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## Original Research Article

## Experimental test of assisted migration for conservation of locally range-restricted plants in Alberta, Canada

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## ABSTRACT

Given projected rates of climate change, species with limited dispersal may be unable to migrate at the pace necessary to maintain their current climate niches. This could lead to increased risk of extirpation or extinction, especially for locally range-restricted species within fragmented landscapes. Assisted migration has been suggested as a proactive conservation tool to mitigate these risks. We tested assisted migration for *Liatris ligulistylis* and *Houstonia longifolia*, two perennial forbs considered ‘vulnerable’ and ‘imperilled’, respectively, in Alberta, Canada, where they are at their northern and western range limits. Both mature plants and seeds were translocated to replicate sites at four geographic locations along a north-south gradient representing the current ranges of the species (central) and areas south (warmer) and north (cooler) of their current range. *L. ligulistylis* adult plants thrived ~500 km north of the species current range with survival, growth, and flowering similar to or exceeding performance in the current range, the influence of soil was also tested by comparing the performance of transplanted mature plants in soil from the source location versus the translocation (recipient) site. Plants planted into soil from the source location had increased flower bud production at all sites. Seedling establishment was significantly higher at sites north of the current range, but much lower in the southern locations. These results suggest that *L. ligulistylis* is in climate disequilibrium, potentially due to migration lags, and that it might be vulnerable to near-future climate vulnerability. For *H. longifolia*, the influence of flower morph type and location were tested. Only 8 out of 130 translocated adult plants survived, five with thrum flowers and three with pin flowers; no seedling establishment was observed in the first growing season, which experienced drier than normal conditions. Among the eight adult plants, seven survived in the central location and one in the north demonstrating specific habitat requirements and conditions that may make this species difficult for translocation and establishment. Overall, locally rare and range-restricted plants with limited dispersal demonstrate climate sensitivity to current conditions and potential for assisted migration, yet species-by-species testing is needed to understand vulnerability and efficacy of this approach.

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## 1. Introduction

Climate change is altering the distributions and geographical ranges of species (IPCC, 2014; Parmesan, 2006) with these shifts projected to be even more pronounced in the future (Thomas et al., 2004; Urban, 2015; Zhang et al., 2017). Those species that are unable to keep pace with their shifting climatic niches will decline (Chauvenet et al., 2013; Early and Sax, 2011); this is especially so for species with low dispersal, small population sizes, long generation times, high habitat specificity, and in areas lacking connectivity (Barber et al., 2016; Gallagher et al., 2015; Loss et al., 2011). To address these factors, assisted migration has been proposed as a proactive conservation tool (McLachlan et al., 2007; Schwartz et al., 2012; Thomas, 2011).

Assisted migration, also referred as managed relocation (Richardson et al., 2009; Schwartz et al., 2012) or assisted colonization (Hällfors et al., 2014), involves moving organisms to locations that are predicted to be more suitable under future climate conditions (Loss et al., 2011; McLachlan et al., 2007). This can help combat multiple stresses due to climate change, while overcoming dispersal barriers when these occur. Liu et al. (2012) assessed the effects of two extreme weather events, a cold spell and a drought event, on the survival of 20 species of wild orchids with 462 individuals translocated beyond their current ranges and compared to individuals within their ranges. They found a 10% mortality in the cold spell, but no mortality in a drought suggesting that assisted migration may be a viable conservation tool for endangered orchids. However, not all trials establish that well. Drayton and Primack (2012) conducted a re-census of eight perennial plant species 15 years post-reintroduction finding that almost all the populations had disappeared. Ongoing assisted migration trials (e.g., four species of *Quercus* (Martín-Alcón et al., 2016), *Picea glauca* (White spruce, Prud'homme et al., 2018), and *Ochotona princeps* (American pika, Wilkening et al., 2015)) have provided further ecological information. However, there may be an underlying bias in reported information on translocations with emphasis on successful projects (Hällfors et al., 2018).

The translocation of species has a long history of use (Thévenin et al., 2018; Vitt et al., 2010) but it requires that social, political, economic and ecological issues all be addressed. Risks, such as that of invasiveness, and the uncertainty of outcomes must be weighted against the risk of species extinction or severe genetic impoverishment. Proper planning is essential before assisted migration is attempted (Abeli et al., 2014; Mueller and Hellmann, 2008). Climates of the translocation sites should match as closely as possible to the bioclimate envelope of the species range (Reichard et al., 2012) and measures should be taken to avoid herbivory (Fenu et al., 2016). It can be especially difficult to get social acceptance from the public.

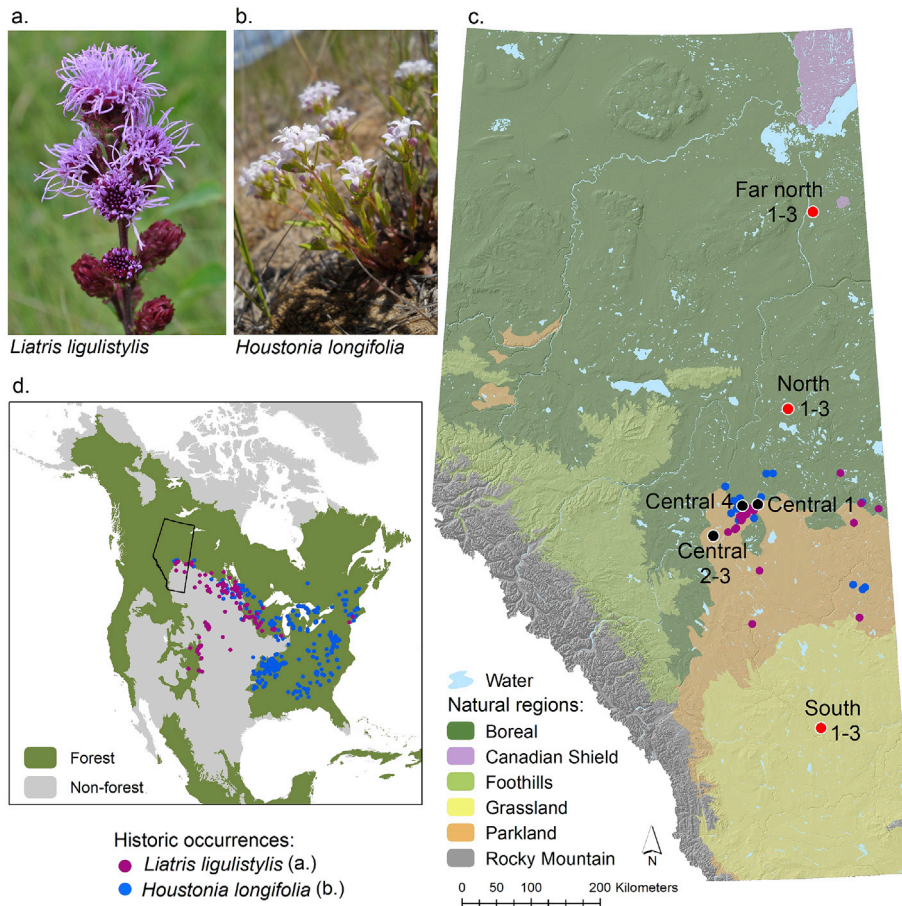
Assisted migration has also been regarded as the strongest method for testing the relationship of range and niche limits (Gaston, 2003). A recent synthesis of translocation experiments showed that range limits are often niche limits (Lee-Yaw et al., 2016). However, another meta-analysis of translocation experiments found weaker support for a coincidence between range and niche limits (Hargreaves et al., 2014) with the exceptions being largely explained by dispersal. Dispersal limitation depends on the species' intrinsic dispersal ability and on environment characteristics (e.g., fragmentation) that constrain a species' geographic distribution (Lawler et al., 2013; Svenning et al., 2008).

