

CONGRUENCE BETWEEN GEOGRAPHIC RANGE DISTRIBUTION AND LOCAL COMPETITIVE ABILITY OF TWO *LUPINUS* SPECIES¹

RUBÉN MILLA², ADRIÁN ESCUDERO, AND JOSÉ M. IRIONDO

Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, c/ Tulipán s/n., E-28933 Móstoles, Madrid, Spain

- **Premise of the study:** In spite of its relevance, we lack rigorous evidence on whether widespread species are superior local competitors compared with coexisting narrowly distributed congeners. We ran a competition experiment between two lupins that coexist at their shared geographic range: *Lupinus angustifolius* L. (widespread) and *L. gredensis* Gandoger (narrow endemic).
- **Methods:** We set up mixed and monospecific populations of the two species, monitored survival and fecundity until the death of the whole cohorts, and measured variables of putative relevance to the competition process. We used aster modeling to address lifetime individual fitness and generalized linear models to assess the effect of species, type of competition, and competition environment on a suite of competition indices.
- **Key results:** *Lupinus angustifolius* showed higher fitness and exerted a stronger competitive effect on its heterospecific neighbors. This occurred through higher fecundity late in the season rather than through differential survival at earlier stages.
- **Conclusions:** This is the first evidence of lifetime superior competitive potential of a widespread species over a narrow endemic congener. This competitive response might scale up to the geographic distribution range and may partially explain the limited distribution of the narrow endemic. Extension to other carefully selected study cases and more in-depth field experiments may help to assess the generality of this pattern and understand how local processes translate into geographic patterns.

Key words: aster models; competition; geographic distribution; lifetime fitness; *Lupinus*; narrow endemics.

The success of a particular species in occupying space is highly variable. What shapes the extent of geographic occurrence of species has been of primary interest for research in animal and plant sciences (Gaston, 2009). This topic remains a basic and still poorly resolved research question for biogeographers.

Biotic interactions are increasingly being recognized as relevant drivers of species geographical boundaries. In plant sciences, interactions with specialized mutualists such as pollinators, commensalists such as nurse plants, competitors, or predators are suggested to constrain or expand species ranges (Lavergne et al., 2005; Holt and Barfield, 2009). One special case of competition arises from the co-occurrence of two congeneric species. Because congeneric species share many morphological and physiological traits, competition between them is frequently more intense than between unrelated species (Silvertown et al., 2001, but see Losos, 2008). If coexisting congeners differ markedly in the extent of their geographic occupancy, the widespread species is argued to be a superior competitor to the narrowly distributed counterpart, which may contribute to constraining the expansion of the narrowly distributed congener and thus help explain its narrow range (Griggs, 1940; Drury, 1974; Lavergne et al., 2003; Saldaña et al., 2005; Matesanz et al., 2009).

The idea that widespread plant species are superior competitors to their narrowly distributed congeners is mostly supported by indirect evidence (see, e.g., references in previous paragraph), whereas information coming from more direct experimental approaches is scarce. A literature search of competition experiments between widespread and narrow endemic congeners yielded only six studies (Appendix S1, see Supplemental Data with the online version of this article), the results of which are inconclusive. Three studies assigned higher competitive ability to the widespread species, two reported context-dependent results, and one experiment found equal competitive ability of the widespread and narrow endemic species (Gottlieb and Bennett, 1983; Prober, 1992; Aplet and Laven, 1993; Snyder et al., 1994; Walck et al., 1999; Bush and van Auken, 2004). Thus, given the current knowledge, there is little room for generalization or support of the putative superior local competitive abilities of widespread species. Moreover, distinguishing the superior competitor from a lifetime fitness viewpoint is not an easy task, considering lifetime fitness as the number of viable offspring produced by an individual throughout its whole life cycle. None of the previous experiments uses lifetime fitness estimates as comparative performance metrics.

The study of lifetime fitness has been hindered because the two most relevant components for its estimation, survival and reproductive success, are analyzed separately (see, e.g., Shaw, 1986; Milla et al., 2009). For example, in a narrow vs. widespread competition experiment, one species may have higher survivorship, whereas its survivors may produce fewer offspring than those of its competitor. Because survival and reproduction cannot be assessed jointly, we cannot assign superior competitiveness to either of the species. However, the recent release of aster models permits the examination of survivorship and reproductive fitness in a single joint analysis (Geyer et al., 2007; Shaw et al., 2008). We used aster models to estimate individual fitness integrated over the whole lifetime of each seed

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²Author for correspondence (e-mail: ruben.milla@gmail.com); phone: +34 91 4888517; fax: +34 91 6647490

sown in our experiment in a single statistical analysis. In spite of the qualitative advancement introduced by aster models, few empirical studies have made use of them to date (Lowry et al., 2008; Wagenius et al., 2009; Leinonen et al., 2010; Ridley and Ellstrand, 2010; Shaw and Geyer, 2010; Westberg et al., 2010).

Here we report results of a widespread vs. narrow endemic competition experiment in which we simulated field growing conditions and followed the fate of single seeds of each species from germination to the production of the next generation offspring, integrating all demographic processes. This approach imitates a seed dispersal event in a local plant community that harbors either mixed or monospecific populations of the two species. In this experimental setting, we controlled several factors that could modulate the interaction between both congeners, such as seed size, which is a surrogate of early maternal provisioning for seedling growth; genetic relatedness between interacting individuals of the same species; and the presence and abundance of other constituents of the plant community. We calculated several indices of competition in addition to fitness estimates of competition intensity.

