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Research article

Idiosyncratic shifts in life-history traits at species' geographic range edges

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Anthropogenic changes drive shifts in species' geographic distributions and increase the occurrence of leading or trailing-edge marginal populations. Theoretical predictions and empirical observations indicate substantial changes in life-history traits in marginal populations, often involving dispersal and reproductive abilities. Using a common garden experiment, we studied the variation of life-history traits of populations sampled on spatial gradients extending from range-core to range-edge habitats for three expanding (miner's lettuce *Claytonia perfoliata*, Danish scurvygrass *Cochlearia danica* and rock samphire *Crithmum maritimum*) and one receding plant species (dune pansy *Viola tricolor* subs. *curtisii*). We monitored life-history traits related to dispersal, phenology, survival, reproductive output and selfing ability. Significant shifts in life-history traits between central and marginal populations strongly differed among species. Marginal populations of the three expanding species displayed modified seed weight in natura, suggesting increased dispersal abilities in leading-edge populations. Discarding unassessed maternal effects, this trait modification can be due to phenotypic plasticity or to genetic differentiation. In miner's lettuce, marginal expanding populations show advanced phenology and higher reproductive output, that may potentially influence their colonization ability. In rock samphire, life-history traits showed large intra- and inter-population variability that did not follow a core-to-edge geographic trend, except for seed size. Finally, the receding populations of the dune pansy displayed a shift towards a plant architecture maximizing survival but reducing individual reproductive success. Altogether, our results indicated a common trend for increased dispersal abilities in marginal populations of expanding species. However, shifts in species' distributions may drive idiosyncratic changes in other life-history traits, for which we observed no general evolutionary syndrome at range edges. These findings go along a stochastic view of trait evolution during range expansion, and question how to draw predictive projections of species' distribution shifts under current global change.

Keywords: *Claytonia perfoliata*, *Cochlearia danica*, *Crithmum maritimum*, dispersal abilities, phenology, reproductive success, shifting geographic range, trailing and leading edge, *Viola tricolor* ssp. *curtisii*

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Introduction

There is ample evidence that environmental changes are reshuffling the geographic distribution of many taxa worldwide (Parmesan 2006, Vilà-Cabrera et al. 2019). In particular, anthropogenic effects such as land conversion, or habitat modification through the setting up of roadways or cultivated fields may impact species' geographic ranges (Gaston 2003, Cheptou and Dornier 2012, Bullock et al. 2020). Species' capacity to face and track human-driven environmental change via range shifts depends on their ability to successfully colonize new areas and establish viable populations in areas where new selective pressures strongly affect the evolution of life-history traits (Angert et al. 2011). Thus, range expansions may drive rapid life-history trait evolution despite successive founder events that are likely to enhance the loss of standing genetic variation (Pannell 2015, Lustenhouwer et al. 2019). Overall, life-history trait evolution at range margins has far-reaching consequences on the fate of species distribution over ecological timescales, and has major implications on management strategies for protecting species of conservation concerns or for limiting the harmful impact of invading species (Urban 2015, Chuang and Peterson 2016).

In leading-edge populations, theoretical predictions and empirical observations often support the intuitive view of shifts in life-history traits promoting colonization: increased dispersal and reproductive abilities and/or selfing rates, ecological generalization and earlier phenology especially when considering latitudinal gradients (Parmesan 2006, Hargreaves and Eckert 2014, Estrada et al. 2016). These changes in dispersal capabilities and phenology also particularly hold in new human-modified inland habitats such as urban areas (Cheptou and Dornier 2012), transit zones (Bullock et al. 2020) or cultivated areas (Arnaud et al. 2011). Strong dispersal ability and ecological generalization are indeed correlated with range shift ability in plants (Angert et al. 2011, Hargreaves and Eckert 2014, Estrada et al. 2016; see however MacLean and Beissinger 2017). Increased dispersal ability on the expanding edge is expected to evolve because of spatial sorting, a runaway evolutionary process during population spread (Phillips et al. 2010, Hargreaves and Eckert 2014, Chuang and Peterson 2016, MacLean and Beissinger 2017). In many plant species, traits facilitating efficient seed dispersal evolve in invading or leading-edge populations (reviewed in Hargreaves et al. 2014, Chuang and Peterson 2016). Earlier phenology or high fecundity may also increase colonization opportunities, depending on the environmental context (Angert et al. 2011). For example, invasive *Impatiens* species show earlier germination than native congenerics (Perglová et al. 2009). Shifts towards earlier phenology (Colautti and Barrett 2013, Lustenhouwer et al. 2018) or greater reproductive output also occur near the leading edge of the geographic distribution of a large number of species (reviewed by Chuang and Peterson 2016; see however Krapek and Buma 2018). Earlier phenology can also prevent from herbivory in ecologically marginal habitats (Benning et al. 2019). Finally, selfing ability is also of crucial importance for successful colonization because it prevents mate limitation (Baker 1955, Grossenbacher et al. 2015, Pannell 2015). Selfing rates may indeed increase in peripheral plant populations (as shown in *Arabidopsis lyrata*, Griffin and Willi 2014; in dune pansies; Latron et al. 2020, and in other plant species, Darling et al. 2008, Mimura and Aitken 2010).

However, theoretical expectations for changes in life-history traits are not systematically verified and there is still no real consensus regarding causal links between expanding range shifts and life-history traits under rapid environmental changes (Angert et al. 2011, Estrada et al. 2016, MacLean and Beissinger 2017, Pironon et al. 2017, Cross and Eckert 2020, Miller et al. 2020, Beissinger and Riddell 2021). Indeed, some of the expectations mentioned above may not be met for several reasons. First, dispersal ability may tradeoff with other traits related to colonization, such as germination rate or dormancy (Burton et al. 2010, Chuang and Peterson 2016). Fast life-history in marginal populations can go along with reduced longevity, lower competitive ability or reduced fitness (reviewed by Angert et al. 2020). Second, marginal populations may have low census sizes and low levels of genetic diversity which facilitates the stochastic fixation of deleterious mutations, creating an expansion load that reinforces the species' geographic range limit (Eckert et al. 2008, Peischl et al. 2015, Angert et al. 2020, Perrier et al. 2020). Moreover, the infrequent nature of new colonization and successful settlement events, along with elevated extinction risks during the initial stages of range expansion, may allow sufficient stochasticity to offset clear-cut deterministic signals of shifts in life-history traits during range expansion (Angert et al. 2011, Krapek and Buma 2018, Williams et al. 2019). Finally, in different marginal populations, genetic drift may cause different mutations to increase in frequency, thus different shifts in life-history traits may be observed on different expansion fronts (Williams et al. 2019).

Besides, anthropogenic disturbances drive habitat loss and range contractions. In that respect, trailing-edge populations remain less studied than leading-edge populations. Nevertheless, these eroding, generally low-latitude, populations deserve conservation priority even if they display somewhat low genetic variation. Indeed, their genetic and ecological distinctiveness shaped by past climate-driven range dynamics confers great potential for local adaptation. This is particularly true in the face of current environmental changes (Hampe and Petit 2005). This evolutionary potential is exemplified by the annual wild flower *Clarkia pulchella*: gene flow from historically warm locations contributed to adaptive genetic variation in populations located more northerly (Bontrager and Angert 2019). However, due to a lack of empirical investigations, there is no general consensus regarding shifts in life-history traits that may occur on trailing edges (Vilà-Cabrera et al. 2019).

Overall, the underlying evolutionary processes driving species distributions may be explored using multifaceted species-level case studies that go beyond static ranges (Cross and Eckert 2020). Here, we set out to investigate the generality of theoretical expectations of changes in life-history traits during

contemporary range expansions and retractions. We characterized the variation of key life-history traits related to dispersal abilities, reproductive output and phenology between central range-core and marginal range-edge populations in four range-shifting plant species facing human-mediated habitat modifications. We studied three expanding plant species: Danish scurvygrass *Cochlearia danica* (Brassicaceae), miner's lettuce *Claytonia perfoliata*, (Montiaceae) and the rock samphire *Crithmum maritimum* (Apiaceae). We also examined a receding and protected species: the dune pansy *Viola tricolor* subsp. *curtisii* (Violaceae). For all these species, the delineation between central and marginal populations was facilitated because their native distribution is strictly coastal (i.e. linear). In range-expanding species, we expected more dispersive propagules in marginal populations as compared to central populations, i.e. smaller seeds for wind-dispersed species and larger achenes for hydrochorous species. If geographically marginal sites are also ecologically marginal, poorly suitable environments, increased predation or increased interspecific competition may also trigger selection for earlier phenology in geographically marginal populations (Chuang and Peterson 2016, Benning et al. 2019, Angert et al. 2020). Finally, marginal populations may sometimes have lower reproductive output and/or survival than central populations, due to tradeoffs between life-history traits (Chuang and Peterson 2016). These expectations are summarised in Table 1 for all studied species. We measured the variation in life-history traits on individuals produced from seeds collected in natura in central and marginal populations of each species and cultivated in a common garden experiment over two generations. We specifically asked the following questions:

1) In range-shifting species, do marginal populations show a shift in dispersal ability, ability for autonomous selfing, phenology and reproductive output compared with central populations?
2) If so, do the observed differences match theoretical predictions expected at range margins?
3) Are these life-history traits undergoing adaptive divergence through genetically based adaptive evolution, or are they showing phenotypic plasticity?