Here we examine translocations for two locally rare and range-restricted forbs – northern blazing star (*Liatris ligulistylis* (A. Nelson) K. Schum.; Moss, 1983) and long-leaved bluets (*Houstonia longifolia* Gaertn., Moss, 1983), which are restricted locally to the Central Parkland natural sub-region (ACIMS, 2015) in Alberta, Canada. A region that has experienced some of the highest levels of habitat loss and fragmentation in the province (Barber et al., 2016) mainly as a result of conversion to till cropping and grazing and some areas of oil and gas exploration and extraction (Alberta Natural Regions Committee, 2006). This region also occurs at a high latitude where climate warming is expected to be higher than at lower latitudes, with substantial impacts projected for species (Santangeli et al., 2017; Zhang et al., 2015). Our purposes were to evaluate the species' local vulnerabilities to projected climate change, provide empirical data on how range limits relate to niche limits, and assess the potential use of assisted migration as a conservation tool for these species. To do this, we test two hypotheses: (1) plant performance (survival, growth, reproduction and colonization) will be poorer at southern translocation sites that represent projected future (~2080's) climate conditions (Schneider, 2013) within the species' current ranges; and 2) translocations north of these species' current ranges will lead to poorer performance (survival, growth, reproduction and colonization) when compared to their current ranges, but better performance than at sites south of the current range. Support for the first hypothesis would suggest local vulnerability to near future (2080s) warming, while lack of support would suggest adaptability to projected climate change. Support for the second hypothesis would suggest that the species is in climate equilibrium within the current range and thus locally adapted to a narrow climatic range, especially if the first hypothesis was also supported. Alternatively, if plant performance in the north is similar to, or exceeds that of, its current range it would suggest that the current distribution of the species is limited by dispersal barriers, supporting hypotheses of migration lags and climate disequilibrium. The use of assisted migration strategies would be a suitable conservation tool if the two hypotheses were supported, and strongly suitable if the first hypothesis (climate vulnerability) was supported and the second hypothesis (climate equilibrium) was rejected.

## 2. Material and methods

### 2.1. Study area and species

*L. ligulistylis* and *H. longifolia* are two perennial forbs that are found in Alberta (Fig. 1). This semi-arid western province of Canada encompasses 66.2 million hectares including six natural regions: Boreal, Canadian Shield, Foothills, Grasslands, Rocky



**Fig. 1.** Geographical locations of *Liatris ligulistylis* (a) and *Houstonia longifolia* (b) translocation sites (c) and historic element occurrence locations in Alberta, Canada (d). Locations north of these species' ranges were established to test the success of assisted migrations to higher latitudes (cooler climates). The south location was established to test the species' climate change vulnerabilities, as this area is predicted to be similar to the predicted future (2080s) climate in the species' current range (warmer climate). All replicate sites contained seeds and adult plants of both species, except Central-4 (Gibbons Field) which had only *H. longifolia*. Location of Alberta in North America shown as a dark outline in inset map that also depicts historic occurrences of each species in North America relative to the distribution of forested ecosystems (d). Base maps are from Alberta Natural Regions Committee (2006). North American records of species from Global Biodiversity Information Facility (2019).

Mountains and Parkland (Alberta Natural Regions Committee, 2006) (Fig. 1). These regions all have short summers and long and cold winters. Mean annual temperature ranges from  $-2.6^{\circ}\text{C}$  in the Canadian Shield to  $4.0^{\circ}\text{C}$  in the Grasslands. Mean annual precipitation varies from 374 mm in the Grasslands to  $\sim 800$  mm in the Rocky Mountains (Zhang et al., 2015). Altitude ranges from 152 m near the Northwest Territories border in the north to 3747 m in the Rocky Mountains along the southwest border (Faramarzi et al., 2017). Both these species' current ranges occur at their northern and western limits and are locally restricted to the Central Parkland natural sub-region in Alberta (ACIMS, 2015) with boreal forests to the north and grasslands to the south.

*L. ligulistylis* is in the family Asteraceae. It has stem heights between 30 and 80 cm, alternate leaf arrangement, and multiple purple heads with disc florets (Royer and Dickinson, 2007). The root system contains corms, which when dormant are useful for translocation of adult plants. It is distributed in Canada (Alberta, Saskatchewan and Manitoba) and the Mid-western USA (Colorado, Iowa, Nebraska, Wyoming, Connecticut, Illinois, Minnesota, Montana, New Mexico, North Dakota, South Dakota, and Wisconsin), with a conservation status of 'vulnerable' (S3) in Alberta (NatureServe, 2013) (Fig. 1d). In the U.S. it is found in more eastern locations where warmer temperatures would be compensated by increased precipitation. Within the grasslands it is found on sites close to where forests are present (e.g., Black Hills of South Dakota) and in the mountainous states of west-central U.S. it is limited to the front ranges of the mountains associated with ecotones with forested environments. Due to its limited distribution in Alberta, it is believed to have a narrow climatic niche, as no occurrences are found to the north (cooler boreal forest) or to the south (drier and warmer grasslands) despite extensive botanical surveys. *L. ligulistylis* is usually found on open woodlands, moist meadows, and sand-hills (Royer and Dickinson, 2007), with extant populations in Alberta restricted to stable isolated eolian sand dunes, and sandy verge habitat such as roadsides. *L. ligulistylis* blooms in late July to mid-August with seeds dispersed from September to November by wind with the