The overall aim of our experiment was to test whether a widespread Mediterranean annual lupin (*Lupinus angustifolius* L.) is a local competitor superior to a coexisting narrow endemic congener that inhabits mountain inland areas in the western Iberian Peninsula (*L. gredensis* Gand.). Additionally, to dissect the competitive process, understand the specific life stages most affected by the interaction, and integrate the relative relevance of processes other than competition that occur after a dispersal event in the wild, we addressed the following specific questions. If present, do differences in lifetime fitness between competitors occur during survival processes, or do they happen later during the reproduction of survivors? Do factors like initial seed size, intraspecific genetic relatedness, or the presence and abundance of other species in the plant community differentially affect individual fitness of the two species?

MATERIALS AND METHODS

Study species and seed collection—The study species were two annual legumes, *Lupinus angustifolius* L., widespread across the Mediterranean Basin, and *Lupinus gredensis*, a narrow endemic of inland mountainous areas in the western Iberian Peninsula (online Appendix S2). Both species are very close phylogenetically, clustered in the Malacospermae section (Käss and Wink, 1997). *Lupinus angustifolius* branches either from the base of the plant or a few centimeters above the soil surface, and it tends to be somewhat taller than *L. gredensis*, which almost always branches from the base (Castroviejo and Pascual, 1990). Leaflets of *L. angustifolius* are narrower than those of *L. gredensis*, and flowers arrange alternately in apical inflorescences in the former and in whorls in the apical inflorescences of the latter species (Castroviejo and Pascual, 1990). Typical seed sizes of both species are equally variable with similar medians, ranging from 4 to 8 mm in diameter (Castroviejo and Pascual, 1990). Both occur in Iberian annual pastures and also inhabit environments subjected to frequent disturbance, such as road or forest edges. *Lupinus angustifolius* grows across a wider altitude range than *L. gredensis*, and both species grow preferentially on acid sandy soils, though *L. angustifolius* also thrives in neutral pH soils (Castroviejo and Pascual, 1990). In the geographic area where the ranges of the two species overlap, they share microhabitat affinities. Thus, they are frequently found co-occurring in the same ephemeral plant communities. Small-scale spatial coexistence of individuals of both species, which provides ground for plant–plant competitive interactions to occur, was the specific criteria followed to select this pair of species as the study system. In our study area, we did not find any interspecific hybrids. Although they have been previously described (Rivas-Goday, 1957), they are seldom found. These species are well suited for this experiment because of their short life cycles, with seeds germinating in late autumn and plants senescing by early summer, which allows

assessment of lifetime fitness. Also, they are predominantly passive selfers, and when outcrossing takes place, flowers are pollinated by an assembly of widely distributed generalist pollinators (see Forbes et al., 1971, for *L. angustifolius*). Consequently, reproduction is not likely to depend on the local assemblage of pollinators when grown in experimental settings. Moreover, seeds are heavy (e.g., mean = 0.07 g; SD = 0.03, for the 1320 seeds used in this experiment), and ballistic dispersal creates an intense clustering of individuals, allowing the replication of a primary seed dispersal event at a pot scale.

In June 2007, seeds were gathered from a plant community that hosted spatially mixed individuals of the two species. The site was located in western Spain (Berruecopardo, Salamanca province). This site was within the main range of distribution of both species, and consequently, neither of the two populations was marginal. Five mother plants per species, at a minimum distance of 10 m from each other, were randomly selected, and mature seeds were harvested from each mother plant (family lines, hereafter).

Experimental set-up and monitoring—On the 16th, 17th, and 18th of November 2007, a total of 1320 seeds (660 per species, 132 seeds per family line) were scarified by gently cracking the seed coat on the side opposite to the embryo with a pair of cutting pliers and were sown in black, round pots 15 cm in diameter by 20 cm in height (261 units). Pots were filled with 8 dm³ of a substrate composed of 28% sand, 15% perlite, and 56% commercial peat, similar to the sandy acidic soils where annual lupins grow in the Mediterranean. Scarification aimed to synchronize seed imbibition to standardize the beginning of the experiment.

Allocation of seeds to pots followed an experimental design that simulated a seed dispersal event at the site of seed origin. Each pot was allocated a set of 10 seeds following one of three competition treatments: (1) monospecific settings of *L. angustifolius*, 40 pots; (2) monospecific settings of *L. gredensis*, 40 pots; and (3) mixtures with five seeds of each species, 40 pots. Seed arrangement within the pots is shown in Fig. 1. The arrangement of family lines in monospecific pots aimed to balance the tendency of siblings to interact with each other because of the short dispersal range of annual lupins and the probability of encountering seeds from other maternal sources (Drummond and Hamilton, 2007). Twelve additional seeds per family line were singly sown as controls of the experiment in the same pot size (single cultures, hereon, 120 pots). Pots were separated ~40 cm from each other and arranged along four planting beds in an experimental field at the Universidad Rey Juan Carlos (Móstoles, Madrid, Spain). Each bed contained an even number of pots representing each competition treatment and family line single culture. Location of pots within beds was randomized. Each pot was subjected to automatic water supply through drip irrigation to maintain pots under common growing conditions. The amount of irrigation was moderate in an attempt to simulate field conditions.

