with water stress, are known to favor reduced allocation to flower size in *Polemonium viscosum* (Galen, 1999, 2000), *Epilobium angustifolia* (Carroll *et al.*, 2001) and *Rosmarinus officinalis* (Herrera, 2005). The small-flowered *Collinsia* species occupied higher mean elevations than their large-flowered sister taxa. One interpretation of this is that the more highly selfing-species are able to move into more marginal-high elevation sites in part because they are also better at coping with a stressful environment. Conversely, autonomous selfing may be a by-product of correlated selection on flower size (Takabayashi & Morrell, 2001).

One assumption that we make is that sister species arise with similar range sizes. There is little evidence that range size

is heritable (Webb & Gaston, 2003; but see Waldron, 2007) and thus the range sizes of sister taxa are not necessarily expected to be similar. Differences in range size among sister taxa could be affected by the mode of speciation (Paul & Tonsor, 2008). In the case of peripatric speciation, the two sister species would begin with very different range sizes. Here, the small-flowered selfing species are most likely to evolve at the periphery of the large-flowered outcrossing species' range (Lloyd, 1965; Herlihy & Eckert, 2005; Moeller & Geber, 2007). If this were true, then we would expect small-flowered species to have, in general, smaller range sizes than their large-flowered sister taxa. This is clearly not the case for *Collinsia*. Alternatively, many peripheral populations of the 'selfing species' may evolve at the range margin of the large-flowered outcrossing species, resulting in a multiple 'selfing species' that are more closely related to their outcrossing sister-taxa progenitor than they are to each other. This would result in a ring of small flowered (selfing) daughter species surrounding the range of the outcrossing species. This could give the appearance of a larger range size for the small-flowered sister taxa using our methods of delineating range size. However, this does not appear to be the case with the majority of *Collinsia* species, because the small flowered taxa are found throughout the ranges of their large-flowered sister taxa, and not just at their margins. With a vicariance event, it is unlikely that sister taxa would arise with similar range sizes (Glazier, 1987; Price *et al.*, 1997; Gaston & Chown, 1999; Barraclough & Vogler, 2000; Webb *et al.*, 2001). Thus, as in peripheral isolates, sister-taxa may begin with very different range sizes, but which taxa has the small vs. the large range size should be random with respect to traits of the species. Regardless of starting conditions for range size when the *Collinsia* sister taxa split, our data show that over evolutionary time, the small-flowered selfing species obtain a larger range size than the large-flowered outcrossing species for all six sister-taxa pairs.

Although our data across all six species-pairs support the general pattern of larger range sizes for small-flowered selfing species, the difference in range size between *C. bartsiiifolia* and *C. corymbosa* is probably driven by additional ecological factors. While *C. bartsiiifolia* and *C. corymbosa* differ significantly in their flower size, and thus meet the criteria for inclusion in our study, *C. bartsiiifolia* (the smaller-flower species) has relatively large flowers within the genus (Fig. 1) and lacks many of the selfing traits of other small-flowered species (Fig. 2a–c). Interestingly, *C. bartsiiifolia* did have significantly greater autonomous fruit set than *C. corymbosa*. More importantly, unlike our other sister-taxa comparisons, *C. bartsiiifolia* and *C. corymbosa* inhabit strikingly different habitats. *C. corymbosa* is restricted to Pacific Ocean coastal dunes, while *C. bartsiiifolia* inhabits a broader range of habitat, including open sandy places (Neese, 1993). The limited distribution of *C. corymbosa* could be attributable to many factors, but little is known about the ecology of this endangered species. Thus, the large range size of *C. bartsiiifolia* may be, in part, a result of its relative proficiency at self-pollination, but we do not think that this is the

only factor driving the huge difference in range size between these two sister-taxa (Fig. 5). Rather, *C. corymbosa* is probably restricted in its range size by unmeasured ecological or physiological factors.