help of a bristly pappus attached to the achene (Royer and Dickinson, 2007). Although data on this species' dispersal abilities are lacking, as is the case for many plant species (Royal Botanic Gardens Kew, 2015), a status report for the related *Liatris spicata* with similar seed morphology indicated only moderate dispersal success over short distances (COSEWIC, 2010). With limited dispersal and high fragmentation levels of 78% within the Central Parkland natural sub-region (Barber et al., 2016) this species may be unable to migrate with its shifting climate range. Therefore, *L. ligulistylis* is considered a good candidate for testing both climate/range limits and possible use of assisted migration.

*H. longifolia* is in the madder family (Rubiaceae). This species has multiple (1–100) short (~15 cm) reproductive stems, opposite leaves, and purplish to white funnel-shaped flowers (Beliveau and Wyatt, 1999; Royer and Dickinson, 2007). It is a distylous species having two distinct floral forms (pins – long style with short stamen, thrum – short style with long stamen) with a strong self-incompatibility system (Beliveau and Wyatt, 1999). *H. longifolia* is found in five Canadian provinces of Alberta, Saskatchewan, Manitoba, Ontario, and Quebec, as well as being distributed in the Midwestern and Eastern USA (every state east of the Mississippi River except Delaware, plus North Dakota, Minnesota, Missouri, Arkansas and Oklahoma, Kansas, and Texas). The conservation status is 'imperilled' (S2) within Alberta (NatureServe, 2013). Like *L. ligulistylis* its habitat is primarily sandy woodlands and dunes (Royer and Dickinson, 2007), or along sandy roadside verge habitat. *H. longifolia* flowers from early June through July (Beliveau and Wyatt, 1999) with seeds maturing by September. This species' seeds lack any features designed to improve dispersal, with only gravity dispersal occurring from seeds falling out of split ovoid capsules at the top of the stem (Kershaw et al., 2001). Based on its limited dispersal, current level of habitat fragmentation within its range, and the expected rate of climate change, it has recently been ranked the 10th most vulnerable plant to climate change out of 419 rare plant species assessed for Alberta (Barber et al., 2016). Therefore, *H. longifolia* is deemed to be an ideal candidate for testing climate/range limits and use of assisted migration.

## 2.2. Translocation experiments

Four geographical locations for assisted migration were established from 2012 to 2014 across Alberta (Tables S1 and S2), each with three replicate sites for *L. ligulistylis* and *H. longifolia*, except for the central location of *H. longifolia* which had four replicates (Fig. 1). The most southern sites were located at ~450 km south of the species' current range; this area experiences about 1.8 °C higher temperature and 21 mm lower precipitation than the current range (i.e., the central location) during the growing season (April–August) (Fig. S1). It is expected to reflect the future (2080s) climate (Schneider, 2013) within the current range and thus would indicate vulnerability to future climate change. Six translocation sites were established north of the species' current range (three ~200 km north of the current range, and three ~500 km north of the current range) to test the success of immediate assisted migrations and the presence of a possible current climate disequilibrium. Compared to the current range, these north sites show the similar, but slightly cooler trend in temperature (~0.6 °C lower) and different trends (North: ~5 mm lower, Far North: ~16 mm lower) in precipitation during the growing season (April–August) (Fig. S1). From the mid-20th to the end of 21st, the climate tends to be hotter and drier in the southern location and presents a relatively stable tendency in the northern locations relative to the current range. Three translocation sites for both species and a fourth one for *H. longifolia* were established within their current climatic ranges to provide a control for the effects of translocation. These four locations will herein be referred to as south, central, north and far north (Fig. 1). Among them, only the central location of the study species has naturally occurring populations of these species in Alberta. In all instances, recipient sites were selected to be semi-open sites with sandy silt soils derived from stabilized (vegetated) dunes arising from post-glacial periods. The translocations were set up in the style of "Common garden" type trials, being established in "natural" sites (unmanaged, not subject to human disturbance) and were mildly prepared (competing vegetation removed) prior to planting of mature plants and sowing of seeds.

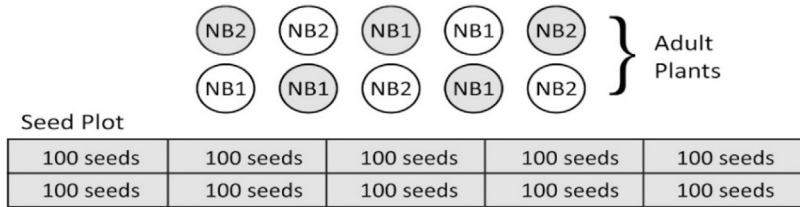
### 2.2.1. *Liatris ligulistylis*

One pilot site was established at each of the south, central, and north locations in October of 2012 (Table S1). At each site 10 mature *L. ligulistylis* corms were translocated from populations collected in two areas: Bruderheim (Fig. 2, Central 2–3) and Ukalta (~50 km northwest of Bruderheim). Before planting, corm weight, width and height were recorded for all collected adult plants. In addition to the translocated corms, seed plots were also established by clearing vegetation to bare sand and sowing 200 seeds collected from those same two areas at each site. However, these plots had little or no seedling emergence and the seeding plot at the southern site was destroyed due to third party activities.