Material and methods

Study species, definition of central and marginal populations and sampling

For four plant species exhibiting contrasting and ongoing geographic range dynamics, we sampled individuals from populations located along a gradient from geographic range centre to range edge (Fig. 1). All four species were native to coastal habitats, which facilitates the identification of central and marginal populations. The rock samphire and the dune pansy still show a strictly coastal distribution, but miner's lettuce and Danish scurvygrass have started colonizing inland habitats in the past few decades. For each species, we sampled 6–10 populations, half of them in central sites and half in marginal sites. Sampling included mature fruits from as many mother plants as possible (up to 23). Details on population locations, surveyed individuals and progeny are provided in the Supporting information.

Miner's lettuce *Claytonia perfoliata* (Montiaceae) is an annual shade-tolerant plant with small unattractive white flowers. Capsules generally contain three seeds, dispersed by myrmecochory (Handel 1978). This species is native to the west coast of North America and was introduced in Europe around 1860 as a market garden plant (de Litardière 1932, Miller 1978, McIntyre 2012). In northern France, miner's lettuce was restricted to dunes and to private gardens along the coastline until 1910–1920. Then, escapees from cultivation started sporadically to occur in inland habitats, presumably through accidental human-mediated dispersal events (de Litardière 1932). For this species, we considered coastal populations as central and inland populations as marginal. Based on presence records obtained from the Botanical Conservatory of Bailleul, we sampled three central coastal populations and three inland leading-edge populations in northern France (Fig. 1A).

Danish scurvygrass *Cochleara danica* (Brassicaceae) is a European annual halophyte whose tiny seeds can be transported by wind after silique dehiscence. It was restricted to the coasts of northern and western Europe until the 1970s, and started expanding inland along salted road banks over the past few decades. It was first observed along inland road banks in the 1970s in the Netherlands, and is now present inland in Germany, the UK, Switzerland, Belgium, France and was recently sporadically detected in Austria where it is still expanding (Cochard 2005, Hohla and Raabe 2012; Supporting information). Seeds are dispersed by car and lorry wheels, resulting in an expansion rate of over 60 km year^{-1} (von der Lippe and Kowarik 2007, Fekete et al. 2018). In northern France, the species is restricted to the coastline (mostly on cliffs) and to a thin strip along motorways, where it can be found just beneath the guardrail and on the central berm. The first inland populations were found in 1999 in this region, and the species is expanding south-eastwards along motorways A25, A27, A23. The most eastwards population included in this study was first recorded in 2011. Despite the species being present much further inland in central Europe, the invasion routes seem to be independent from each other (Supporting information). We therefore considered inland populations in northern France as being marginal. For this species, we defined central populations as those located along the coastline, and marginal populations as those found along motorways inland. We sampled five central populations along the coastline of northern France and five leading-edge expanding populations along national motorways A25, A23 and A27, just beneath the guardrail in safely accessible sites. These leading-edge populations were located 9–110 km away from the coast (motorway distance; Fig. 1B).

Rock samphire *Crithmum maritimum* (Apiaceae) is a heliophilous perennial halophyte found on rocky shores in western Europe. The species is restricted to a thin strip

Table 1. Expected and observed differences in life-history traits between central (C) and marginal (M) populations of miner's lettuce, Danish scurvygrass, rock samphire and dune pansy. ?: no clear expectation, because expectations depend on whether the features observed in G_0 are of plastic or genetic origin. Shifts in life-history traits that followed theoretical expectations appear in bold face and those that departed from expectations are underlined. See the Supporting information for the levels of significance of statistical tests.

Traits	General expectation (range margin versus centre)	Generation	Miner's lettuce		Danish scurvygrass		Rock samphire		Dune pansy	
			Expected	Observed	Expected	Observed	Expected	Observed	Expected	Observed
Seed weight and size	For expanding species: more dispersive seeds; i.e. smaller in wind-dispersed species, larger [more floatable] in sea-dispersed species.	G_0	C > M	**C > M**	C > M	**C > M**	C < M	**C < M**	?	C ≈ M
		G_1	?	C < M	?	C > M	?	C ≈ M	?	C < M
Germination success	Marginal environments more variable: seeds more dormant (and of lower quality?) i.e. lower germination success.	G_0	C > M	C < M	C > M	**C > M**	C > M	C ≈ M	C > M	**C > M**
		G_1	?	C < M	?	C ≈ M	?	C < M	?	C ≈ M
Time to germination	Lower habitat quality and unpredictable habitat should select for earlier phenology: this is expected for marginal populations in expanding species. For receding species: marginal populations come from lower latitudes and should have delayed phenology.	G_1	C > M	**C > M**	C > M	C < M	C > M	**C > M**	C < M	C > M
Phenology of later life events	Same as above	G_1	C > M	**C > M**	C > M	C ≈ M	C > M	C ≈ M	C < M	**C < M**
Reproductive effort	Lower in marginal populations (allocating more to survival, especially perennial species)	G_1	C > M	C ≈ M	C > M	C < M	C > M	C ≈ M	C > M	**C > M**
Fitness	For expanding species: increased fitness of marginal populations under optimal conditions (common garden). For receding species: genetically impoverished marginal populations should have lower fitness	G_1	C < M	**C < M**	C < M	C ≈ M	C < M	**C < M**	C > M	**C > M**