In addition to the competition treatment and family line effects, we also took into account the following independent variables, which we considered relevant to the dispersal and subsequent competition process in field conditions. Initial seed size (mass, g) was measured to the nearest 0.01 mg as a surrogate of early provisioning for seedling growth (Leishman et al., 2000). Weeds were allowed to grow in all competition pots to simulate a typical old-field colonization event, where not only lupins, but also other species from the local pool of species enter into play. The common garden site is located within the geographic range of coexistence of both species, and the local community of ruderal species is similar to that at the seed collection site. High variability in weed cover was observed between pots throughout the experiment (Appendix S6, see Supplemental Data with the online version of this article), probably because of subtle differences in the arrival of weed seeds and propagules from the surroundings and their differential performance in competition. Thus, we included total weed cover as an additional independent variable in models. Weed cover was estimated to the nearest 5% by the same observer from vertical photographs of each pot in late February and at the flowering stage coinciding with the phenological peak of the community.

We monitored the experiment from the sowing date to mid July, when all plants had finished maturing the seed and began senescence. During this period, we recorded the presence/absence of each target individual at the germination stage (survival to seedling stage, verifying that all scarified seeds that did not germinate were dead), after winter in late February, and at the fruiting stage around early mid June. Survival rates are thus considered from the seed stage, including the transition from seed to seedling, up to the production of the new cohort seeds. At flowering time, maximum and minimum plant canopy diameter and canopy height of each lupin individual were measured to the nearest 0.5 cm, and plant size was estimated by calculating the volume of the corresponding ellipsoid (cm³). After fruit ripening, the number of mature and viable seeds (offspring) per individual was counted.

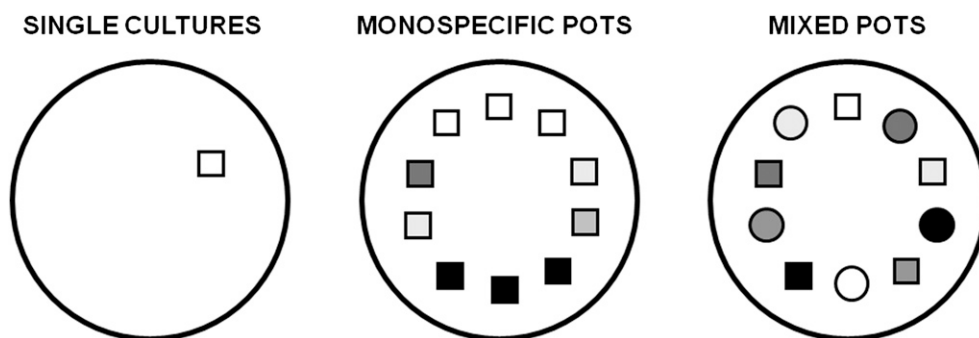


Fig. 1. Arrangement of seeds sown in single cultures, in monospecific competition pots, and in mixed competition pots. Squares: species *i*; circles: species *j*. Different values of gray are different family lines within each species. The 132 seeds of each family line were distributed so that each family line had an equal number of seeds in mixture pots and in each of the four possible positions within monospecific pots (surrounded by one sibling, surrounded by two siblings, with no sibling nearby but with a sibling at the opposite side of the pot, and without siblings in the pot). See Materials and Methods for justification of the arrangement of family lines in monospecific pots.

Competition indices—We assessed three main aspects of competition: intensity, effect, and outcome. To assess competition intensity, instead of computing the widely used relative competition intensity index (Wilson, 1988), we directly modeled individual lifetime fitness using the average performance of each family line grown in single culture as a fixed-effect predictor in the models (see “Statistical analyses” below). To estimate the competitive effect of each individual *i* of family line *j* on its neighbors, we first computed the decrease in yield (i.e., number of viable seed produced) of each neighbor relative to the performance of its family line sown in single culture (RY_{ij}):

$$RY_{ij} = \log(Y_{imixture}) - \log(Y_{jsingle})$$

where RY_{ij} is relative yield of individual *i* of family line *j*, $Y_{imixture}$ is yield of a given individual *i*, and $Y_{jsingle}$ is average yield of the 12 individuals of its family line *j* sown in single culture. Then we calculated the RY of the nine individuals in a pot, discarding the focal individual, and averaged the RY of those nine individuals to obtain a measure of the effect of the focal individual (EFF_k) on the performance of its pot neighbors:

$$EFF_k = \frac{1}{9} \sum_{i=1}^9 RY_{ij}$$

It is worth noting that the greater the magnitude of the effect, the more negative this index becomes. Aggressive competitors will generate a low EFF_k index (Weigelt and Jolliffe, 2003).

Finally, to estimate the outcome of competition for the mixture pots, we used the relative efficiency index (REI) (Connolly, 1987):

$$REI = \sum_{i=1}^5 Y_{angl} - \sum_{m=1}^5 Y_{gredm}$$

where $\sum_{i=1}^5 Y_{angl}$ is the sum of the number of offspring produced by all five individuals of *L. angustifolius* in a mixture pot, and $\sum_{m=1}^5 Y_{gredm}$ is that of the five *L. gredensis* plants. If $REI > 0$ in a given mixture pot, then the outcome of competition is favorable for *L. angustifolius* in that pot; whereas if $REI < 0$, *L. gredensis* is the species yielding more offspring.

