

STUDIES

Assessment of biogeographic variation in traits of Lewis flax (*Linum lewisii*) for use in restoration and agriculture

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Abstract

Lewis flax (*Linum lewisii*) is widely distributed across western North America and is currently used in native ecosystem restoration. There is also growing interest in *de novo* domestication of Lewis flax as a perennial oilseed crop. To better understand this species and facilitate both restoration and domestication, we used common gardens to assess biogeographical variation in a variety of seed and growth traits from 37 flax accessions, consisting of 35 wild populations from the Intermountain West region, the pre-variety germplasm Maple Grove (*L. lewisii*) and the cultivar 'Appar' (*L. perenne*) and related this variation to collection site geography and climate. Results from linear mixed models suggest there is extensive phenotypic variation among populations of Lewis flax within the Intermountain West. Using a multivariate approach, we identify a key suite of traits that are related to latitude and climate and may facilitate adaptation, including flowering indeterminacy, seed mass and stem number. These traits should be taken into account when considering the release of new germplasm for restoration efforts. We also find that Lewis flax seed contains desirably high amounts of alpha-linolenic acid and is otherwise mostly indistinguishable in fatty acid composition from oil-type varieties of domesticated flax (*L. usitatissimum*), making it a strong candidate for domestication. This study provides fundamental knowledge for future research into the ecology and evolution of Lewis flax, which will inform its use in both restoration and agriculture.

Keywords: Agriculture; ecology; evolution; restoration ecology; seed biology.

Introduction

Heritable phenotypic diversity is the raw material for both natural and artificial selection. In natural settings, differential selection among populations can result in geographic or environmental clines in trait variation; such clines are often

used as initial clues as to which traits may be involved in local adaptation (Endler 1986; Kooyers et al. 2015). Understanding patterns of intraspecific diversity and adaptation is of increasing importance as climate change accelerates, especially in the

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contexts of ecosystem restoration and sustainable agriculture (Cochrane *et al.* 2015; Des Roches *et al.* 2021). Both of these pursuits rely on leveraging adaptive variation in order to maximize ecosystem and agricultural services with economic efficiency.

Degradation of landscapes and a growing market of carbon offsets have caused increasing demand for restoration projects and, consequently, large amounts of native seed (Galatowitsch 2009; Suding 2011; Broadhurst *et al.* 2016). Obtaining native forb seed can be especially difficult, as relatively few species (or plant materials) are commercially available. Wild populations may be unreliable seed producers, difficult to collect, low in seed quality and/or genetically compromised, with collection being potentially harmful to natural populations (Jones 2019).

Efforts to increase the availability and diversity of native seed should take into account basic evolutionary processes. Adaptation of a species to local conditions can influence the success of restoration efforts, though local adaptation should not be the sole deciding factor for seed sourcing, since not all species exhibit strong local adaptation (Gould *et al.* 1979; Hamilton 2001; Broadhurst *et al.* 2008; Leimu and Fischer 2008; Hereford 2009; Kramer and Havens 2009; Breed *et al.* 2013; Jones 2013). Strategies such as admixture provenancing and composite provenancing involve the use of diverse germplasm from non-local sites and can be beneficial if inbreeding/genetic drift (e.g. via habitat fragmentation), and/or species range shifts are a concern (Ellstrand and Elam 1993; Broadhurst *et al.* 2008; Breed *et al.* 2013).

In parallel, the use of broad genepools (e.g. landraces, wild relatives) in crop breeding improves chances of discovering beneficial genetic variation, which can be used to develop new varieties for agriculture better adapted to various stressors related to climate change, including drought, disease and salinity (Raza *et al.* 2019; Zhang and Batley 2020). There is also growing interest in the *de novo* domestication of crop wild relatives (CWRs)—especially those that are native and perennial—as new grain, oilseed and biofuel crops that could provide increased ecosystem services compared to existing domesticated annual relatives (DeHaan *et al.* 2005; Glover *et al.* 2010). New perennial crops at various stages of development include intermediate wheatgrass (*Thinopyrum intermedium*), switchgrass (*Panicum virgatum*), silflower (*Silphium* spp.), sorghum (*Sorghum bicolor*), various legumes (*Phaseolus* spp.) and various wild flax (*Linum*) species (Nabukalu and Cox 2016; Van Tassel *et al.* 2017; DeHaan *et al.* 2018; Schlautman *et al.* 2018; Tork *et al.* 2019; Lovell *et al.* 2021). A major goal of perennial crop systems such as these is to promote the restoration of biodiversity and sustainable ecosystem function, while producing food.