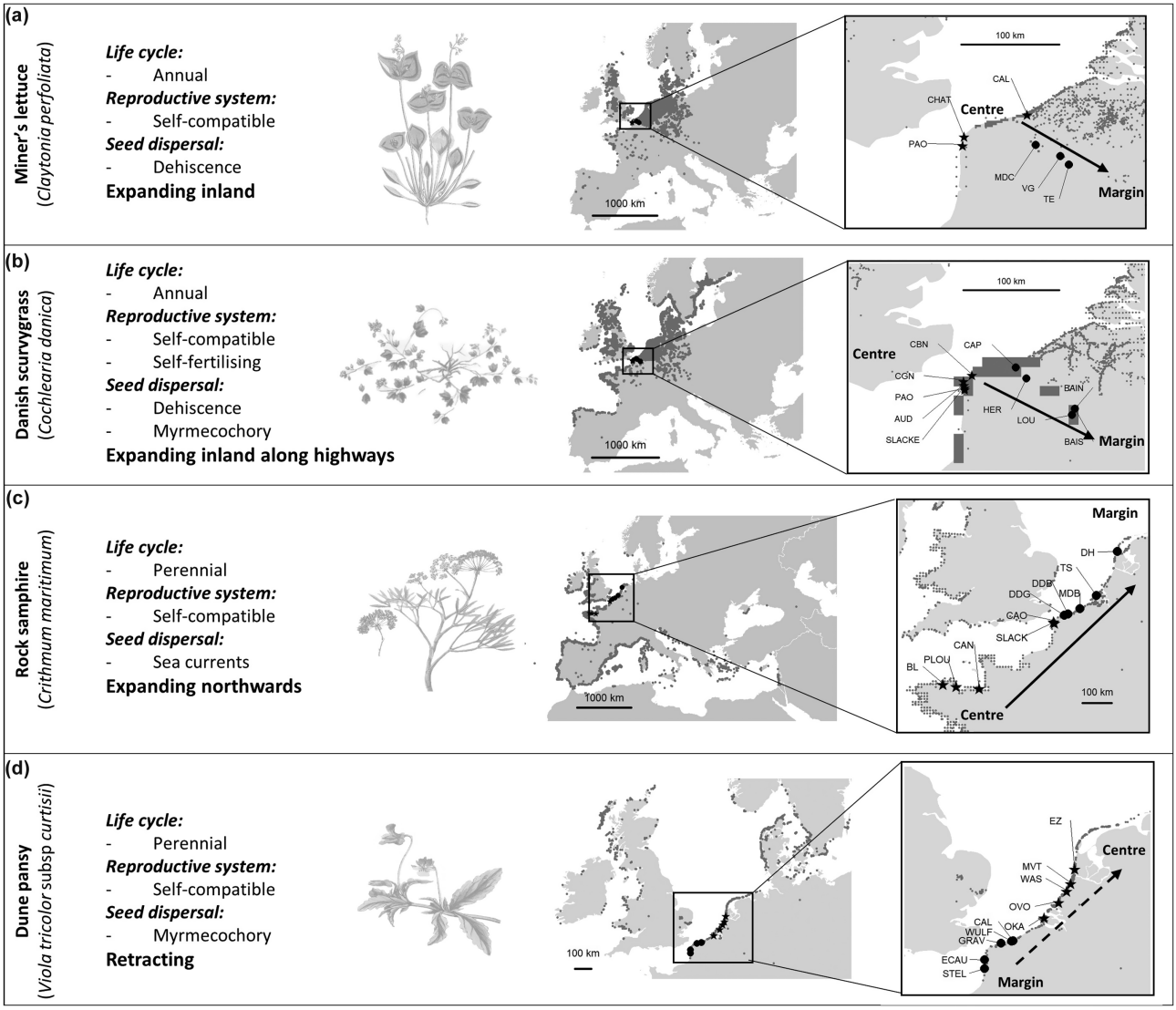


Figure 1. Geographic distribution of miner's lettuce *Claytonia perfoliata*, Danish scurvygrass *Cochlearia danica*, rock samphire *Crithmum maritimum* and dune pansy *Viola tricolor* subsp. *curtisii* (data from GBIF www.gbif.org/ and SIFLORE http://siflore.fcbn.fr/). Stars and circles indicate respectively the central and marginal populations sampled and used for the common garden experiment. Key life-history traits of the species are provided. The dashed arrow indicates a contracting range margin whereas solid arrows indicate an expanding range margin.

along the shoreline, just above the highest tide level. Its large umbels attract various floral visitors, and its corky achenes can drift in marine currents, with seeds remaining viable after several months drifting (Ridley 1930). Over the past decades, its geographic distribution expanded northwards in artificial habitats along the coastlines of northern France, Belgium and the Netherlands (Crawford 1982, Lambinon et al. 2012). For this species, microsatellite markers have been developed and used to define biogeographic patterns (Latron et al. 2018, 2020). Briefly, there was no decrease in allelic richness from core populations located on the northern coast of Brittany (western France) to more recently founded populations in the Netherlands. No significant spatial genetic structure was detected, suggesting efficient long-distance dispersal. Yet, four genetic groups were identified along the Atlantic and North Sea French coastline, with a substantial genetic discontinuity among populations along the English Channel and those located along the North Sea. Furthermore, while we were able to find the species in natural habitats along the Atlantic coast and along the English Channel, populations are strictly restricted to artificial habitats along the North Sea. Both the genetic break and the shift in habitats (natural to artificial) occurred at a very short geographical scale, near the strait of Dover; the Slack population is located west of this limit (Fig. 1C). Therefore, we defined central populations as those found along the Atlantic and English Channel coastline (five populations from Brittany to northern France) and marginal leading-edge populations as those found along the North Sea (five populations ranging from northern France to the Netherlands; Fig. 1C).

The dune pansy is an endangered perennial plant native to semi-stabilized sand dunes along the English Channel and North Sea. Its bright terminal flowers attract many insects, but natural populations are often characterized by substantial selfing rates (Latron et al. 2020). After capsule dehiscence, seeds are dispersed over short distances by ants (Oostermeijer 1989, Rix 2014). In northern France, urbanization and dune management policies have made the dune pansy's habitats scarcer, whereas central populations in the Netherlands are more continuously distributed. For this species, spatial genetic structure was described in Latron et al. (2018, 2020) that showed a clear genetic break between French and Dutch populations. While Dutch populations have high allelic richness and show low genetic differentiation (suggesting efficient dispersal among these populations), French populations showed lower allelic richness and were genetically disconnected from each other (Latron et al. 2020). For these reasons, we considered Dutch populations as central (five populations) and French populations as trailing edge populations (five sampled populations; Fig. 1D). The lack of populations sampled in Belgium reflects our inability to find populations there, despite cautious prospection.

Common garden design

We investigated whether life-history traits related to dispersal abilities, ability for self-fertilization without pollination vectors, phenology and reproductive output differed between central and marginal populations. To this end, we set up a common garden experiment using seeds collected in natura and their offspring (Fig. 2). Because we monitored life-history traits from in natura collected seeds and from offspring seedlings in controlled conditions, trait differences measured in the common garden may mirror either maternal effects or genetically-based variation among populations. The Supporting information shows the location of the common garden, and variations in monthly temperature and precipitations for each sampled location. These mean climatic variables do not differ much for central and marginal populations of all species except rock samphire. In addition, conditions in the common garden are not different from those encountered in the sampling sites, except those from Brittany. For rock samphire, some central populations were collected in Brittany, where winter temperatures are milder and winter precipitations are higher than those of the common garden (Supporting information).

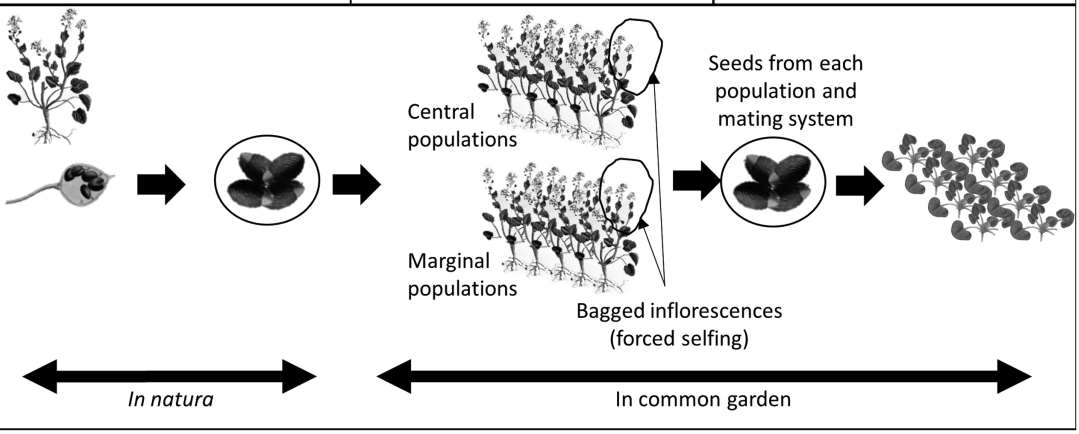
	G_0	G_1	G_2
Plant material	Mother plant *in natura*	Seeds sown in common garden	Seeds collected in common garden
Measurement level	Individual (Seedling family)	Individual	Population
Traits measured	- Seed weight - Germination rate	- Time to germination, to first flower bud, to first flowering, and to first fructification - Number of fruits - Seed weight - Vegetative biomass - Reproductive effort - Fitness	Mean weight, germination rate and germination time of seeds produced by the G_1 populations, using open pollination and forced self-fertilization.
Flowchart			

Figure 2. Flowchart of the common-garden experiment and of the life-history traits measured at the individual or population level on individuals sampled in natura and on their offspring raised in the common-garden. G_0, G_1 and G_2 refer to the generations studied. G_0 corresponds to the plants in natura, for which we measured the weight and the germination rate of their seeds (both are collective measures, collected at the level of the mother plant). These seeds were sown and grown in the common garden, where they were named G_1. The seeds produced by G_1, here named G_2, were measured for seed weight and germination rate and time. Since these measures are collective (and performed at the level of the G_1 population), they are referred to as G_1 measures in the text. The G_2 plants were not studied further than the germination stage.

Seeds were kept dry at room temperature until sowing. Just prior to sowing, seeds of miner's lettuce were stored 10 days at 5°C to release seed dormancy. No treatment was needed to activate germination in the other studied species. For each populations of each species, we sowed 150 seeds and randomly transplanted 40 seedlings in a common garden where we monitored life-history traits for one growing season. Seeds were sown indoors during winter and seedlings were transplanted outdoors after the last frosts in flower pots; the common garden was located at the University of Lille (50°36'27"N, 3°8'36"E). As compared to coastal sites, this location is slightly colder in winter but the temperature is similar in spring and summer (the time periods when the plants were outdoors). In the same way, the rain regime in April–September is comparable in Lille and in the sampling sites (Supporting information). For all species, phenological traits were measured until the senescence of aerial parts, and plants were then harvested and dried for vegetative biomass assessment.