Statistical analyses—Analyses of the effect and outcome of competition—The competitive effect of each individual plant on its nine neighbors (EFF_k) was modeled using generalized linear models (GLMs) (McCullagh and Nelder, 1989). A model was run, using competition, species, and their interaction as categorical fixed-effect factors, and initial seed size, weed cover, single culture survivorship, number of offspring produced in single culture, and planting bed as continuous predictors. Poisson error distribution and log link function were specified. Type 3 option of PROC GENMOD (SAS v. 9, SAS Institute, Cary, North Carolina, USA) was used to analyze main effects. The outcome of competition (REI) was not modeled because, due to the nature of this index, fixed-effect factors cannot be specified (only mixture pots are used, and the species factor is included in the calculation of the index itself). As REI was distributed normally, we ran a Student’s *t* test analysis against $REI = 0$ to assess whether

the competitive outcome was favorable for *L. angustifolius*, *L. gredensis*, or neither of the two species. Generalized linear models were computed using SAS v. 9. T-tests were run with SPSS 17.0 (SPSS, Chicago, Illinois, USA).

Analyses of the competition intensity: aster models—We considered lifetime fitness as the expected number of offspring produced per each seed initially sown in the competition treatment pots. We used aster models to calculate and model expected lifetime fitness (Geyer et al., 2007; Shaw et al., 2008). The use of aster models was prompted by the bimodal distribution of fitness of the individuals in this experiment (Fig. 2). The usual procedure under this scenario is to analyze survivorship and reproduction of survivors separately (e.g., Shaw, 1986; Milla et al., 2009). However, aster models overcome this limitation through the use of forest graph exponential family of canonical models that combine generalized linear modeling with survivorship analysis in a single statistical test, accounting for the dependence of fitness components expressed later in ontogeny (e.g., fecundity) on processes expressed earlier (e.g., survival) (Geyer et al., 2007; Shaw et al., 2008). Abundant information and resources on the mathematical basis and usage of aster models is available at <http://www.stat.umn.edu/geyer/aster/>. Appendix S3 (online) shows a life-history graph containing the several stages of survival and fecundity considered in this experiment and the assumed statistical distribution for the expected output of each stage.

We generated four nested aster models for lifetime fitness (the so-called initial, family, weeds, and full models, described later) following the procedures of Shaw et al. (2008). This four-step approach was intended to sequentially dissect the effects of the considered factors on lifetime fitness and to follow their order of appearance throughout the experiment. Each model contained a predictor variable that accounted for the survival status of individuals in previous stages (see aster manual at <http://www.stat.umn.edu/geyer/aster/>), explanatory variables included in previous models, and some others added de novo for the ongoing model (see Table 1). (1) Initial model: this model included the factors affecting the initial conditions of the experiment, i.e., initial seed size and the planting bed where the pot was located. (2) Family model: the initial model was expanded by the inclusion of family effects through average survival to fruiting stage and average number of offspring of each family line when grown in single culture. (3) Weeds model: this model incorporated percentage cover by weeds in late spring. Note, however, that several of the models aimed to predict survival after winter. In those models, weed cover came from data gathered at the end of winter. (4) Full model: finally, the fixed-effect factors competition (mixture or monospecific) and species (*L. angustifolius* or *L. gredensis*) were added to the model. These four models were used separately to predict lifetime fitness. The same four models also were used to explain individual survivorship at three stages as shown in Appendix S3 (see Supplemental Data with the online version of this article): survival to seedling stage, survival after winter, and survival at the fruiting stage. For example, the weed model, applied to the “survival after winter” stage, attempted to predict the probability of survival of a given individual to winter on the basis of (1) its probability of survival to the seedling stage, (2) its initial seed size, (3) the planting bed where its pot was allocated, (4) the average survival and fecundity of its family line representatives sown in single culture, and (5) weed cover in its pot.

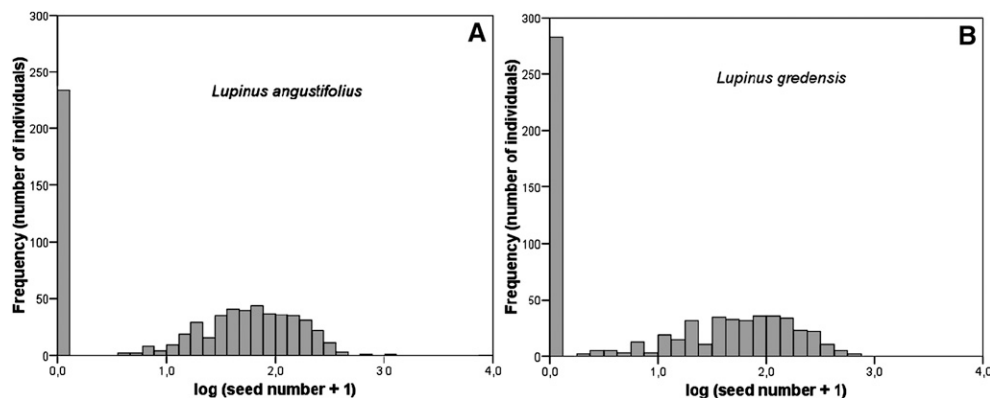


Fig. 2. Histogram of observed log-transformed (seed number + 1) produced per each individual sown in the experiment. Panel A is for *Lupinus angustifolius* (widespread species), and B is for *L. gredensis* (narrow endemic species).