One wild plant with dual potential in restoration and agriculture is Lewis flax (*Linum lewisii*), a blue-flowered, perennial forb native to western North America. Its distribution extends from northern Mexico into Alaska and is found in a wide variety of habitats and plant communities, ranging from salt desert shrublands to subalpine ecosystems in the Sierra Nevada and Rocky Mountains (Mosquin 1971; Meyer and Kitchen 1994; Ogle *et al.* 2009). It is one of just two described blue flax species native to North America, the other being *Linum pratense*, a closely related annual species of smaller stature and overlapping but more limited range (Mosquin 1971). Both are grouped in *Linum* section *Linum*, which mostly comprises blue-flowered Eurasian species, such as their more distant relative annual domesticated flax, *L. usitatissimum* (McDill *et al.* 2009; McDill and Simpson 2011).

Lewis flax is capable of outcrossing but also has no apparent self-incompatibility mechanisms. It is homostylous, displaying a single flower morph with styles as long or longer than anthers, thus typically requiring insect pollinators to move pollen upwards to the stigma in order to self; therefore, its mating system is facultative autogamy (Kearns and Inouye 1994). The degree of inbreeding versus outcrossing in natural populations of Lewis flax is unknown, although the relative distance between anthers and stigmas has been observed to vary geographically, which suggests inbreeding rates may vary as well (Mosquin 1971). Lewis flax attracts generalist insect pollinators, with most observations being of dipterans and hymenopterans (Kearns and Inouye 1994). As seed capsules mature, they dry and split open along boundaries between 10 separate segments, each containing one seed. Seeds are easily dislodged from open capsules and fall beneath the mother plant. We are unaware of any work that has explored mechanisms for secondary dispersal across space; however, limited work on seed dormancy and germination regulation suggests the opportunity for dispersal through time, especially in environments with unpredictable fall and winter precipitation (Meyer and Kitchen 1994). We have observed seed dormancy to diminish fairly rapidly with after-ripening in dry warm storage. Seed viability under laboratory conditions is somewhat limited (losses observed in 5–7 years).

Lewis flax has been used by Indigenous peoples in North America for centuries, both for its nutritious seed and strong fibres (Moerman 1998). Beyond its perennial growth habit, several traits make Lewis flax a promising candidate for domestication, namely its comparatively large seeds (Ogle *et al.* 2019), self compatibility (Kearns and Inouye 1994; Pendleton *et al.* 2008b) and relatively small genome size of approximately 600 Mb (Wang *et al.* 2012; You *et al.* 2018; unpublished data 2021). Together these traits should provide a favourable starting point and allow for efficient genomics-assisted breeding. Other traits that will be valuable for a Lewis flax oilseed 'ideotype' moving forward include a compact and upright growth habit—similar to oilseed varieties of annual flax—as well as seeds that resist shattering (Tork *et al.* 2019). These traits reduce crowding, improve ease of harvesting and limit contact with soil-borne pathogens (Tork *et al.* 2019).

Because of its robust adaptability and striking blue flowers, Lewis flax is popular for use in restoration and landscaping contexts in the western USA, especially when conservation of native species and ecosystems is a priority (Meyer and Kitchen 1994; Ogle *et al.* 2009, 2019; Leger and Baughman 2015). The US Department of Agriculture (USDA) has an ongoing tri-agency effort to develop Lewis flax for these purposes. The pre-variety germplasm Maple Grove, derived from a collection in Millard County, UT, was released in 2004, following the realization that the previously released cultivar 'Appar' was actually *Linum perenne*, a close relative of *L. lewisii* native to Eurasia (Meyer and Kitchen 1994; Pendleton *et al.* 2008a, b). Despite recognition of this error, *L. perenne* continues to be planted in North America as an ornamental and sometimes mistakenly in restoration settings (personal observation). For detailed descriptions of *L. perenne* and 'Appar', especially in the context of North American restoration plantings, see Nicholls (1986) and Pendleton *et al.* (2008a, b).