To assess mating system effects on seed traits, we applied two pollination treatments: 1) free intra-population mating (with possibility of selfing); 2) forced selfing, with no biotic pollination vector. To do so, we created one block per population per species, where 40 plants were arranged in staggered rows and enclosed in a mosquito net cage that prevented inter-population mating. We successively opened each cage for several hours throughout the flowering season, which allowed intra-population cross-pollination. To test if autonomous self-fertilization was possible, we bagged one flower stalk on 10 randomly chosen plants in each population block. Seeds or achenes resulting from open mating and from enforced self-fertilization were then collected for a germination survey.

Measurements of life-history traits

Traits were measured on the seeds of the G_0 progenitor plants that were collected in natura, on the plants grown from these seeds in the common garden (G_1) and on their offspring (G_2). All traits were measured at the individual level except those related to G_2 (Fig. 2). Seeds produced by G_0 were measured at the family level (one measure per progenitor G_0 plant). The seeds produced by G_1 (i.e. those grown to be G_2) were measured for seed weight and germination rate and time. Seed weight could be measured at the family level (i.e. at the level of each G_1 plant), but not germination rate nor time, because it can only be measured on a seed lot, and some G_1 plants had low reproductive output. Thus, these traits were measured at the level of each whole G_1 population. Hence, they are hereafter referred to as G_1 measures. The G_2 plants were not studied further than the seedling stage.

For each G_0 mother plant growing in natura, we measured its mean diaspore weight (fruit weight for rock samphire, seed weight for the other three species). We monitored the germination rate and phenology of 8.6 ± 5.8 seeds from each G_0 mother plant every two days, until no new germination was observed for a full week. For each population, 39 ± 3 of these seedlings were transplanted to the common garden to constitute the generation G_1 (Supporting information). We monitored the phenology of each G_1 individual twice a week until senescence by recording the dates of first flower bud, first open flower and first mature fruit. We counted the fruits of 20 randomly chosen individuals and measured the mean weight of seeds produced by the G_1. For the rock samphire, we also measured achene size with an optical sensor (Elmor C3, Elmor Angewandte Elektronik, Schwyz, Switzerland). For the dune pansy, we additionally measured plant height at senescence. Finally, we assessed the vegetative biomass of each dried harvested plant (root biomass for rock samphire, and aerial biomass for the other species).

We defined reproductive effort as the ratio of the number of fruits to the vegetative biomass. We finally sowed 150 seeds produced by open pollination and by autonomous self-fertilization (when it occurred) in each G_1 population to assess germination rate and phenology. Differences in genotypes and phenotypes obviously interact with multiple environmental factors, such that individual fitness may vary among populations as a function of both local environment and local adaptation (Valladares et al. 2014). We estimated G_1 individuals' fitness as the product of their number of fruits and the germination rate of their offspring issued from open pollination. Keeping in mind that relative fitness of individuals belonging to different populations is dependent on the environmental context, this estimation thus accounted for reproductive output and early offspring survival: it is the number of viable offspring produced by each individual in a common environment.

Data analysis

To determine which traits were correlated, we performed a principal component analysis (PCA) for each species separately, using all measured traits. Each G_1 individual plant was attributed the seed weight of its maternal G_0 plant, and the G_1 seed weight measured on the seeds that it produced. To assess whether central and marginal individuals differed in sets of traits, i.e. in their position in the principal component space, we then performed a permutational multivariate ANOVA (R library vegan, function *adonis*). For uncorrelated traits, we then compared trait values of individuals from central and marginal populations using Wilcoxon tests, and corrected p-values for multiple testing using Benjamini and Hochberg's false discovery rate method (Benjamini and Hochberg 1995). Throughout, the reported p-values are adjusted ones. Effect sizes (Cohen's d, Cohen 1988) were assessed using R library rstatix (function *wilcox_effsize*). Effect sizes were computed as the ratio of the Z statistic of the Wilcoxon test on the square root of the number of the sample size. Effect sizes below 0.2 were considered very small, those between 0.2 and 0.5 were considered small, those between 0.5 and 0.8 were considered moderate and those above 0.8 as large (Cohen 1988, p. 24).

Phenotypes may be plastic, i.e. individuals carrying the same genotype may have different phenotypes if they live in different environments. To investigate whether the differences in seed weight, seed size and seed germination rates from G_0 were genetically based or due to phenotypic plasticity, we assessed the reaction norms of central and marginal populations from

G_0 to G_1. Indeed, phenotypic plasticity can be visualised with the reaction norm, which is a plot showing how environmental conditions affect how a phenotype is expressed (Franks et al. 2014). All analyses were performed using R ver. 4.0 (www.r-project.org) and libraries rstatix (Kassambara 2021), vegan (Oksanen et al. 2020), corrplot (Wei and Simko 2017), FactoMineR (Lê et al. 2008), factoextra (Kassambara and Mundt 2020) and ggplot2 (Wickham 2016).

Results

Life-history trait covariation

Depending on species, the first two dimensions of the PCA expressed 37–50% of the total inertia (Fig. 3, Supporting information). These axes were correlated with 1) phenological variables and 2) reproductive effort and fruit number. Seed traits contributed mostly to dimensions 3, 4 and 5 (Supporting information). To avoid redundancy, we will focus our subsequent analyses on traits that were not or only weakly correlated (Supporting information): seed weight in natura, germination rate and phenology, reproductive effort, vegetative biomass and the weight of G_2 seeds.

Life-history trait differences among sampled localities

In all species except the rock samphire, individuals of central and marginal origin were differentiated in the multivariate space of the PCA (permutational ANOVA, $p = 0.015$ for miner's lettuce, $p = 0.006$ for Danish scurvygrass and $p = 0.001$