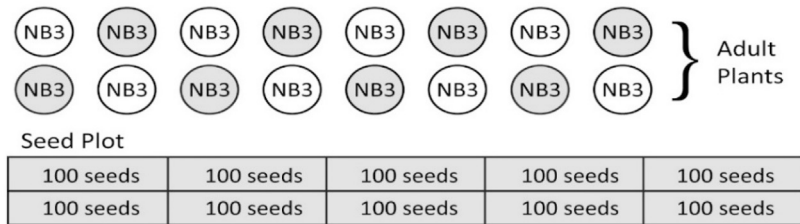
A preceding survey of *L. ligulistylis* found a large population (~88,000) in North Bruderheim in 2013 (largest population known in the province). In 2013 a new sowing trial was established in the pilot sites in which 1000 seeds, collected from *L. ligulistylis* plants from North Bruderheim, were sown evenly into 10 seed plots at each site (Fig. 2a). Also, in 2013, two new replicate sites were added at the south, central and north locations and three new replicates were established at the far north location (Table S1). These replicates were established using 144 of the 150 corms collected from the Bruderheim population, as well as seed from these plants. At both the 2012 and 2013 replicate sites, adult corms were planted into 2-gallon plastic pots with either recipient (the translocation site) or source soil randomly assigned to each pot. Enclosures made from chicken wire were established around each pot to prevent herbivory of adult plants, as deer grazing on the plants was observed in natural populations. At each of the 2013 replicate sites, 10 seed plots (~30 cm × 30 cm) were delineated and separated by a 20 cm buffer. The soil was lightly raked in each of the 10 plots and 100 seeds were sown in the middle of each plot and thinly covered



**(a) 2012 Experimental Design**



**2013 Experimental Design**

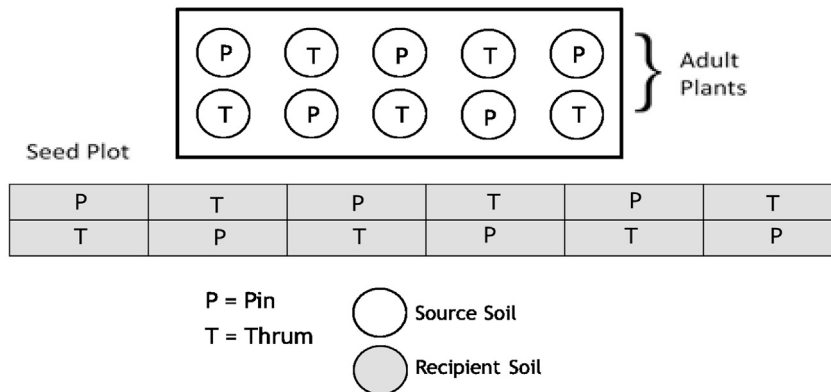


**Legend**

NB1 = 1 Northern Blazing Star Corm from Ukalta, AB      NB2 = 1 Northern Blazing Star Corm from Bruderheim, AB      NB3 = 1 Northern Blazing Star Corm from North Bruderheim Provincial Recreation Area, AB

○ Source Soil      ○ Recipient Soil

**(b)**



**Fig. 2.** Experimental design for *Liatris ligulistylis* (a) and *Houstonia longifolia* (b) translocations. (a) NB number represents the source area of adult plants of *L. ligulistylis*: Ukalta (NB1), Bruderheim (NB2) and the North Bruderheim Provincial Recreational Area (NB3); the color of circle represents soil origin: source soil from the collection site (white) or recipient soil from the translocation site (grey). (b) P and T represent different floral morph (Pin vs. Thrum) of *H. longifolia* adult plants. Each quadrat (rectangles in b) contained seed from one plant, although due to a limitation of seed, seed from some plants was divided between two quadrats. The number of seeds sown per quadrat varied from 8 to 2817.

with soil (Fig. 2a). Time lapse cameras (Wingscapes TimelapseCam 8.0) were used at each site in the spring of 2014 to capture phenology of adult plants with four pictures per day programmed between 11:30 a.m. to 1:00 p.m.

Composite soil samples were collected from each site and analyzed to determine variations between source and recipient soils. The Dumas combustion method was used to determine total nitrogen (TN) and total organic carbon (TOC) of these soil samples. Then electrical conductivity (EC) and pH were recorded with the use of a pH/EC meter. Finally, to determine phosphorus and potassium levels a Modified Kelowna extraction was used, followed by an Atomic Absorption analysis for potassium and Colorimetric methods for phosphorus.

**2.2.2. *Houstonia longifolia***

A native pasture (privately owned) containing a large population (~50,000) of *H. longifolia* was discovered near the town of Gibbons, Alberta (Central 4). Collections from this site (Gibbons Field) were split evenly between pin and thrum floral morphs; whole plants were collected along with soil to prevent damage to their fine fibrous roots. Collected individuals were

then planted into half gallon plastic pots with source soil from the collection site. In September 2014, 10 of these adult plants were translocated to each site (Table S2), with an even proportion of pins (five) and thrums (five). Chicken wire enclosures were used around each pot to prevent herbivory by ungulates. Experimental seed plots were also established; at two sites for each of the four locations (south, central, north, and far north) these consisted of 12 quadrats (30 cm × 30 cm) separated by a 20 cm buffer while, due to seed limitations, the remaining sites had six quadrats. Seed from pins and thrums was sowed in different quadrats to examine differences in establishment rates between morph types. Since *H. longifolia* does not require wet stratification for germination (only light is needed to break dormancy) (Baskin and Baskin, 1998), seeds were sowed in the spring (May) of 2015 shortly after snowmelt and soil thawing. Within each seed plot, the sandy soil surface was moistened with water and seeds were then dispersed evenly in each quadrat after which a thin cover of moistened sand was applied to prevent loss of small seeds due to wind. The number of seeds sown per quadrat ranged from 8 to 2817 (Fig. 2b).

Growing season (May–August 2014 for *L. ligulistylis* and April–July 2015 for *H. longifolia*) monthly temperature and precipitation data were obtained for each location from the software ClimateWNA (Wang et al., 2016), along with 30-year normals (1981–2010) to assess variations from normal conditions during the translocation experiment.

### 2.3. Plant performance measures

#### 2.3.1. Adult plants

In 2014, multiple plant performance measures were recorded for adult *L. ligulistylis* plants at each translocation site. Survival rate (proportion of plants producing aboveground leaves from 2012 to 2014) and flowering (proportion of plants that produced a flowering stem) were recorded separately for source and recipient soil at each site. From time lapse cameras we determined dates on which the first plant started to sprout and when the first (top) flower bud opened. Stem heights were measured to the tip of the stem for non-flowering stems and to the base of the flower bud at the top of the stem for those with flowering stems. Height of the tallest stem from each plant was recorded as the plant's maximum height. Maximum height was used instead of average height as it gave a more accurate representation of growth since plants with multiple shoots can contain short stems that lead to underestimation of height. Number of flower buds per plant was recorded by summing the number of buds on each flowering stem.