Only models with biological soundness were run (e.g., a weeds model to predict early survival to the seedling stage before winter was not run, as no weeds had developed yet). To predict survival after winter, weed cover was taken from winter data, not from spring data.

Comparison of more complex models over reduced models was calculated using log-likelihood ratio tests (Shaw et al., 2008). This permitted the dissection of the effects of events that occurred successively during the development of the experiment (initial conditions, further growth of weedy vegetation, etc.) on lifetime fitness. Aster models were run using the aster package (Geyer et al., 2007; Shaw et al., 2008) available for the R platform (R Core Development Team, 2008).

RESULTS

Controls grown in single culture produced more offspring than their family line siblings sown in competition pots ($P < 0.01$, results not shown), indicating that individuals set to compete had competitive interactions. In general, competition was more intense in mixture than in monospecific pots because both the number of survivors and viable seeds produced per pot tended to be lower in the mixture pots than in the monospecific pots of both *L. angustifolius* and *L. gredensis* (online Appendix S4,

TABLE 1. Log-likelihood ratio tests for the comparison of aster models predicting lifetime fitness, survival at fruiting stage, survival after winter, and early survival to the seedling stage. (A) Each subsequent model adds survival at the preceding stages, and a suite of explanatory variables, to the previous model (i.e., models are nested). Change in deviance is twice the log-likelihood ratio. (B) Statistical comparisons were made sequentially between nested models. A significant change in deviance indicates improvement of the previous model after the addition of a new set of predictors and takes into account factors already present in the previous model. Explanatory variables included in each of the nested models are shown in the upper part of the table (see Materials and Methods for details on each variable). Null is a model including only survival at the preceding stages and a dummy predictor to provide a baseline against which to compare the initial model.

(A) Partial model name		Model formula			
Null	Response = survival at preceding stages + dummy predictor				
Initial	Response = survival at preceding stages + seed size + planting bed				
Family	Response = survival at preceding stages + seed size + planting bed + family line _{surv} + family line _{seed#}				
Weeds	Response = survival at preceding stages + seed size + planting bed + family line _{surv} + family line _{seed#} + weed control				
Full	Response = survival at preceding stages + seed size + planting bed + family line _{surv} + family line _{seed#} + weed control + competition + species				
(B) Component of fitness predicted	Model comparison	Model df	Model deviance	Change in deviance	<i>P</i> value of log-likelihood ratio test
Lifetime fitness	Null		−473899		
	Null vs. initial	1	−473943	45	<0.05
	Initial vs. family	2	−474003	60	<0.05
	Family vs. weeds	1	−474004	0.05	1
	Weeds vs. full	2	−474984	66	<0.05
Survival to fruiting stage	Null		2546.28		
	Null vs. initial	1	2503.21	43.07	<0.05
	Initial vs. family	2	2497.95	5.26	0.02
	Family vs. weeds	1	2497.06	0.89	0.35
	Weeds vs. full	2	2449.04	0.48	0.92
Survival to winter	Null		1843.32		
	Null vs. initial	1	1783.85	50.46	<0.05
	Initial vs. family	2	1781.76	2.09	0.15
	Family vs. weeds	1	1775.82	5.95	0.01
	Weeds vs. full	2	1744.06	0.58	0.90
Survival to seedling stage	Null		1143.25		
	Null vs. initial	1	1116.16	27.09	<0.05
	Initial vs. family	2	1115.87	0.29	0.59
	Family vs. full	2	1089.68	0.85	0.84

$P < 0.001$ for viable seeds and $P = 0.011$ for survivorship, on the basis of GLMs analyses). The family lines sown in single culture exhibited different fecundity and survival rates, providing ground for maternal effects to play a role in predicting the fitness of individuals in competition treatments (online Appendix S5). Moreover, the quantitative variables employed as predictors in statistical models showed ample and continuous ranges of variation among pots and individuals, which make their effects readily detectable (online Appendix S6).

Competitive abilities of *Lupinus angustifolius* and *Lupinus gredensis*—The results of the aster models for lifetime fitness, the indexes of the effect of competition, and competitive outcome all consistently indicated that widespread *L. angustifolius* is a superior competitor to narrow endemic *L. gredensis* (Tables 1 and 2, Figs. 3 and 4).

Lupinus angustifolius individuals produced more offspring than those of *L. gredensis* when set to compete in mixture pots (Fig. 3A). On the contrary, *L. gredensis* had more viable descendants than *L. angustifolius* in monospecific pots (Fig. 3B).

The competitive effect of individuals on their neighbors (EFF_i) showed similar patterns to those of lifetime fitness. The competitive effect that an *L. angustifolius* individual exerted on pot neighbors was significantly higher in mixture pots than in monospecific pots (Fig. 4, Table 2). If we transform the log-scaled data of Fig. 4 back to raw data (note that EFF_i is based on RY_{ij} data, which are log-scaled), it can be observed that the neighbors of *L. angustifolius* individuals in mixture pots produced, on average, ca. 7 descendants fewer than their siblings grown in single culture, whereas the neighbors of *L. angustifolius* individuals in monospecific pots experienced a decrease of 3.5 descendants. This was not the case for *L. gredensis*, which inhibited the development of neighbors to a similar extent in both mixture (ca. 6.4 descendants) and monospecific (ca. 6.6 descendants) pots (Fig. 4, and note significant species \times competition interaction in Table 2).