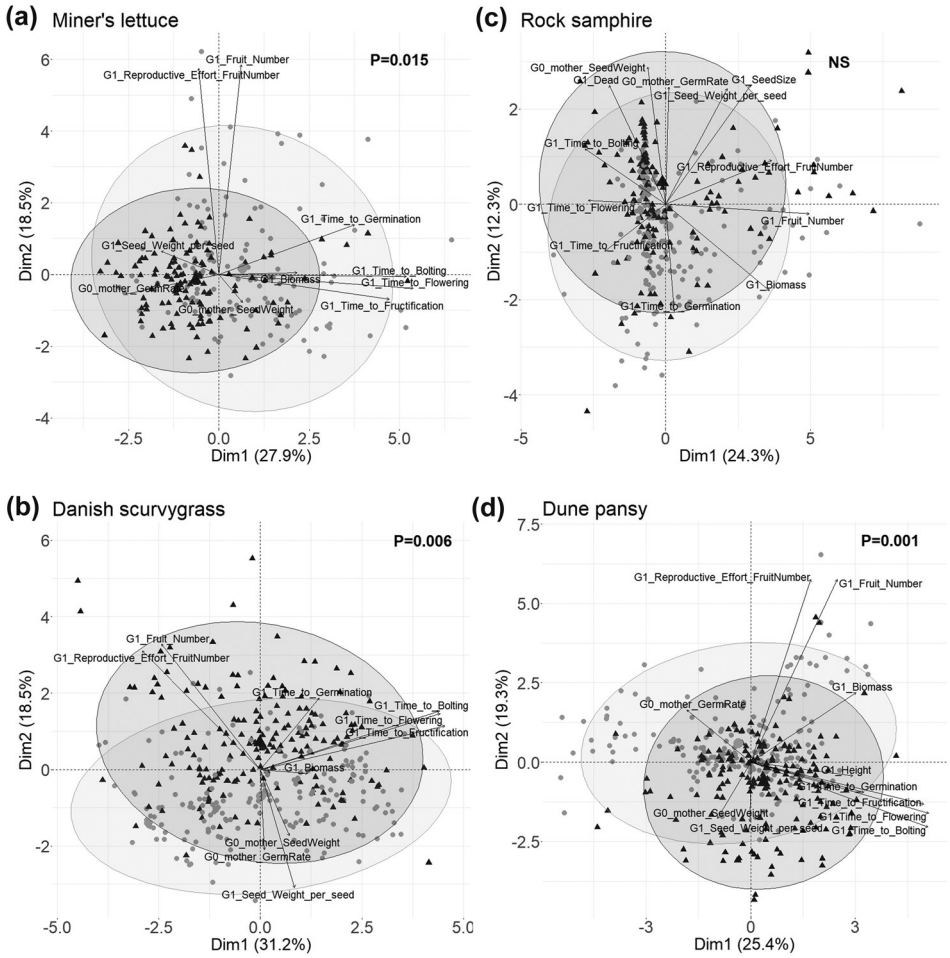


Figure 3. Principal component analysis (PCA) on life-history traits for miner's lettuce, Danish scurvygrass, rock samphire and dune pansy. Ellipses include 95% of individuals sampled from central sites (light grey; individuals pictured by circles) or marginal sites (darker grey, individuals depicted by triangles). Levels of significance of the multivariate ANOVA testing for differences among the suite of traits are indicated on each panel (ns: not significant). Traits included in this analysis are: G0_mother_SeedWeight, the weight of seeds of the progenitor G0 plant that led to G1; G0_mother_GermRate, the germination rate of these seeds; G1_Time_to_Germination, G1_Time_to_Bolting, G1_Time_to_Flowering and G1_Time_to_Fructification, the phenological traits of the G_1 plants; G1_Fruit_Number, the fruit number of G_1 plants; G1_Biomass and G1_Reproductive_Effort their biomass and reproductive effort. Because we observed some mortality in rock samphire, we also added this variable for that species (G1_Dead).

for dune pansy). Qualitatively, identical same results were obtained when removing the G_0 traits from the analysis (not shown). This indicates a shift in traits between central and marginal populations for all species except rock samphire.

More specifically, Table 1 summarizes initial expectations and observed trait differences between central and marginal populations. Expectations, when possible, were species-specific, depending for example on dispersal mode. For each species, there were significant differences for some traits. Nonetheless, no common pattern recurred across all studied species.

Consistent with increased seed dispersal abilities in marginal populations, in natura (G_0), seeds of marginal populations were lighter than those of central populations for miner's lettuce and Danish scurvygrass ($p < 0.001$, Fig. 4A–B), and the opposite was observed in the rock samphire ($p < 0.001$, Fig. 4C), all with a small effect size. In dune pansy, seed weight did not differ between central and marginal populations (Fig. 4D). Seeds of miner's lettuce marginal populations showed higher germination rates than those from central populations ($p < 0.001$; Fig. 5A, medium effect size), whereas Danish scurvygrass and dune pansies showed the opposite trend ($p = 0.002$ and $p = 0.025$; Fig. 5B, D). Furthermore, seeds from marginal populations of miner's lettuce, rock samphire and dune pansy germinated a few days faster than those from central populations (respectively, $p < 0.001$, $p < 0.001$ and $p = 0.030$; Fig. 6A, C, D), whereas the opposite trend was observed in Danish scurvygrass ($p < 0.001$; Fig. 6B). The differences described above, observed for seeds collected in natura, may be due to genetic effects or to phenotypic plasticity.

At later stages of the individual life cycle (traits measured on the G_1 common-garden-raised populations), phenological differences among central and marginal populations vanished in rock samphire and Danish scurvygrass (Supporting information). In miner's lettuce, central populations still displayed a slower reproductive phenology than marginal populations. On the contrary, in dune pansy, central populations exhibited faster reproductive phenology compared to marginal populations (Supporting information).

We should keep in mind that this common garden experiment may not perfectly reflect differential strategies modulating environmental specific fitness. However, because their germination rate was higher, marginal populations of miner's lettuce produced more offspring than did central populations, despite having a similar number of seeds produced per g biomass (Supporting information). In Danish

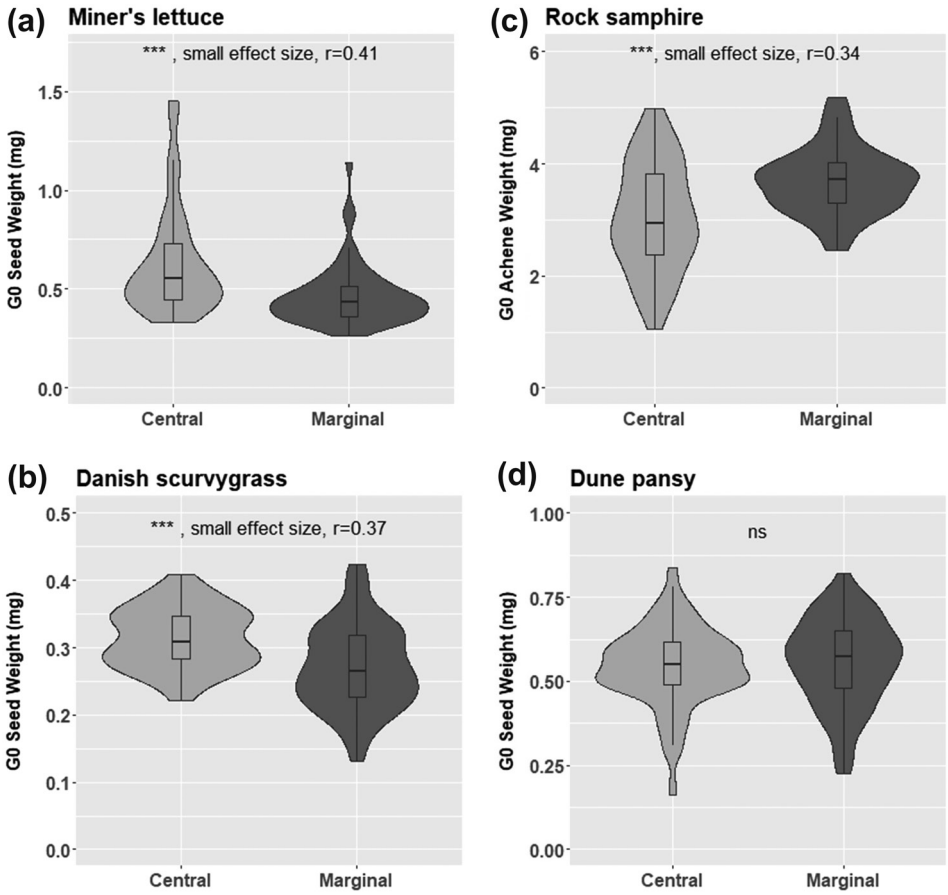


Figure 4. Violin plots and boxplots showing the distribution of the seed weight (G_0, in natura) for individuals from central (left) and marginal (right) populations of miner's lettuce, Danish scurvygrass, rock samphire and dune pansy. Results of the test for differences among central and marginal populations is provided. ns: not significant; ***: $p < 0.001$.