In summary, we attribute the majority of the differences in range size between sister taxa to differences in mating system and conclude that those species most proficient at autonomous selfing are best at establishing populations, and thus can more readily expand their range. Understanding the factors that contribute to range size differences among species is important to conservation. Factors that lead to range expansion are intimately related to processes that facilitate the establishment and spread of invasive and weedy species (Baker, 1974; Mack *et al.*, 2000). Likewise, factors that result in range contraction or limit expansion are critically important, as range size is inversely related to the probability of extinction (McKinney, 1997; Purvis *et al.*, 2000; Jones *et al.*, 2003; Gaston & Fuller, 2008). Our data clearly support the importance of the mating system, particularly autonomous selfing ability, as an adaptive trait that influences establishment success in a novel location. Species that can autonomously self-fertilize and establish new breeding colonies, but switch to outcrossing as their numbers increase locally, may provide an additional adaptive explanation for the prevalence of mixed mating. Hence, mating-system traits related to autonomous selfing may play a vital role in explaining variance in range size amongst species. Future studies that explore the relationship between mating system and range size in a variety of other taxa will help to shed light on the generality of this pattern.

Acknowledgements

We thank Bruce Baldwin, John Paul, Melisa Faigeless, David Chaiffetz, Aileen Butera and Ryan Unks for contributions and feedback on this manuscript. We also thank the Kalisz and Angert Labs for helpful discussions. This work was supported with an NSF DDIG (DEB 0709638) awarded to S. Kalisz and A. Randle and an NSF (DEB 0324764) awarded to S. Kalisz.

References

- Abbott RJ, Brennan AC, James JK, Forbes DG, Hegarty MJ, Hiscock SJ. 2009. Recent hybrid origin and invasion of the British Isles by a self-incompatible species, Oxford ragwort (*Senecio squalidus* L., Asteraceae). *Biological Invasions* 11: 1145–1158.
- Anderson GJ, Bernardello G, Stuessy TF, Crawford DJ. 2001. Breeding system and pollination of selected plants endemic to Juan Fernandez Islands. *American Journal of Botany* 88: 220–233.
- Armbruster SW, Mulder CPH, Baldwin BG, Kalisz S, Wessa B, Nute H. 2002. Comparative analysis of late floral development and mating-system evolution in Tribe Collinsieae (Scrophulariaceae s.l.). *American Journal of Botany* 89: 37–49.
- Baker HG. 1955. Self-compatibility and establishment after 'long-distance' dispersal. *Evolution* 9: 347–348.
- Baker HG. 1967. Support for Baker's law-as rule. *Evolution* 21: 853–856.
- Baker HG. 1974. The evolution of weeds. *Annual Reviews* 5: 1–24.
- Barracough TG, Vogler AP. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. *The American Naturalist* 155: 419–434.
- Barrett SCH, Morgan MT, Husband BC. 1989. The dissolution of a complex genetic polymorphism: the evolution of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae). *Evolution* 43: 1398–1416.
- Barrett SCH, Shore JS. 1987. Variation and evolution of breeding systems in the *Turnera ulmifolia* complex (Turneraceae). *Evolution* 41: 340–354.
- Bernardello G, Anderson GJ, Stuessy TF, Crawford DJ. 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Botanical Review* 67: 255–308.
- Bertin RI, Newnam CM. 1993. Dichogamy in angiosperms. *Botanical Review* 59: 112–152.
- Biodiversity occurrence data provided by: (Accessed through GBIF Data Portal, www.gbif.net, 2008-10-01 to 2008-12-31)
- Böhning-Gaese K, Caprano T, van Ewijk K, Veith M. 2006. Range size: eisentangling current traits and phylogenetic and biogeographic factors. *The American Naturalist* 167: 555–567.
- Brändle M, Stadler J, Klotz S, Brandl R. 2003. Distributional range size of weedy plant species is correlated to germination patterns. *Ecology* 84: 136–144.
- Brown JH. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124: 255–279.
- Brown JH, Stevens GC, Kaufman DM. 1996. The geographic range: size, shape, boundaries and internal structure. *Annual Review of Ecology and Systematics* 27: 597–623.
- Burd M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *The Botanical Review* 60: 83–139.
- Carlquist S. 1966. The biota of long-distance dispersal. IV. Genetic systems in the floras of oceanic islands. *Evolution* 20: 433–455.
- Carr GD, Powell EA, Kyhos DW. 1986. Self-incompatibility in the Hawaiian Madiinae (Compositae): an exception to Baker's Rule. *Evolution* 40: 430–434.
- Carroll AB, Pallardy SG, Galen C. 2001. Drought stress, plant water status, and floral trait expression in fireweed, *Epilobium angustifolium* (Onagraceae). *American Journal of Botany* 88: 438–446.
- Colautti RI, Grigorovich IA, MacIsaac HJ. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8: 1023–1037.
- Cox PA. 1989. Baker's Law: plant breeding systems and island colonization. In: Bock JH, Linhart YB, eds. *The evolutionary ecology of plants*. Boulder, CO, USA: Westview Press, 209–224.
- Crawford DJ, Archibald JK, Stroemer D, Mort ME, Kelly JK, Santos-Guerra A. 2008. A test of Baker's Law: Breeding systems and the radiation of *Tolpis* (Asteraceae) in the Canary Islands. *International Journal of Plant Science* 169: 782–791.
- Cruden RW. 1977. Pollen-ovule ratios: a conservative indicator of breeding system in flowering plants. *Evolution* 31: 32–46.
- Flinn KM. 2006. Reproductive biology of three fern species may contribute to differential colonization success in post-agricultural forests. *American Journal of Botany* 93: 1289–1294.
- Galen C. 1999. Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. *Bioscience* 49: 631–640.
- Galen C. 2000. High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum* (Polemoniaceae). *The American Naturalist* 156: 72–83.
- Gaston KJ. 1996. Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution* 11: 197–201.
- Gaston KJ. 1998. Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 353: 219–230.
- Gaston KJ. 2003. *The structure and dynamics of geographic ranges*. New York, NY, USA: Oxford University Press.