Finally, the index of competitive outcome in mixed pots was significantly greater than zero, indicating that *L. angustifolius* was more competitive at the pot scale ($REI_{\text{mean}} = 33.8 \pm 10.5$ SE, $t = 3.2$, $P = 0.0026$).

TABLE 2. F ratios and their statistical significance for the effects of the several predictors included in a generalized linear model with the effect of competition (EFF_i) as response variable. See Materials and Methods for details on the EFF_i index.

Predictor	F ratio	P value
Planting bed	17.6	<0.05
Initial seed size	5.3	0.0211
Family line survival in single culture	1.7	0.1957
Family line fecundity in single culture	0.1	0.7102
Weed cover	0.1	0.8121
Species (<i>Lupinus angustifolius</i> vs. <i>L. gredensis</i>)	17.4	<0.05
Competition (mixed vs. monospecific)	14.0	<0.05
Competition \times species	140.0	<0.05

Dissection of the competition process—*Lupinus angustifolius* seeds were heavier than *L. gredensis* seeds (Appendix S6). Its family lines also showed more uniform lifetime survival rates than those of *L. gredensis* (Appendix S5). However, no significant differences were found between competition treatments for *L. angustifolius* and *L. gredensis* lifetime survival (Table 1). More importantly, lifetime survival rates did not differ among mixture and monospecific pots (Fig. 5). This means that the superior competitive ability of *L. angustifolius* in mixture pots was only revealed during the reproduction of survivors. In contrast to models built for lifetime fitness, the partial models for survival yielded predictions similar to those of the full model, further reinforcing the result that competition and species did not influence survival rates (Fig. 5). Lifetime fitness of *L. angustifolius* was greater in mixture pots, whereas *L. gredensis* reached higher fitness in monospecific pots (Fig. 3). All partial models, except the weeds model, produced different predictions of lifetime fitness relative to their prior, more reduced models (see fitness models in Table 1). The full model, where the effect of competition is explicitly entered, predicted a strong reduction of *L. gredensis* fitness in mixture pots, accompanied by a significant but moderate increase of *L. angustifolius* performance (Fig. 3).

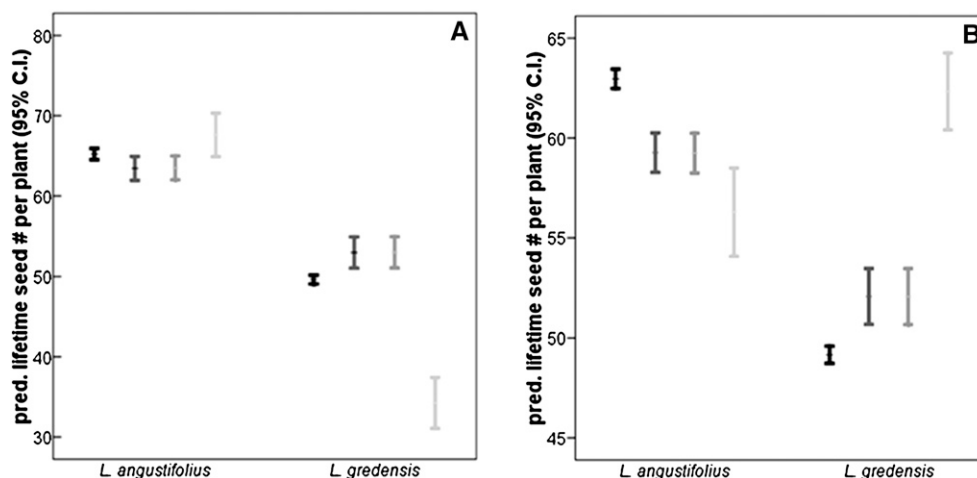


Fig. 3. Aster model predicted lifetime fitness of a typical individual of each species set to compete in mixture (A) or monospecific pots (B). Predicted (pred.) means ($\pm 95\%$ C.I.) are shown for four different models. Models are nested, with each one including the explanatory variables of all previous models. Models are arranged in a gray scale from initial (black), family (dark gray), weeds (medium gray), to full (light gray). See Materials and Methods for details on each specific model.

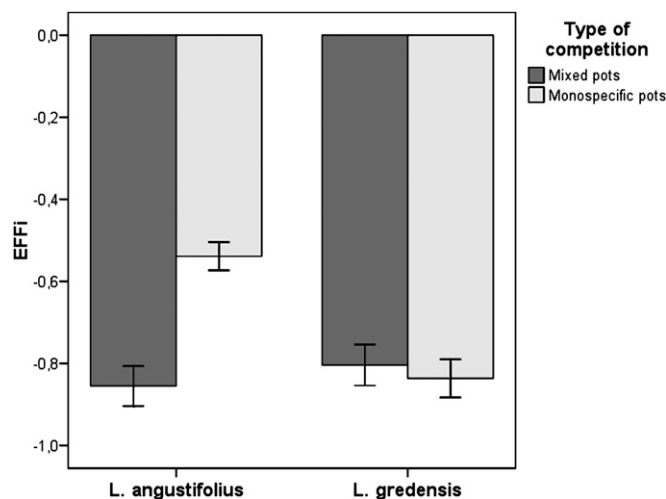


Fig. 4. Competitive effect of each individual on the fitness of its neighbors in mixture and monospecific pots (EFF_i ; see Materials and Methods). EFF_i is the average seed number ($\pm 95\%$ CI) of the nine neighbors of the focal plant i , relative to that of their family line representatives sown in single culture.