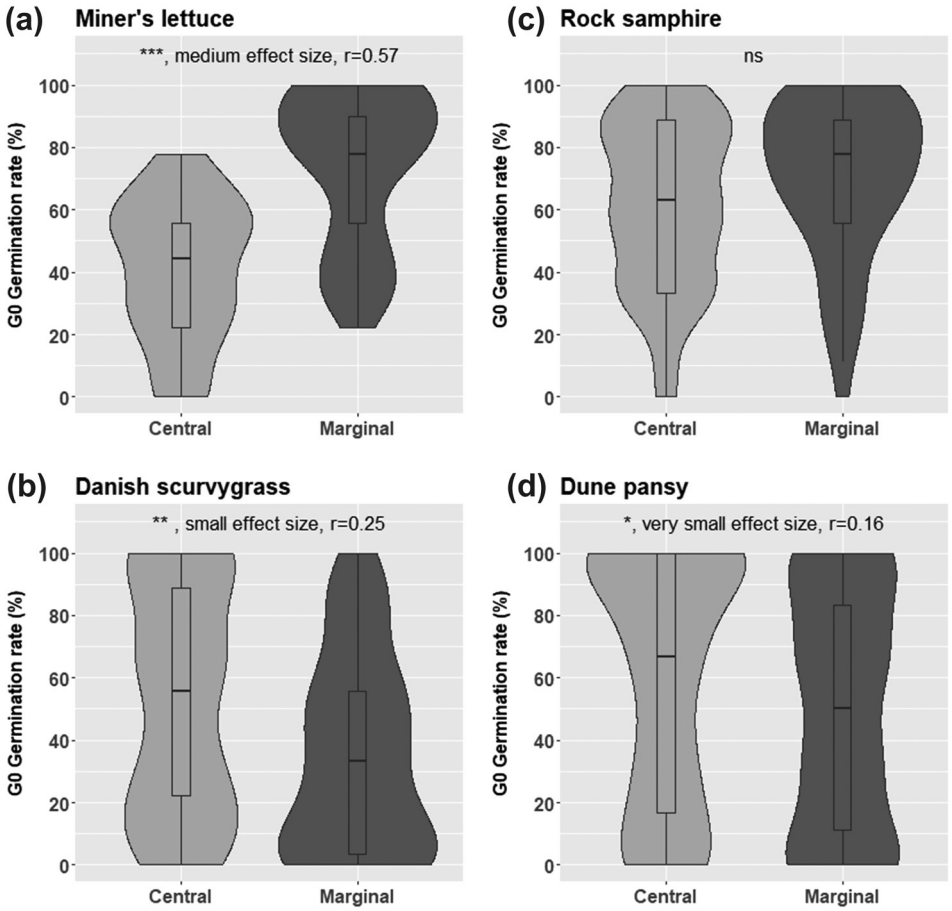


Figure 5. Violin plots and boxplots showing the distribution of the germination rate of seeds collected from central (left) and marginal (right) populations of miner's lettuce, Danish scurvygrass, rock samphire and dune pansy. Results of the test for differences in germination rate is provided: ns: not significant. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

scurvygrass, the reproductive effort of marginal populations outperformed that of central populations owing to a larger number of fruits per individual, for an equivalent biomass (Supporting information). However, this did not translate into increased fitness because the germination rate of marginal populations was lower (Supporting information). For rock samphire, marginal populations showed lower individual biomass than central populations but similar reproductive output and lifetime fitness (Supporting information). Finally, for dune pansy, marginal populations displayed reduced individual reproductive effort as compared to central populations (Supporting information).

Basis of phenotypic variation in seed traits: trait variation from G_0 to G_1

In miner's lettuce and rock samphire, seed weights converged in G_1, suggesting that variations observed in G_0 were mostly attributable to either maternal effects or phenotypic plasticity (Fig. 7A, C). In Danish scurvygrass and dune pansy, G_1 seeds were consistently heavier than G_0 seeds, and all populations showed similar slopes from G_0 to G_1 (Fig. 7B, D). Aside from transgenerational maternal effects, this result suggests a genetic basis for the differences in seed weight observed between central and marginal populations of Danish scurvygrass, despite environmental effects.

Finally, the previously observed differences in germination rates between central and range limit populations persisted from the field to the common garden, but this difference decreased for all species except miner's lettuce (Supporting information).

Geographic origin and mating system effects on seed traits

In contrast to miner's lettuce and Danish scurvygrass, dune pansies and rock samphires were unable to produce seeds in self-pollination bags, providing evidence for the need of biotic pollination vectors even though these latter two species are known to display a mixed mating system (Latron et al. 2020).

In miner's lettuce, open-pollinated seeds were lighter than selfed seeds, for both central and marginal populations (all at $p < 0.001$; Supporting information), and had a lower germination success ($p < 0.001$, data not shown). In contrast, for Danish scurvygrass, open-pollinated seeds were heavier

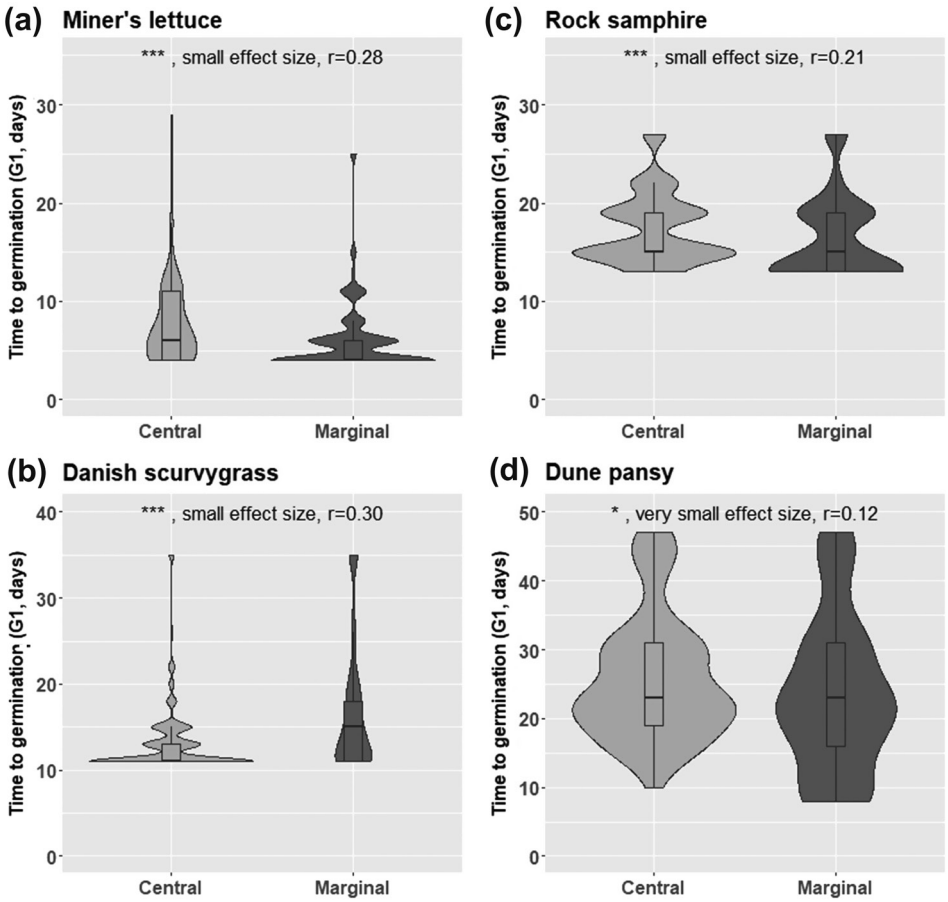


Figure 6. Violin plots and boxplots showing the distribution of the time to germination for seeds collected from central (left) and marginal (right) populations of miner's lettuce, Danish scurvygrass, rock samphire and dune pansy. Results of the test for difference in germination time is provided: *: $p < 0.05$; ***: $p < 0.001$.

than selfed seeds, for both marginal and central populations ($p = 0.01$ and $p = 0.03$ respectively; Supporting information), but did not differ in germination rate ($p > 0.05$, data not shown). Whether outcrossed or selfed, seeds of central populations were heavier than those from marginal populations (all at $p < 0.001$; Supporting information).

Discussion

Restriction in species' geographic ranges may stem from declining environmental suitability with increasing distance from the core of the species' ranges (Parmesan 2006, Phillips et al. 2010, Bontrager and Angert 2019; but see Pironon et al. 2017). This decline can result in reduced growth and reproductive output for peripheral populations, especially for expanding or receding populations that face suboptimal environmental conditions (Angert et al. 2020). These suboptimal conditions can select for modifications in life-history traits: marginal populations are theoretically expected to show higher dispersal ability, faster development, higher selfing rates and higher reproductive investment than central populations (reviewed by Chuang and Peterson 2016, Angert et al. 2020). Yet, empirical evidence supporting these intuitive predictions remain puzzling, and different traits can evolve independently among replicated populations located at leading edges (Williams et al. 2019, Miller et al. 2020), which questions the power of species' traits to predict range shifts (Beissinger and Riddell 2021). Our study focused on species with ongoing shifts in distribution ranges. Each of the above predictions was validated for at least one species. Nonetheless, the only prediction that was validated for all expanding species was increased seed dispersal abilities, through phenotypic plasticity or adaptive evolution in marginal populations of expanding species (at least for the seeds collected in natura).