To determine seed production of *L. ligulistylis*, we placed mesh bags around flowering heads at the start of senescence to prevent seed loss. After senescence, stems were cut and taken to a lab at the University of Alberta for further drying and seed counts (done by hand). Two plants were removed from analysis because their seed bags were ripped by the chicken wire enclosures during collection and thus some seeds were lost. Recounts of a 5% sub-sample of seed counts were used to assess accuracy of seed counts and these indicated an average error rate of 0.27%. During seed counting, seed set was determined by lightly pressing the outer seed coat between fingers to determine whether seeds were 'full' (with an embryo) or 'empty' (without an embryo). Seed set for each plant was calculated by dividing the number of full seeds by the total number of seeds produced. No individual plant contained all full seeds, but there were several which contained none.

In the summer of 2015, all 13 *H. longifolia* translocation sites were visited and multiple measures of plant performance were recorded. Survival rate was recorded for each plant, with those plants which turned brown being considered dead. For surviving plants, stems were counted and average height – based on up to 10 stems per plant – was measured. From July 2nd to July 4th flowers, including unopened flower buds, were counted for each plant.

#### 2.3.2. Seeds and seedlings

Emergence of *L. ligulistylis* seed sown in the fall of 2013 was assessed in the 2014 growing season. The number of seedlings that appeared between May–August 2014 was expressed as a percent of the number of sown seeds and referred to as seedling emergence. The number of seedlings still alive at the beginning of September was also recorded and referred to as seedling establishment. Average seedling height, based on measurements of up to 10 seedlings in each quadrat, was also recorded. Quadrats seeded with *H. longifolia* in the spring of 2015 were monitored throughout the course of the summer of 2015 to measure seedling establishment, as described above.

### 2.4. Data analyses

All statistical analyses were completed using the R statistical software (R.3.1.2; R Core Team, 2014). We used models to test the effects of soil (source vs. recipient) and location on the different response variables with replicate site (within location) included as a random effect. Model residuals were examined for normality and homogeneity of variance. If the interaction between location and soil type was not significant it was removed from the models. Post-hoc comparisons were completed using the R package *lsmeans* with a Tukey adjustment (Lenth and Hervé, 2015).

Response variables for adult plants of *L. ligulistylis* of each translocation site included survival, flowering, maximum height, number of flower buds, and seed set. A generalized linear model with a binomial distribution - using the R package *nlme* (Pinheiro et al., 2015) - was used for analyses of plant survival and flowering. Then a likelihood ratio test was performed using the function *drop1* to determine the significance ( $\chi^2$  distribution) of location and soil by single term deletions. A linear mixed-effect model using the package *nlme* was used for analysis of maximum height in the 2014 growing season. Generalized linear

mixed-effects models with a Poisson distribution using the package *lme4* (Bates et al., 2015) were used for analyses of the number of flowers/flower buds and total seed production per plant (flowering stem nested within plant ID nested in replicate site as an additional random effect). Outliers were removed for both these models, with one observation removed for number of flowers/flower buds and four observations removed for the seed production. Significance of factors was estimated by parametric bootstraps at 4999 iterations using the package *afex* (Singmann et al., 2015). Due to convergence issues in analyses of the seed production data, a likelihood ratio test, using the package *afex*, was used to determine significance ( $\chi^2$  distribution) of location and soil origin. A linear mixed effects model using the package *nlme* was used for analysis of seed set (flowering stem nested within plant ID nested in replicate site as the random term). Seed set data were subjected to an arcsine transformation prior to analysis, plants with zero seed set were changed to a proportion of full seeds of 0.001 to allow for this transformation.

Linear mixed effects models were used to determine the effect of corm size on plant height and number of buds in the 2013 and 2014 growing season with the replicate sites as a random effect. For this analysis one outlier of corm size was removed (79.02 cm<sup>3</sup>) from the data set, as well as one outlier of 49 buds for a plant in 2013.

The response variables for the sown seeds of *L. ligulistylis* were emergence, establishment and height. A negative binomial generalized linear mixed effects model was used (R package *lme4*; Bates et al., 2015) for analyses of emergence and establishment since the Poisson model indicated significant over-dispersion ( $\phi > 4$ ). Because only recipient soil was used, location was the only predictor in this analysis, with replicate site as a random effect. Significance values were estimated from parametric bootstraps with 4999 iterations using the package *afex*. A linear mixed effects model was used for analysis of seedling height (based on average per seed plot). Due to the low number of surviving plants and seedling establishment, no statistical analyses for *H. longifolia* were conducted with only summary statistics presented.

### 3. Results

#### 3.1. Adult plant translocations

##### 3.1.1. *Liatrix ligulistylis*

Location had no significant effect on adult plant survival, proportion flowering, flower bud production, or seed production (Table 1). Adult survival was high overall (south: 73.8%, SE = 7.0, central: 86.4%, SE = 5.6, north: 87.8%, SE = 5.1, far north: 79.2%, SE = 5.9). On average about 50% of plants flowered (south: 41.5%, SE = 8.9, central: 41.5%, SE = 8.8, north: 44.9%, SE = 8.3, far north: 50.0%, SE = 8.1) with an average of 9–12 flower buds per plant across all locations (Table 1, Fig. 3). Seed production per plant ranged from 39 to 2865 seeds (south: 209.5, SE = 48.6, central: 372.8, SE = 82.0, north: 246.8, SE = 53.1, far north: 423.3, SE = 95.2). There was a marginally significant difference ( $p = 0.068$ , Table 1) in average maximum height among locations with the far north location having the greatest average maximum plant height (37.4 cm, SE = 2.4 cm), followed by the north (34.1 cm, SE = 2.4), south (28.1 cm, SE = 2.6), and central (27.8 cm, SE = 2.6) locations. However, none of the pairwise comparisons among locations were significant (Table S3).

Soil origin did not significantly affect adult plant survival, proportion flowering, average maximum height, or seed production (Table 1); plants in source soil were marginally taller (34.8 cm, SE = 1.67 cm) and produced slightly more seeds (319.1, SE = 38.5) than those planted in recipient soil (Height: 30.1 cm, SE = 2.3 cm; Production: 283.0, SE = 39.9). In contrast, soil origin had a significant effect on flower bud production with those plants in source soil producing nearly 1.5 times as many buds as those placed in recipient soil (Table 1, Fig. 3).