- Gaston KJ, Chown SL. 1999. Geographic range size and speciation. In: Magurran AE, May RM, eds. *Evolution of biological diversity*. Oxford, UK: Oxford University Press, 236–259.
- Gaston KJ, Fuller RJ. 2008. Commonness, population depletion and conservation biology. *Trends in Ecology and Evolution* 23: 14–19.
- Gerber MA, Moeller DA. 2006. Pollinator responses to plant communities and implications for reproductive character evolution. In: Harder LD, Barrett SCH, eds. *Ecology and evolution of flowers*. Oxford, UK: Oxford University Press, 102–116.
- Glazier DS. 1987. Toward a predictive theory of speciation – the ecology of isolate selection. *Journal of Theoretical Biology* 126: 323–333.
- Grant V. 1958. The regulation of recombination in plants. *Cold Springs Harbor Symposium on Quantitative Biology* 23: 337–363.
- Hamrick JL, Godt M. 1990. Effects of life-history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 351: 1291–1298.
- Hanna AI. 2007. *AAMToolbox user guide*. Norwich, UK: John Innes Centre.
- Harvey PH, Pagel MD. 1991. *The comparative methods in evolutionary biology*. Oxford, UK: Oxford University Press.
- Hedrick PW, Ginevan ME, Ewing EP. 1976. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics* 7: 1–32.
- Henslow G. 1879. On the self-fertilization of plants. *Transactions of the Linnean Society of London* 1: 317–398.
- Herlihy CR, Eckert CG. 2005. Evolution of self-fertilization at geographical range margins? A comparison of demographic, floral, and mating system variables in central vs. peripheral populations of *Aquilegia Canadensis* (Ranunculaceae). *American Journal of Botany* 92: 744–751.
- Herrera J. 2005. Flower size variation in *Rosmarinus officinalis*: Individuals, Populations and Habitats. *Annals of Botany* 95: 431–437.
- Hijmans RJ, Guarino L, Cruz M, Rojas E. 2001. Computer tools for spatial analysis of plant genetic data: 1. DIVA-GIS. *Plant Genetic Resources Newsletter* 127: 15–19.
- Holt RD, Keitt TH. 2005. Species' borders: a unifying theme in ecology. *Oikos* 108: 3–6.
- Holtsford TP. 1996. Variation in inbreeding depression among families and populations of *Clarkia tembloriensis* (Onagraceae). *Heredity* 76: 83–91.
- Jain SK. 1976. The evolution of inbreeding in plants. *Annual Review of Ecology and Systematics* 7: 469–495.
- Jones KE, Purvis A, Gittleman JL. 2003. Biological correlates of extinction risk in bats. *The American Naturalist* 161: 601–614.
- Kalin-Arroyo MT, Armesto JJ, Primack RB. 1985. Community studies in pollination ecology in the high temperate Andes of central Chile II. Effect of temperature on visitation rates and pollination possibilities. *Plant Systematics and Evolution* 149: 187–203.
- Kalisz S, Vogler D. 2003. Benefits of autonomous selfing under unpredictable pollinator environments. *Ecology* 84: 2928–2942.
- Kalisz S, Vogler D, Fails M, Shepard FE, Herman T, Gonzales R. 1999. The mechanism of delayed selfing in *Collinira verna* (Scrophulariaceae). *American Journal of Botany* 86: 1239–1247.
- Kearns CA, Inouye DW. 1993. *Techniques for pollination biologists*. Niwot, CO, USA: University Press of Colorado.
- Kelly CK. 1996. Identifying plant functional types using floristic data bases: Ecological correlates of plant range size. *Journal of Vegetation Science* 7: 417–424.
- Klinkenberg B. ed. 2008. E-Flora BC: Electronic Atlas of the Plants of British Columbia. Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, Vancouver. URL: www.e flora.bc.ca. [accessed 2008-12-01].
- Lawton JH. 1993. Range, population abundance and conservation. *Trends in Ecology and Evolution* 8: 409–413.