DISCUSSION

The widespread species is a superior competitor to its narrowly distributed coexisting congener—The initial motivation of this study was to rigorously test whether a widely distributed plant species is a superior competitor to a narrowly distributed coexisting congener at a local scale. Our findings highlight that *L. angustifolius*, the widespread species, generally thrives better under the conditions of this experiment than *L. gredensis*, its narrowly distributed counterpart. A given *L. angustifolius* individual is at a greater advantage when sharing space with *L. gredensis* than when sharing with conspecifics, whereas the opposite is true for *L. gredensis*. To our knowledge, this is the first report of higher lifetime fitness and competitive abilities of a widespread species in comparison to a coexisting narrow

endemic in a competitive artificial setting. We detected this in an experimental setting that mimics field conditions, through the simulation of hypothetical but realistic dispersal events in each mesocosm but then allowing each experimental pot to develop freely in terms of establishment and death.

On the basis of these results, we cannot discard that mechanisms acting through interspecific plant–plant competition at a very local spatial scale may scale up to affect a process occurring at an extremely larger spatial scale, like the extent of geographic occurrence (see Gaston, 2003, for examples on other biotic interactions). At this stage of research, direct causal links cannot be established, but we can propose hypotheses compatible with the results found here to be tested in the future. For instance, if *L. angustifolius* performs better locally, how can we expect increased performance to translate into larger geographic distribution? Because seed shape and dispersal mechanisms are similar, improved local performance should imply an initial advantage in long-distance dispersal probabilities. Ballistic seed dispersal in *Lupinus* species is limited, and a vast majority of seeds disperse near the mother plant (Drummond and Hamilton, 2007). However, mid- and long-distance seed dispersals do occur, and spatial distribution of populations in the field shows a clear discrete pattern (personal observation), probably as a consequence of secondary dispersal agents. *Lupinus angustifolius* individuals produced an average of 34 more descendants than *L. gredensis* in mixture settings, so more dispersal propagules are available for low-probability mid- and long-distance dispersal events. In situ experiments in the field are clearly needed to test this hypothesis and its relative role, compared with other biotic and abiotic mechanisms, and to answer questions about how processes occurring at contrasting scales may be linked. For example, does competition grow even more asymmetrical toward the range margins of *L. gredensis* (see Jump and Woodward, 2003)? Do long-distance dispersal events become rarer for *L. gredensis* at its margins compared with *L. angustifolius*? How does *L. gredensis* maintain viable populations at the core of the geographic range shared with *L. angustifolius* (Higgins et al., 2000; Levine and Rees, 2002)?

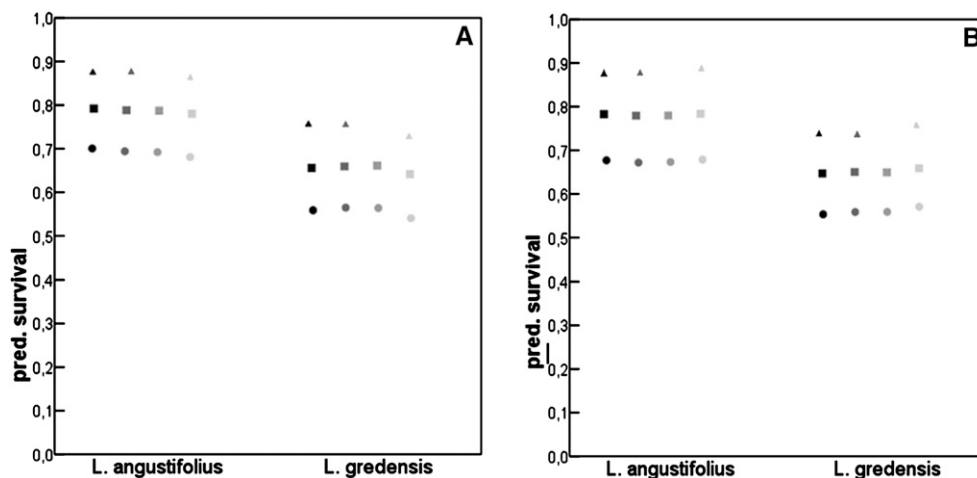


Fig. 5. Aster model predicted (pred.) mean values (CI are not shown for clarity) for survival to seedling stage (triangles), survival after winter (squares), and survival at fruiting stage (circles) for a typical individual of each species set to compete in mixture (A) or monospecific pots (B). Models are arranged in a gray scale from initial (black), family (dark gray), weeds (medium gray), to full (light gray). Note that predictions of weeds model are absent for the seedling stage (no weeds yet).

Higher fecundity late in the season, rather than higher survival, allowed the widespread species to achieve superior competitive performance—We found that each species had similar survival rates in mixture and monospecific pots. Fecundity, however, was different between competitive environments in each species. *Lupinus angustifolius* individuals clearly benefited from sharing pots with *L. gredensis*, but *L. gredensis* did not. Therefore, the fecundity of survivors may be the major factor generating differences in the competitive effects on neighbors and in the final competitive outcome, all of which were favorable for *L. angustifolius*. This is an expected result, since competitive interactions are more prone to occur later in ontogeny, when neighbors are larger and interfere more readily with each other (Inouye et al., 1980; Gould and Gorchov, 2000). However, in the field, survival is often highly relevant to the lifetime fitness of a given cohort of plants. For instance, Latta and McCain (2009) found that selection gradients have a greater effect on survival components than on fecundity in the field, whereas the only relevant fitness component in the greenhouse was fecundity. Our results, obtained in near to field conditions, indicate that mortality does occur, but its magnitude is similar in intraspecific and interspecific competition settings and thus is unlikely to exert a significant effect on the process of interest here, i.e., the local extinction of a putative inferior competitor by a stronger one. Traits that confer high fecundity in *L. angustifolius* include early flowering phenology, high seed and fruit set rates, and high early resource provisioning for growth (Milla et al., 2009). Putative differences between *L. angustifolius* and *L. gredensis* in those traits may have prompted the disparity in competitive abilities through contrasting fecundity. In this sense, we have evidence only for seed size, as a surrogate of resource provisioning for early growth, which was indeed higher in *L. angustifolius*.