Seed set ranged from nearly zero to 0.857, averaged 0.229 per plant, and there was a significant location by soil interaction (Table 1). For the recipient soil, seed set was higher at the central location than at the south or far north location, while intermediate at the north location (Fig. 3). There were no significant differences in seed set among locations for those plants in the source soil. At the south location, plants in the source soil had a higher percentage of full seeds than those in the recipient soil. In contrast, at the central and north locations plants in the recipient soil had a marginally higher percent of full seeds than those in source soil (Table 1, Fig. 3).

Corm size had no significant effect on maximum height or number of flowers/flower buds of adult plants produced in 2013 or 2014.

Time lapse photographs in 2014 demonstrated that plants at the south location sprouted earliest (May 6–20), followed by the central (May 11–25), north (May 19 - June 1), and far north (May 31 - June 4) locations. Date of first sprouting for the species was therefore inversely related to latitude and presumably early spring climate conditions (2.6 days per 100 km). A similar trend with latitude was observed for first flower bud burst. Initial flower bud burst occurred first at the south site (July 13–21), followed by the central (July 20–24), north (July 18 - August 1) and far north (July 28 - August 3) sites (Table S4) resulting in a latitudinal difference of first bud burst of 1.6 days per 100 km distance.

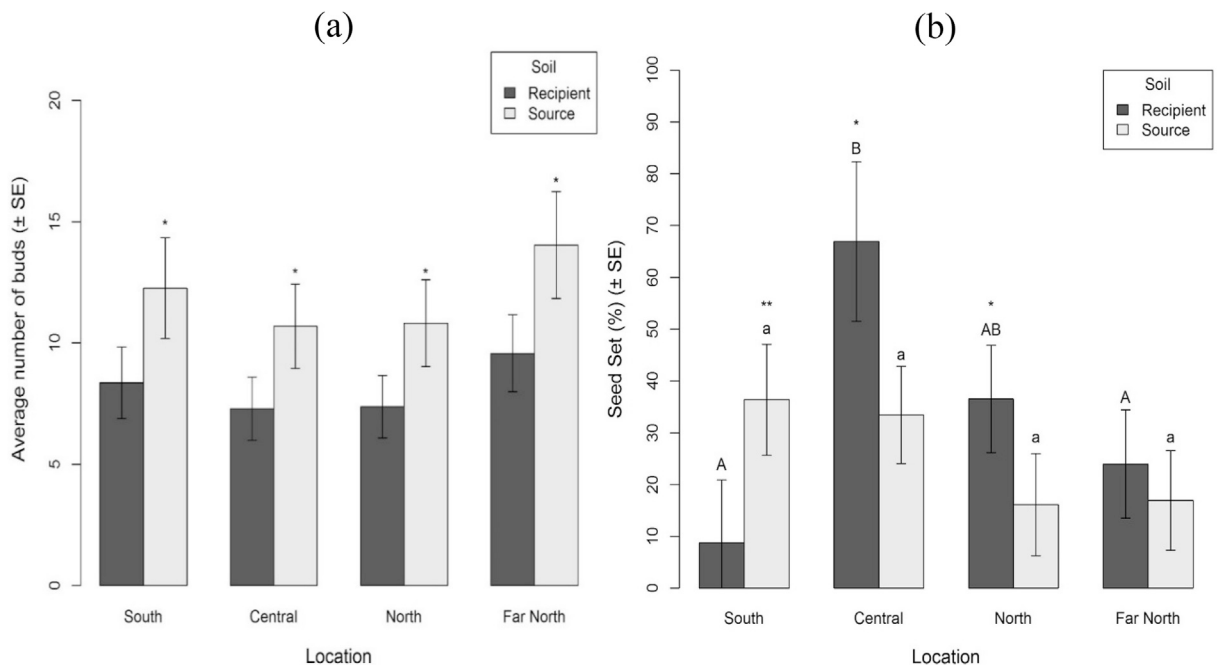
Recipient soil at the south location and Central-1 location had higher total organic carbon (TOC), total nitrogen (TN), pH, electrical conductivity (EC), and potassium (K), but lower phosphorus (PO<sub>4</sub>-P) than the source soil from Central 2–3 locations. In contrast, the north and far north recipient soils had opposite properties but similar pH values (except North-1) than the source soil. Recipient soils at all locations also had similar textures with silt having the highest percentage particle concentration followed by sand and clay (Table S5).

**Table 1**

Effects of soil origin, location, and their interaction on performance of translocated *Liatris ligulistylis* plants and sown seed. The interaction between soil origin and location was only significant for seed set and was therefore only retained for that model. Seedling emergence refers to the number of seedlings that appeared between May–August 2014, whereas seedling establishment refers to the number of seedlings that were still alive in the beginning of September 2014. **Bolded text** indicates values obtained by running a likelihood ratio test (LRT). ‘–’ indicates an alternate method<sup>a</sup> for obtaining p-values. ‘na’ indicates a lack of interaction term. Soil origin was not tested for the sown seeds. Distribution refers to the probability distribution used for each model.

Measures of Success	Distribution	Soil Origin			Location			Soil Origin: Location		
		F-value	Stat	p-value	F-value	Stat	p-value	F-value	Stat	p-value
Adult plant translocation										
Survival (%)	Binomial	–	<b>0.11</b>	<b>0.744</b>	–	<b>3.50</b>	<b>0.321</b>	na	na	na
Flowering (%)	Binomial	–	<b>0.82</b>	<b>0.364</b>	–	<b>0.68</b>	<b>0.890</b>	na	na	na
Maximum Height (cm)	Gaussian	2.10	–	0.150	3.48	–	0.068	na	na	na
Flower Buds/plant	Poisson	–	17.61	<0.001	–	1.78	0.740	na	na	na
Total Seeds/plant	Poisson	–	<b>5.24</b>	<b>0.800</b>	–	<b>0.80</b>	<b>0.370</b>	na	na	na
Seed Set (%)	Gaussian	1.49	–	0.229	1.16	–	0.372	3.7	–	0.018
Seed translocation										
Emergence (%)	Negative Binomial	–	–	–	–	25.98	<0.001	–	–	–
Establishment (%)	Negative Binomial	–	–	–	–	26.69	<0.001	–	–	–
Seedling Height (cm)	Gaussian	–	–	–	1.08	–	0.410	–	–	–

<sup>a</sup> The column “F-value” gives a F-value and calculates p-value using F test, and the column “stat” gives a Chi-square value and calculates p-value using parametric bootstrap method.