Miner's lettuce: marginal populations showed increased germination rates and earlier phenology

Using a common experimental environment, and keeping in mind the potential limitations related to varying adjusted fitness in different local environments, the most salient difference between central and marginal populations of the annual miner's lettuce was earlier and higher germination rates of seeds from marginal sites, resulting in an overall higher

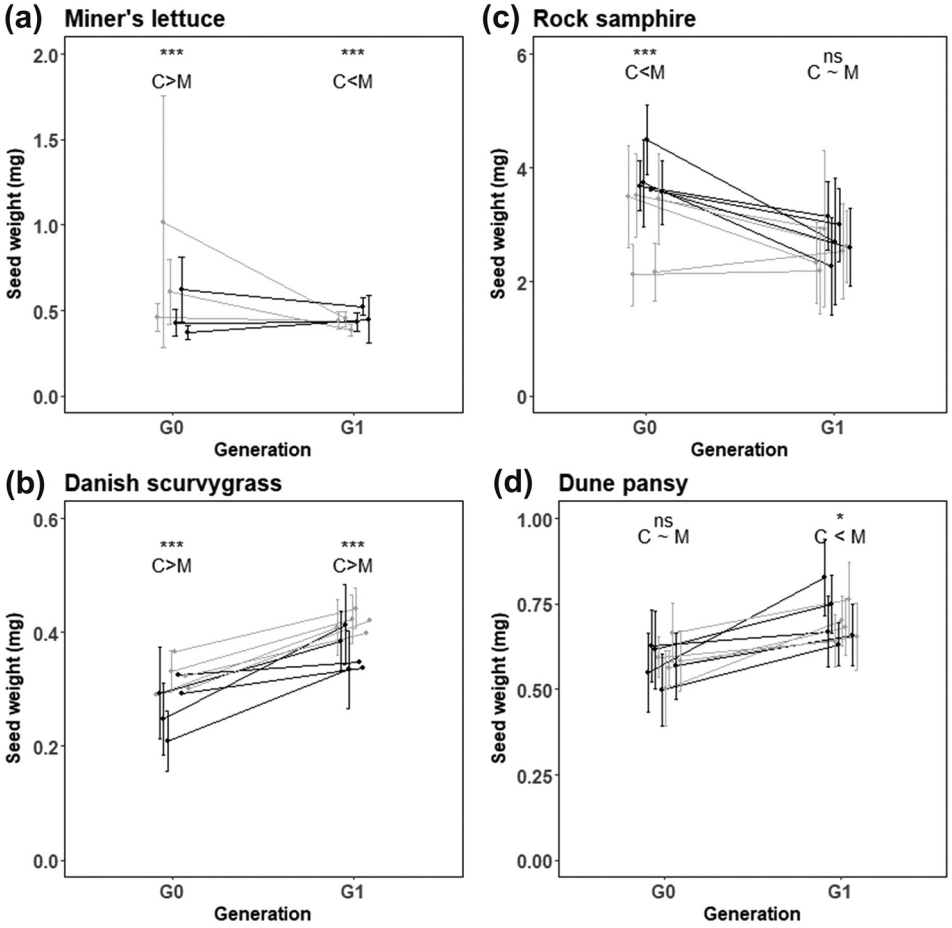


Figure 7. Mean seed weight of seeds collected in central populations (grey symbols) and marginal populations (black symbols) in natura (G_0) and of their common-garden raised offspring (G_1) for miner's lettuce, Danish scurvygrass, rock samphire and dune pansy. Error bars indicate standard deviations. Differences among central (C) and marginal (M) populations is provided for each generations; ns: non significant; * : $p < 0.05$; *** : $p < 0.001$.

individual fitness. Faster germination is expected in marginal populations (Chuang and Peterson 2016). Higher germination success is however more puzzling. Often observed in invasive species, seed dormancy loss in marginal populations may explain the higher germination success because it can speed up the colonization of marginal sites (Baskin and Baskin 2014). Seed dormancy is often highly heritable but can also show substantial phenotypic plasticity (Donohue et al. 2005, Wagmann et al. 2012, Blossey et al. 2017). In miner's lettuce, significant differences in germination rate persisted even after one generation in the common garden, indicating a putative genetic basis. One plausible explanation may be that marginal populations were founded by escapees from cultivation and that seed dormancy was selected against in cultivated populations, as commonly observed in crops (Fuller and Allaby 2009). These seed traits translate into a much higher fitness for marginal miner's lettuce populations, consistent with theoretical and empirical studies on expanding species (Burton et al. 2010, Colautti and Barrett 2013, Lustenhouwer et al. 2018). Faster germination in marginal populations translated in generally advanced phenology of these populations throughout their life cycle.

Theoretical expectations involving spatial sorting for increased dispersal (Phillips et al. 2010) were not expected – nor observed – in the case of miner's lettuce, because of accidental human-mediated dispersal events in inland habitats.

Regardless of their origin, all populations were able to autonomously self, with no evidence for inbreeding depression in early life stages. Moreover, selfed seeds even germinated better than open-pollinated ones. This result is in line with the high selfing rates observed in American miner's lettuce populations (Miller 1978). Altogether, self-fertilization and evolvable seed traits make miner's lettuce a good candidate for expansive dynamics (Pannell 2015).

Danish scurvygrass: smaller seeds in marginal populations

Consistent with the spatial sorting hypothesis (Phillips et al. 2010), individuals from marginal roadside populations produced smaller – and likely more dispersive – seeds than those from central populations. This effect persisted in the common garden, indicating an evolutionary shift towards smaller seeds in marginal populations.

These smaller seeds also showed delayed germination and a lower germination rate than those from central populations, consistently with dispersal trading off with other components of individual fitness, as expected from simulations of range-expanding populations (Burton et al. 2010). Two non-mutually exclusive hypotheses can be put forward. First, smaller seeds may show reduced germination success (Moles and Westoby 2004). Alternatively, weak competition in marginal habitats – i.e. the first few centimetres from the asphalt along motorways – may release the pressure for earlier germination in marginal populations (Rathcke and Lacey 1985). Despite delayed germination, the phenology of marginal populations of Danish scurvygrass did not differ from central populations for later life stages, indicating faster development. Faster growth rate in expanding edge populations is a common feature (Chuang and Peterson 2016), which has been observed both in non-invasive (Lustenhouwer et al. 2018) and invasive plant species (Colautti et al. 2006).

Regarding selfing ability, bagged inflorescences were able to set fruits and seeds that germinated at least as well as free-crossed flowers, for all populations. This indicates autonomous selfing regardless of geographic origin, with no or weak inbreeding depression, at least until the seedling stage. Autonomous selfing and evolvable seed dispersal capabilities have likely contributed to the rapid expansion of Danish scurvygrass along European roadsides, again supporting theoretical expectations (Angert et al. 2011, Pannell 2015).

Rock samphire: highly variable populations, no obvious differences between central and marginal populations

Most traits in the rock samphire showed large inter-individual and inter-population variance that did not follow a core-to-edge geographic trend. In the multivariate trait space, central and marginal populations were not significantly differentiated (Fig. 3).

Marginal rock samphire populations showed slightly larger achenes than did central populations, which may translate into higher buoyancy and longer-distance dispersal. However, because seeds remain viable for several months in seawater, this species seems to be a good colonizer regardless of achene size (Ridley 1930). Accordingly, this species shows weak spatial genetic structure (Kadereit et al. 2005, Latron et al. 2020). Continuous gene flow among populations probably rapidly wipes out any phenotypic differentiation over large spatial scales. Finally, autonomous selfing was not possible in this species, despite high selfing rates observed in natural populations (Latron et al. 2018, 2020). Provided that pollinators are present, rock samphire is thus a good colonizer because mates are likely to be present in marginal habitats owing to frequent long-distance dispersal of seeds drifted by marine currents (Latron et al. 2020), a pattern also documented in the coastal hydrochorous wild beet *Beta vulgaris* ssp. *maritima* (Leys et al. 2014).

Dune pansy: trailing-edge populations showed reduced individual reproductive output

Compared with individuals located in trailing-edge populations, those from central populations showed better germination success, earlier flowering and a better reproductive output, which resulted in a higher overall individual fitness. Low reproduction is thus likely to threaten the persistence of marginal receding populations of the dune pansy. Although dune pansies from central populations were small with many stems and ramifications, those from marginal sites were tall with a single stem and fewer ramifications, resulting in fewer flowers (Supporting information). This difference in plant architecture persisted in a common environment, indicating a genetic basis or maternal effects. The difference in plant architecture may result from increased competition for light from gorse and marram grass in marginal populations: while central populations were found in semi-stabilised sand dunes with low vegetation, marginal populations were found on older, more vegetated dunes. Thus, in concert with habitat fragmentation, dune management strategies in marginal sites have indirectly driven a lower seed production through increased interspecific competition for light. This brings into question the long-term demographic stability and persistence of rear-edge dune pansy populations, a concern of general importance for rear-edge populations (Hampe and Petit 2005, Vilà-Cabrera et al. 2019). Lastly, dune pansy individuals were not able to autonomously self-fertilize. Pollinator scarcity and mate limitation may be additional factors threatening marginal dune pansy populations by increasing levels of inbreeding, as observed using progeny arrays (Latron et al. 2020).