- Levin DA. 1968. Breeding system of *Lithospermum carolinense* – adaptation and counteradaptation. *The American Naturalist* 102: 427–441.
- Lewis H. 1993. *Clarkia*. In: Hickman JC, ed. *The Jepson manual: higher plants of California*. Berkeley CA, USA: University of California Press, 786–793.
- Lloyd DG. 1965. Evolution of self-compatibility and social differentiation in *Leavenworthia* (Cruciferae). *Contributions of the Gray Herbarium, Harvard* 195: 3–133.
- Lloyd DG. 1980. Demographic factors and mating patterns in angiosperms. In: Solbrig OT, ed. *Demography and evolution in plant populations*. Berkeley and Los Angeles, CA, USA: University of California Press, 67–88.
- Lloyd DG. 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Science* 153: 370–380.
- Lockwood JL, Cassey P, Bmackburn T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20: 223–228.
- Longhurst AR. 1955. Evolution of the Notostraca. *Evolution* 9: 84–86.
- Lowry E, Lester SE. 2006. The biogeography of plant reproduction: potential determinants of species' range sizes. *Journal of Biogeography* 33: 1975–1982.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.
- Malo JE, Baonza J. 2002. Are there predictable clines in plant-pollinator interactions along altitudinal gradients? The example of *Scoparius* (L.) Link in the Sierra de Guadarrama (Central Spain). *Diversity and Distributions* 8: 365–371.
- McKinney ML. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28: 495–516.
- McMullen CK. 1987. Breeding systems of selected Galápagos Islands angiosperms. *American Journal of Botany* 74: 1694–1705.
- McNaughton SJ, Wolf LL. 1970. Dominance and the niche in ecological systems. *Science* 167: 131–139.
- Moeller DA, Geber MA. 2007. Ecological context of the evolution of self-pollination in *Clarkia xantiana*: population size, plant communities and reproductive assurance. *Evolution* 59: 786–799.
- Moldenke AR. 1975. Niche specialization and species diversity along a California transect. *Oecologia* 21: 219–242.
- Neese EC. 1993. *Collinsia*. In: Hickman JC, ed. *The Jepson manual: higher plants of California*. Berkeley, CA, USA: University of California Press, 1024–1027.
- Pannell JR. 1997. Widespread functional androecy in *Mercurialis annua* L. (Euphorbiaceae). *Biological Journal of the Linnean Society* 61: 95–116.
- Pannell JR, Barrett SCH. 1998. Baker's Law revisited: Reproductive assurance in a metapopulation. *Evolution* 52: 657–668.
- Paul JR, Morton C, Taylor CM, Tonsor SJ. 2009. Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant genus *Pycotria* (Rubiaceae). *The American Naturalist* 173: 188–199.
- Paul JR, Tonsor SJ. 2008. Explaining geographic range size by species age: a test using Neotropical *Piper* species. In: Carson WP, Schnitzer S, eds. *Tropical forest community ecology*. Oxford, UK: Blackwell Publishing, 46–62.
- Pither J. 2002. Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society of London Series B, Biological Sciences* 270: 475–481.
- Pound GE, Cox SJ, Doncaster CP. 2004. The accumulation of deleterious mutations within the frozen niche variation hypothesis. *Journal of Evolutionary Biology* 17: 651–662.
- Price SC, Jain SK. 1981. Are inbreeders better colonizers? *Oecologia* 49: 283–286.
- Price TD, Helbig AJ, Richman AD. 1997. Evolution of breeding distribution in the old world leaf warblers (genus *Phylloscopus*). *Evolution* 51: 552–561.
- Primack RB. 1987. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* 18: 409–430.
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London Series B, Biological Sciences* 267: 1947–1952.