**Fig. 3.** Average number of flowers or flower buds (a) and the percentage of seed set (i.e. full seeds) (b) produced per translocated adult plants of *Liatris ligulistylis* at each location by soil origin (recipient or source). Different letters above bars indicate significant differences between locations for plants in recipient soil (capital letters) or source soil (small letters). \*\* indicates significant difference ( $p < 0.05$ ) and \* indicates marginal significant difference ( $0.05 < p < 0.1$ ) between soil origins at a given location (see also Table S6 & Table S7 for analysis of seed set). Note that the ‘Central’ location represents the species’ current range.

### 3.2. *Houstonia longifolia*

Only eight out of 130 translocated adult plants survived, with no plants surviving at the south and far north locations, seven surviving in the central location (17.5%, SE = 4.8) and only one in the north location (3.3%, SE = 3.3) (Table 2). Out of the eight plants that survived, five were thrums and three were pins. The one plant that survived in the north had 22 stems with a maximum height of 6.5 cm and 52 flowers. For the seven plants that grew in the central location, average number of stems was 15 (SE = 3), with an average maximum height of 4.7 cm, and an average number of flowers per plant of 23 (SE = 5) (Table 2).

The growing season of the year 2015 was dry with temperatures being slightly above normal and most sites experiencing less precipitation ( $z < 0$ ) than the historical precipitation norms from May to June (Fig. S2). During this species’ growing



**Table 2**

Summary of attributes of adult plants of *Houstonia longifolia* after translocations. Short dash refers to adult plants failing to survive, thus no measurements recorded of them.

Site	Survivals	ID	Morph	Stems	Flowers	Mean Height (cm)	Max Height (cm)
South-1	0	–	–	–	–	–	–
South-2	0	–	–	–	–	–	–
South-3	0	–	–	–	–	–	–
Central-1	1	59T	Thrum	33	34	4.4	6.1
Central-2	2	112P	Pin	19	40	3.5	4.3
		22T	Thrum	5	11	3.1	4.2
Central-3	3	87T	Thrum	11	17	3.7	5.0
		106P	Pin	6	21	2.6	3.1
		109T	Thrum	23	35	3.0	4.1
Central-4	1	15P	Pin	10	5	3.5	6.4
North-1	0	–	–	–	–	–	–
North-2	0	–	–	–	–	–	–
North-3	1	124T	Thrum	22	52	5.8	6.5
Far North-1	0	–	–	–	–	–	–
Far North-2	0	–	–	–	–	–	–
Far North-3	0	–	–	–	–	–	–

season, temperatures were marginally above normal in April and July, and far higher in June, but close to normal in May (Fig. S2(a)). However, precipitation levels at all locations in May and at the far north location in June were much less than the historical norms ( $z$ -scores are around  $-2$ ), while north locations in April experienced a higher precipitation level than normal (North:  $z = 1$ ; Far North:  $z = 1.7$ ) (Fig. S2(b)). Overall, the growing conditions of the species in 2015 were dry (Fig. S2).

### 3.3. Seed translocations

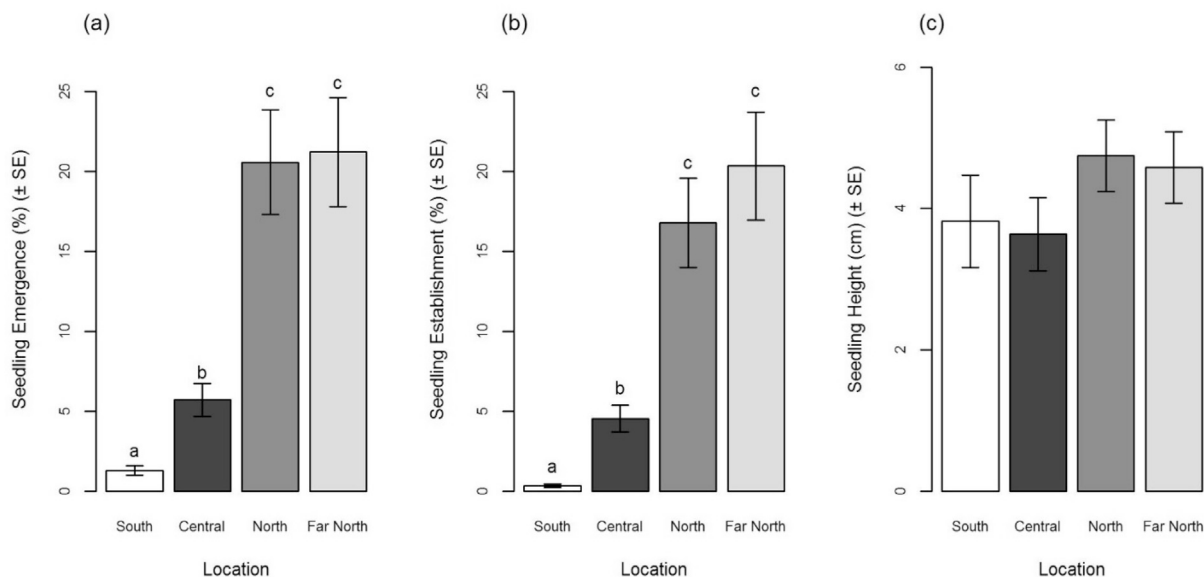
For *Liatris ligulistylis*, location had a significant effect on both seedling emergence and seedling establishment (Table 1). Post hoc comparisons illustrated that seedling emergence and establishment were significantly different among all locations except the north and far north locations, with the north and far north locations having significantly higher emergence rates than the south and central locations (Fig. 4, Table S8, Table S9). However, location had no significant effect on maximum seedling height suggesting that once seedlings emerged, growth did not differ among sites (Table 1, Fig. 4).

For *Houstonia longifolia*, no seedling establishment was observed in 2015 despite laboratory germination trials that found viable seed with pin morph seed having a germination rate of 46.7% and thrum morph seed a rate of 32.3%.