Caveats and perspectives

Limits of the study: interplay between phenotypic plasticity and adaptive evolution, and environmental drivers of variation between central and marginal locations.

Given the increasing pace of human-induced environmental changes, species responses to environmental changes are critical to their persistence. Phenotypic changes under novel conditions may occur either through phenotypic plasticity or through adaptive evolution (Franks et al. 2014, Fox et al. 2019). Phenotypic plasticity reflects the ability of one genotype to adjust its phenotype as a function of the environment. It may be adaptive or not. Adaptive phenotypic plasticity would result in modified phenotypes having increased fitness (Fox et al. 2019). In contrast, adaptive evolution for a particular phenotype involves changes in the genetic variation as the result of natural selection. Yet, the interplay between genotypes, environment and phenotypes may be not straightforward, in particular because phenotypic plasticity is itself a trait that can evolve and that may, or not, be adaptive (Fox et al. 2019). Reaction norms help to detect the occurrence of phenotypic plasticity.

In this respect, and beyond maternal effects that are inherently difficult to detect (Kuijper and Hoyle 2015), our results suggested a substantial effect of plastic variation for seed traits

potentially involved in dispersal capabilities, as shown in various plant species (Schlichting 1986, Thomann et al. 2015, Gan et al. 2020). Increased dispersal abilities at leading edges are expected to be selected for (Phillips et al. 2010, Chuang and Peterson 2016), whether from genetic adaptation, or through evolved phenotypic plasticity (which would confer higher dispersal abilities in ecologically marginal sites). The adaptive value of the observed general trend for increased dispersal in marginal populations for the three expanding species we surveyed needs further investigation. Indeed, reaction norms may evolve provided there is standing genetic variation for phenotypic plasticity, a challenging field of research which is far beyond the scope of our study.

Besides, significant changes in life history traits are often related to differences in biotic and abiotic factors between central and marginal locations (Pironon et al. 2017). Although there are no obvious differences in coarse climatic factors (mean temperature and mean precipitation) among sampled locations and the location of the common-garden we used, we cannot rule out the influence of several other factors, such as habitat suitability, level of competition, variation in soil type or of finer climatic cues on the surveyed life-history traits regardless of centrality or marginality of sampled populations. Nonetheless and keeping in mind these potential limitations, a set of general considerations can be drawn from our results.

Is self-fertilization more frequent in marginal populations?

If marginal populations are of small census size, self-fertilization is supposed to be favoured by natural selection, regardless of whether these populations are on the leading or trailing edge of their distribution (Baker 1955, Levin 2012, Grossenbacher et al. 2015). This trend is however likely to be transient (Pannell 2015). We did not find differences between central and marginal populations in their ability to self-fertilize autonomously for any of the investigated species. However, in natura, receding marginal populations of the dune pansy indeed showed higher local inbreeding levels than did central populations (Latron et al. 2020). Thus, the only conclusive support for increased selfing rates was observed in a receding plant species, whereas no clear trends were discerned for expanding mixed-mating species on their colonization front. The propensity for shifts in mating system may thus not be as common as expected towards range margins for recently expanding species (Barrett 2010, Pannell 2015). In addition, we only have sampled one replicate of range expansion for each species, while theory suggests that eco-evolutionary dynamics may lead to variability across replicates of a geographic range expansion (Williams et al. 2019).

Does dispersal ability increase in marginal expanding populations?

Expanding populations are theoretically expected to show high dispersal ability through spatial sorting (Phillips et al. 2010, Shine et al. 2011). These changes can be due to genetic adaptation. Alternatively, adaptive phenotypic plasticity for increased long-distance dispersal could be more extensive at range margins to cope with heterogeneous and fluctuating environment, especially in anthropogenic areas (Valladares et al. 2014). In natura, we observed this pattern of increased dispersal in marginal populations of the three expanding species: smaller seeds in marginal populations of the wind-dispersed Danish scurvygrass, smaller seeds in marginal populations of the wind and ant-dispersed miner's lettuce, and larger, more corky achenes in marginal populations of the hydrochorous rock samphire. As mentioned above, these trait differences between central and marginal populations disappeared in the common garden for two species, which suggest phenotypic plasticity or maternal effects.

More generally, our results suggest that plastic or evolutionary shifts in dispersal ability in marginal populations can occur, and should be considered when forecasting species' distributions (as in LaRue et al. 2019).

Do marginal populations show faster life cycles?

Earlier phenology may be expected in unpredictable environments and when interspecific competition is high (Cohen 1966, 1971, Rathcke and Lacey 1985, Lustenhouwer et al. 2018). Colder climates also select for lower temperature needs to complete plant development (Rathcke and Lacey 1985, Wagmann et al. 2012). Only miner's lettuce showed earlier phenology of marginal populations until fructification. For Danish scurvygrass, germination of marginal populations was delayed, but later phenology was identical to that of central populations. Besides, earlier phenology of marginal populations was expected in marginal rock samphire populations because they extend towards colder sites. However, long-distance episodes of gene flow through achene drifting are likely to prevent local adaptation in this species (Latron et al. 2020). Finally, dune pansies from receding marginal populations showed delayed flowering because they grew to taller sizes before producing flowers, presumably in response to shading (Abrahamson and Gadgil 1973). Therefore, due to tradeoffs and to stochastic processes such as genetic drift, gene surfing and expansion load, marginal environments may drive stochasticity in life-history traits under selection. This explains why expected changes in life-history traits do not necessarily occur at geographic range margins (Williams et al. 2019, Miller et al. 2020, Beissinger and Riddell 2021).

Conservation perspectives in anthropogenic environments

Land use clearly affects habitat availability and connectivity for all surveyed species. Danish scurvygrass has not yet colonized secondary road networks in France as the species did in England or Belgium, perhaps because salinity levels differ. Alternatively, colonization may just be a matter of time, and further investigations are needed as to the habitat requirements of Danish scurvygrass. For miner's lettuce, additional studies of seed dormancy and viability, of population genetic

structure and of levels of ploidy are required. Identification of the locations where miner's lettuce was cultivated would also help to understand the salient pattern of higher germination success of marginal populations. For rock samphire, careful prospecting resulted in no population of this species in natural habitats along the North Sea coast: all populations were located on artificial rocky habitats. Thus, this thermophilic species may benefit from climate warming, but its northeastwards expansion seems to be limited by the availability of anthropogenic rocky shores. This potential limitation stresses the importance of specific habitat availability during migration in response to climate change (Guo et al. 2018).

Finally, dune fixation and fragmentation have led to habitat loss and fragmentation towards the trailing edge of the distribution of the dune pansy and its patterns of genetic structure indicated a loss of efficient connectivity among trailing-edge populations (Latron et al. 2020). Higher vegetation cover in these habitats may increase the level of competition for light, selecting for taller plants with lower reproductive output. As such, rear-edge populations of dune pansy matched all aspects of marginality by their ecological and genetic distinctiveness and by their declining demography (Vilà-Cabrera et al. 2019). However, preliminary interpopulation crosses (Latron et al. unpubl. data) did not reveal outbreeding depression in this species, an encouraging result for potential reinforcement of marginal populations with seeds from central Dutch populations.

Conclusion

Our results showed that marginal populations of four different plant species displayed somewhat contrasting life-history traits compared with central populations. Some of these shifts were conserved in the common garden, indicating significant evolutionary shifts or maternal effects. Nonetheless, only traits potentially related to seed dispersal ability consistently exhibited changes consistent with theoretical expectations. Other shifts in life-history traits were essentially species-specific, involving idiosyncratic responses to ongoing range dynamics, a pattern consistent with evolutionary stochasticity owing to different demographic histories, levels of population connectedness and amount of genetic variation (Angert et al. 2011, Miller et al. 2020). This idiosyncrasy raises concerns as to our capacity to forecast shifts in species' distributions because dispersal ability or other ecological niche-related traits may evolve very fast and stochastically (Williams et al. 2019, Beissinger and Riddell 2021), which could impact the outputs of species distribution models (Bush et al. 2016, LaRue et al. 2019).

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Author contributions

Mathilde Latron: Data curation (equal); Formal analysis (equal); Investigation (lead); Methodology (equal); Validation (equal); Writing – original draft (lead); Writing – review and editing (equal). **Jean-Francois Arnaud**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Eric Schmitt**: Investigation (supporting); Methodology (supporting). **Anne Duputié**: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.gf1vhhmst (Latron et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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