- Rust RW, Clement SL. 1977. The biology of *Osmia glauca* and *Osmia nemoris* (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 45: 523–528.
- Schoen DJ, Morgan MT, Bataillon T. 1996. How does self-pollination evolve? Inferences from floral ecology and molecular genetic variation. *Philosophical Transactions of the Royal Society of London. B. Biological Science* 351: 1281–1290.
- Schueller SK. 2004. Self-pollination in island and mainland populations of the indroduced hummingbird-pollinated plant *Nicotiana glauca* (Solanaceae). *American Journal of Botany* 91: 672–681.
- Stebbins GL. 1950. *Variation and evolution in plants*. New York, NY, USA: Columbia University Press.
- Stebbins GL. 1957. Self-fertilization and population variability in higher plants. *The American Naturalist* 91: 337–354.
- Sytsma KJ, Smith JF. 1991. The use of chloroplast DNA to assess biogeography and evolution of morphology, breeding systems, and flavanoids in *Fuchsia* sect. *Skinnera* (Onagraceae). *Systematic Botany* 16: 257–269.
- Takebayashi N, Morrell PL. 2001. Is self-fertilization an evolutionary dead end? Revisiting an old hypothesis with genetic theories and a macroevolutionary approach. *American Journal of Botany* 88: 1143–1150.
- Thompson K, Ceriani RM. 2003. No relationship between range size and germination niche width in the UK herbaceous flora. *Functional Ecology* 17: 335–339.
- Thompson K, Gaston KJ, Baud SR. 1999. Range size, dispersal, and niche-breadth in the herbaceous flora of central England. *Journal of Ecology* 87: 150–155.
- Waldron A. 2007. Null models of geographic range size evolution reaffirm its heritability. *The American Naturalist* 170: 221–231.
- Webb CJ, Kelly D. 1993. The reproductive biology of the New Zealand flora. *Trends in Ecology and Evolution* 8: 442–447.
- Webb TJ, Gaston KJ. 2003. On the heritability of geographic range sizes. *The American Naturalist* 161: 553–556.
- Webb TJ, Kershaw M, Gaston KJ. 2001. Rarity and phylogeny in birds. In: Lockwood JL, McKinney ML, eds. *Biotic homogenization*. New York, NY, USA: Kluwer-Plenum, 57–80.
- Whibley AC, Langlade NB, Andalo C, Hanna IA, Bangham A, Thébaud C, Coe E. 2006. Evolutionary paths underlying flower color variation in *Antirrhinum*. *Science* 313: 963–966.
- Whitlock MC. 2005. Combining probability from independent tests: the weighted Z-method is superior to Fisher's approach. *Journal of Evolutionary Biology* 18: 1368–1373.
- Wiens JJ, Graham CH. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36: 519–539.
- Willis JC. 1922. *Age and area*. Cambridge, UK: Cambridge University Press.



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 *Early View* – our average submission to decision time is just 29 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 £139 in Europe/\$259 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).