## 4. Discussion

In this study, we use translocations of two range-restricted perennial forbs (*Liatris ligulistylis* and *Houstonia longifolia*) to examine their climate vulnerabilities, assess the alignment between their range limits and niche limits, and to explore the possible use of assisted migration as a proactive conservation tool. We found that *L. ligulistylis* can grow well hundreds of kilometers north of its current range, while the translocations of *H. longifolia* were not successful. These findings provide insight into the use of assisted migration for rare plant species conservation, especially those in high latitude regions that have the greatest absolute and relative differences in climate change (Beever and Woodward, 2011; Zhao et al., 2015) and regions with severe habitat loss and fragmentation. In high latitudes, these effects are projected to amplify through this century (Boisvert-Marsh et al., 2014) and can be more severe in a fragmented habitat where area and isolation effects exert additional pressure on species population and distribution (Travis, 2003).

Based on measurements from the summer of 2014, assisted migrations of *L. ligulistylis* plants grew well up to 500 km north of its current range; in these locations they produced flowering stems and seed in levels similar to those in the species' current range. Seed emergence and establishment rates were also significantly higher in the northern translocation sites than south of, or even within, the species' current range. Although the performance of mature plants was not significantly different among translocation for most measures, seed set was significantly higher in the central location than in the south. That, combined with the poorer performance of translocations started by seeds in the southern location, suggests that *L. ligulistylis* might have near future vulnerabilities to climate warming in its current range, especially for the seedling establishment phase. When the precipitation is similar at all locations in 2014, a temperature gradient from north to south may result in a greater drought effect in southern locations, and these differences might be diminished in a wetter year. The fact that performance of mature plants and seedling at the north locations was just as good as at central locations, and that seedling emergence and establishment were better at the northern than central location, suggest that the northern location(s) was equally or more suitable for *L. ligulistylis* than its current range. This provides empirical evidence that the current range limits for this species are smaller than its niche limits. Further, it suggests dis-equilibrium with the climate in its current range. The current distribution may be due to its dispersal limitation (Hargreaves et al., 2014) and poor habitat connectivity in Alberta.



**Fig. 4.** Measurements of translocated seeds of *Liatris ligulistylis* at each location. (a) Seedling emergence (number of seedlings that appeared between May–August 2014 as a percent of number of sown seeds) at the four translocation locations. (b) Seedling establishment (number of seedlings still present in September 2014 as a percent of number of sown seeds) at the four translocation locations. (c) Seedling height at the four translocation locations. Different letters indicate significant differences between locations. There were no significant differences in seedling height between locations (Table 1). Note that the ‘Central’ location represents the current range.

Based on experimental trials comparing source to recipient soils, future translocation of *L. ligulistylis* should incorporate source soil, as those adult plants placed in their source soil produced a significantly higher number of flower buds and full seeds (south location) than those plants placed in recipient soil. This could be attributed to the source soil having lower pH and EC values, along with higher phosphorus levels than the recipient soil. This species is believed to have vesicular-arbuscular mycorrhizae associations, similar to those in *L. spicata* (Medve, 1985; COSEWIC, 2010). By using source soil, the appropriate mycorrhizae were most likely transplanted along with the plant (COSEWIC, 2010; Schwartz et al., 2006). Even if the recipient soil is judged to be fairly similar to the source soil (Table S7), it may lack certain mutualistic organisms needed to promote a species’ growth (McLachlan et al., 2007; Moeslund et al., 2017). It is worth noting that biological contamination of source soil in translocations should be considered, although we did not detect it in the current work. The differences in performance between the 2013 (little or no seedling establishment) and 2014 seed translocations could be attributable to weather condition and/or number of seeds sown. In any case, this species may be a good candidate for future assisted migrations considering the performance of seeds and adults.

Assisted migration trials of *H. longifolia* failed with only 8 of the 130 translocated plants surviving to one year after translocation and no seedling emergence or establishment. The lower survival rate of seeds than adult plants is consistent with previous studies (Godefroid et al., 2011; Dalrymple et al., 2012; Guerrant, 2012). The poor results for the translocation trial of *H. longifolia* are most likely a result of the dry weather conditions in the spring and early summer of 2015 (Fig. S2), with most translocation sites receiving less precipitation than their normals and marginally higher temperature than normals. Earlier spring or prior fall sowing of seeds and repeated trials may have been more successful (Angadi et al., 2004). On-going management to support plants and seedlings after translocation, for example watering in drought years, may be necessary to ensure survival (Early and Sax, 2011). Future translocations of seed should therefore consider sowing in early spring when conditions are expected to be wetter; or if conditions are unfavourable then translocations may need to be done repeatedly; in drought conditions watering and experimentation with shade tents might be needed.

In addition to fluctuating weather, differing root morphology may be a key cause that led to fewer adult plants of *H. longifolia* surviving than of *L. ligulistylis*. The fine fibrous roots of *H. longifolia* were very likely more sensitive to transplanting than dormant corms of *L. ligulistylis*. Therefore, future assisted migrations should recognize the difficulty of translocating species with shallow fibrous root systems, possibly use plugs grown in nurseries to overcome this challenge. Considering unusual weather, sensitive root structure, and unhelpful third party destruction of a site, development of more elaborate methods for translocation and management of *H. longifolia* is needed.

The main limitation of both experimental assisted migration trials used here is that measurements were only recorded over one growing season on the seeds of *L. ligulistylis* (May to August 2014) and the seeds and adults of *H. longifolia* (May to July 2015). Weather conditions in each year likely affected the survival, growth, and reproduction of these species. Therefore, to determine the true success of assisted migrations, long-term monitoring of these sites will be necessary, along with translocations in different years (Guerrant, 2012). A brief visit to a few of these sites ~4 years after translocation suggested that

establishment has been poor (no further seed germination & reduced adult survival of *Liatris ligulistylis*). The lack of successful establishment of *H. longifolia* emphasizes that translocations also need to be evaluated on a species-by-species basis, as some species may be more suited for assisted migrations than others (Hannah, 2008; Renton et al., 2012). Although there is still much debate over the use of assisted migration, preliminary results here provide insight into the methods and challenges associated with translocations of locally range-restricted plants that may assist gene flow of them to existing adaptive ranges or serve as a comprehensive plan to their management and protection, as well as the empirical data for the analysis of the link between species niche and species geographic distribution. It is hoped that the results will promote the formulation of appropriate assisted migration policy to promote the continuation of research trials and prevent future extinction (McLachlan et al., 2007; Thomas et al., 2004; Thomas, 2011). One future question is how translocations from populations further east or south might affect performance and whether these would differ from ones established using commercial seed.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00572>.

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