We also evaluated the effect of other factors that interfere with the development of lupins in their natural habitats. In accordance with the moderate relevance of survival with respect to fecundity, factors occurring early in the season had little effect on competitive relationships. Neither seed size, allocation of pots to different locations within the experimental field, nor the development of weeds in the mesocosm produced different lifetime fitness predictions for *L. angustifolius* and *L. gredensis* in mixture vs. monospecific pots. This suggests that competition among our functionally and phylogenetically close lupins is much more important for the local performance of the two species, and its putative geographic consequences, than is competition with other components of the community. Competition among close relatives is often more intense than among phylogenetically distant species (Johansson and Keddy, 1991). This supports the idea that interaction among congeners is an important ecological driver of geographic patterns compared with other biotic interactions. Another factor that might have influenced the differential response is competition for rhizobia between the two species.

The full model, which includes overall offspring production in the pot, indicated that individual fitness was higher for *L. angustifolius* in mixture pots, whereas individual fitness for *L. gredensis* was higher in monospecific pots. This suggests that the widespread species makes more efficient use of resources in mixture pots than its narrow endemic counterpart, which responds better when the widespread is absent. Some studies have reported higher growth rates, biomass gain, or height growth for widespread species compared with narrow endemics, which may indicate a more efficient resource use strategy of widespreads

(Prober, 1992; Aplet and Laven, 1993; Walck et al., 1999). However, other studies show no net differences between narrow and widespread species in this sense (Gottlieb and Bennett, 1983; Snyder et al., 1994; Bush and van Auken, 2004).

Finally, it is worthy to comment on the approach to lifetime fitness used in this study. Before the release of aster models, few attempts were made to integrate survival and fecundity in a single statistical model. One common approach was to weight fecundity by the proportion of survivors, which ignores the nonrandom nature of mortality and the dependence of one process on the other (e.g., Galloway and Etterson, 2007). Others have attempted to model lifetime fitness by combining multiple regression over different fitness components or by using an individual's contribution to population growth rate (λ) as a fitness proxy, but none of these or other methods satisfactorily deal with violations of distributional assumptions (e.g., van Tienderen, 2000; Caswell, 2001; Coulson et al., 2003; see Shaw et al., 2008, for a full account). Recently, Latta and McCain (2009) modeled survival and fecundity components of fitness jointly using structural equation models (SEMs; Shipley, 2002). To our knowledge, however, SEMs cannot satisfactorily deal with multimodal response variables or manage a data set with a very high proportion of missing data for all fecundity-related variables (but see d-sep approaches based on path analysis, e.g., Thomas et al., 2007). In addition, absent data for fecundity cannot be assumed to be missed at random because survival is not a random thinning of individuals in a population, but a selective filter. Latta and McCain (2009) solved this by using family line means instead of individual-based data, which sweep the overabundance of zeros in the data set without inflating missing data. However, this is not an exportable procedure for most studies, where the individual level of analysis is the focus. Aster models are rooted on conditional modeling, which is the proper context to account for events that occur subsequently in the life cycle. Other frequently modeled mechanisms in evolutionary ecology, like the dissection of the reproductive process (e.g., Traveset et al., 2003; Giménez-Benavides et al., 2008), could make use of this approach when events occurring later in the process are dependent on the outcome of earlier events. Here, predictions of aster models allowed plotting marginal means and confidence intervals at each experimental treatment level, based on predicted parameters, which would be nonsense using observed data because of its intrinsic bimodal nature. We strongly advocate joint consideration of survival and fecundity in lifetime fitness analyses and thus recommend aster models as the most appropriate tool to address difficulties inherent to this type of analyses.

In conclusion, the application of novel lifetime fitness analyses, and the analysis of several different aspects of competition, provided evidence that a widespread species of *Lupinus* shows higher fecundity and is a superior local competitor to a coexisting narrow endemic. Lower competitiveness may scale up and hinder geographic expansion of the endemic species, as shown by the low dependence of its performance on other factors relevant in the pioneer habitat of both species, like abundance of other weedy species. This study points to two ways forward in this line of research. First, other case studies, encompassing other geographic areas and growth forms, are clearly needed. The results shown here are specific to our study system, and the question arises as to how case-study specific these findings are. Given current knowledge (Appendix S1), we cannot speculate further. In this sense, we think that very careful selection of study peers (e.g., truly coexisting in the field along the shared

geographic range) and adequate approach to comparative fitness and competitive abilities are a requisite for reliability. Second, more detailed knowledge on in situ dynamics, especially at narrow endemic distribution borders, would clarify mechanisms linking competitive abilities to geographic occupancy.

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