Yields of Maple Grove Lewis flax have been low compared to 'Appar', and it has also been observed to suffer from outbreaks of the fungal pathogen flax rust (as far as is known, this pathogen is the same as or closely related to the species affecting domesticated flax, *Melampsora lini*). There is interest in developing and releasing additional germplasm that has more robust seed yield and greater longevity compared to Maple

Table 1. Collection and garden site information. MAT and AP are mean annual temperature and precipitation, respectively, derived from the CHELSA V1.2 bioclim data set. Accession OC_MG is a re-collection from the original collection site of the Maple Grove (MG) pre-variety germplasm. PGJ1 and PGJ2 are collections from the same approximate population but 5 years apart and by different people. Likewise, Crystal1 and Crystal2 are from the same approximate site, collected 2 years apart by different people. Patterson1 and Patterson2 also represent an approximately repeated collection. We chose to analyse these repeat collections as unique accessions because of the potential influence of temporal variation.

Accession name	Accession ID	State	County	Lat	Long	Elevation (m)	MAT (°C)	AP (mm)	Year of collection
Tin_Cup	9106574	ID	Caribou	42.970	-111.257	1973	5.4	445	Unknown
Arbon_Valley	9106566	ID	Bingham	42.631	-112.497	1585	8.3	317	Unknown
McCoy_Creek	9107571	ID	Bonneville	43.182	-111.118	1735	6.6	307	Unknown
Lava	9106553	ID	Bannock	42.630	-112.073	1634	8.1	377	Unknown
Cove_Rd	9106554	ID	Caribou	42.884	-111.884	1595	7	476	Unknown
OC_MG	U31	UT	Millard	39.023	-112.078	1915	8.9	221	2010
DER1	U41	UT	Millard	38.691	-113.812	1848	10.4	201	2011
DER2	U40	UT	Millard	38.011	-113.783	1787	10.5	262	2005
Crystal1	U42	UT	Millard	38.796	-113.589	1915	9.9	204	2011
PGJ1	U34-06	UT	Iron	37.912	-113.030	1691	11.3	342	2006
PGJ2	U34-11	UT	Iron	37.912	-113.030	1691	11.3	342	2011
Provo	U43	UT	Utah	40.299	-111.623	2073	6.5	652	2011
Delta_CP	C1	CO	Delta	38.661	-108.250	1895	9.3	237	2004
Paradox	C2	CO	Montrose	38.221	-108.642	1741	10.5	250	2004
Dow_Mtn	1146 (P8)	CO	Dolores	37.754	-108.210	1976	3.8	577	2007
Crystal2	1143	UT	Millard	38.794	-113.587	1905	9.9	204	2009
Halfway	1150 (P12)	UT	Millard	38.619	-113.845	1905	10.1	214	2009
Water_Canyon	1136 (pssl-84)	NV	Lander	40.630	-116.703	1768	8.9	304	2010
Cave_Valley	1141 (P13)	NV	Lincoln	38.591	-114.768	1977	10	333	2009
LL_Pass	1155 (P1)	NV	Elko	40.826	-114.596	1954	8	328	2008
Long_Hill	1156 (P6)	UT	Iron	37.949	-113.015	1757	10.9	362	2008
Major	1157 (pssl 142)	NV	White Pine	39.032	-114.590	2059	9.3	201	2010
Patterson1	1158 (pssl 162)	NV	Lincoln	38.596	-114.692	2016	9.7	243	2010
West_Ely	1169 (pssl 136)	NV	White Pine	39.253	-114.888	1973	9.3	232	2010
Wilson	1170 (pssl 92)	NV	Elko	41.634	-116.283	1677	8.9	342	2010
Silver_King	1139 (P2)	NV	Lincoln	38.089	-114.896	1639	12.4	294	2008
Deep_Creek	1144 (P5)	UT	Tooele	39.854	-113.857	2469	6.6	191	2008
Crestline	1142 (pssl 176)	NV	Lincoln	37.755	-114.211	1980	10.3	377	2010

Table 1. Continued

Accession name	Accession ID	State	County	Lat	Long	Elevation (m)	MAT (°C)	AP (mm)	Year of collection
Levan	1152 (pssl 146)	UT	Juab	39.592	-111.824	1767	9	405	2010
Pequop	1159 (P3)	NV	Elko	41.076	-114.585	2090	7	339	2008
Rice_Mtn	1161 (P9)	UT	Iron	38.053	-113.969	2013	9.8	252	2009
Soldier_Canyon	56087201	NV	Elko	40.783	-115.343	1860	7.9	426	2009
37	(P11)	Unknown	Unknown	Unknown	Unknown	Unknown	NA	NA	2007
Bear_Lake	FRRL-2 Bear Lake	UT	Rich	41.880	-111.245	2228	4.7	436	Unknown
Patterson2	FRRL-1 Patterson	NV	Lincoln	38.583	-114.700	2036	9.7	244	Unknown
'Appar'	'Appar' SFD-10-8	NA	NA	NA	NA	NA	NA	NA	NA
MG	Maple Grove SBR-02-08	UT	Millard	39.023	-112.078	1915	8.9	221	NA
Millville garden	NA	UT	Cache	41.656	-111.816	1407	9.8	298	NA
Ephraim garden	NA	UT	Sanpete	39.371	-111.578	1686	9.6	459	NA

Grove; this would also provide increased genetic diversity and geographic relevance for this species in restoration settings. Any and all such developments in Lewis flax would benefit its potential agricultural use.

Crop breeding and restoration rely on leveraging existing adaptive variation, but the extent of variation in Lewis flax and the degree to which it exhibits local adaptation are unclear. Variation in potentially fitness-related traits, such as growth form, seed mass, seed oil content/composition and rust susceptibility, has not been explored. We used common gardens to assess variation in multiple seed, structural and other traits among 35 wild-collected accessions of *L. lewisii* from across the Intermountain West, as well as Maple Grove and 'Appar'. We sought to characterize how these traits are associated with each other and with environmental variables, thereby identifying potential trade-offs and growth strategies that may have an ecological basis. We also compared seed oil traits between Lewis flax and domesticated annual flax. Based on these analyses, we discuss the implications of intraspecific variation for both restoration and agricultural applications of Lewis flax and identify accessions with potential promise in these settings.

Methods

Sampling

We collected seed from 35 wild, naturally occurring populations across Idaho, Nevada, Utah and Colorado. Although Lewis flax has a broad ecological niche, our collections were primarily from arid and semi-arid sites where the need for adapted plant materials for restoration is greatest. Collections were made by multiple individuals over the course of multiple years. We attempted to represent a wide range of growing conditions, but collections were largely opportunistic because of variation in seed production year-to-year and the relatively narrow window of time when seeds are mature but have not yet dispersed. Given this, and because individual collectors worked independently over multiple years, some populations are quite close to each other.

For each population, seed was gathered in bulk from at least 50 individual plants representing a range of sizes; we use 'accessions' throughout this paper to refer to these bulked wild collections. There was no additional generation of plants grown between collection and use in our experiment. In addition to 35 wild populations, we also included commercially grown seed of Maple Grove (Foundation seed class) and 'Appar' (Breeder seed class), sourced from 2008 harvests of certified production fields at the USDA Natural Resources Conservation Service's Plant Materials Center in Aberdeen, ID, USA (IDPMC). We mapped the locations of collection and garden sites using the R package *tmap* (Tennekes 2018). Our collections span 37.8 to 43.2° north latitude, -108.2 to -116.7° longitude and an elevational gradient of 1585 to 2469 m above sea level. Additional collection information is contained in Table 1.

Plant preparation

Seeds of flax accessions described above were germinated beginning in February 2012, in a greenhouse at IDPMC. Three to five seeds were directly sown into equal parts peat, perlite and sand in cone-shaped plastic containers (4-cm diameter, 22-cm length). Seedlings were thinned upon emergence and were watered as needed to keep the soil damp and promote root growth. We observed no issues with plants being root-bound. Greenhouse temperatures were maintained between 22 and

29 °C with unmanipulated light regimes. Seedling germination and growth was not blocked or randomized. It was also unequal among sources, but this is unsurprising given differences in maternal sites and seed age [for a separate analysis of Lewis flax seed germination, see [Meyer and Kitchen \(1994\)](#)].

In June 2012, seedlings were transplanted into two separate common gardens: one near Logan, UT, USA (hereafter Millville), and one at the Great Basin Research Center in Ephraim, UT, USA (hereafter Ephraim). We adapted to non-uniform germination by dividing seedlings for each common garden based upon (i) a desire to have as much germplasm as possible represented at both gardens, and (ii) where this was not possible, southern collections were included at Ephraim and northern collections at Millville. Although the authors shared some information about approaches between sites, the experimental design was not identical (plants per plot, care of plants and data collection). Despite this challenge, the two gardens provide valuable independent environments for testing of the accessions. We describe methodology for the two gardens separately below.

Millville garden design and phenotyping

Four accessions (Arbon Valley, McCoy Creek, Desert Experimental Range 2, Crystal1) were not included at the Millville garden due to a shortage of seedlings. Remaining accessions were transplanted into an outdoor field site with Ricks gravelly loam soil (coarse-loamy over sandy or sandy-skeletal, mixed, superactive, mesic Calcic Haploxerolls). A polypropylene weed-barrier fabric (Lumite, Aldo, GA, USA) was installed over the plot area, and holes were burned 30-cm apart with a torch to accommodate transplanting of individual flax seedlings. The accessions were established into 10-plant plots (one accession per plot) on 12 June 2012 in a randomized complete block design with eight replications (blocks). The Millville garden received no supplemental water. The experimental area was circumscribed by a border of Maple Grove, also transplanted 30-cm apart. Quilt Xcel fungicide (azoxystrobin, propiconazole; Syngenta US) was applied at the labelled rate on 6 June 2013 to control flax rust (*M. lini*), though data on amount of rust infection across accessions were not recorded. Plants were clipped at a 15-cm height in early November 2012. Treflan 5G herbicide (trifluralin, Dow AgroSciences) was applied for pre-emergent control of volunteer seedlings on 4 April 2013. Plants were clipped for harvest at 15 cm on 23–24 October 2013 and 8 October 2014. We measured and analysed the following traits in 2013: capsules per stem, capsules per plot, stems per plot, diameter at widest girth, canopy height and second-year biomass; in 2014, third-year biomass. Millville phenotyping details can be found in [Supporting Information—Methods](#).

Ephraim garden design and phenotyping

Transplanting at the Ephraim garden was completed on 18–19 June 2012. The Ephraim garden was planted in a randomized complete block design similar to Millville garden, with eight blocks, but plots containing five instead of 10 plants of the same accession. Thus, there were a total of 40 plants of each accession planted in the Ephraim garden. Spacing within and between rows was 76 cm and 120 cm, respectively. Weeds were controlled with the same fabric as Millville and by subsequent manual removal. Unlike Millville, the Ephraim garden was irrigated immediately prior to planting, and also periodically through the summer of 2012 to aid establishment. No supplemental water was provided in the 2013 growing season. Phenotyping was conducted spring and summer of 2013, when all plants

had reached maturity. We measured vigour, stems per plant, capsules per stem, viable seeds per capsule, remaining buds and flowers per stem, forks per stem, capsule diameter, stem diameter, 50-count seed mass, canopy height and rust presence. Details on Ephraim phenotyping can be found in [Supporting Information—Methods](#).

Seed oil traits

We measured oil characteristics of seeds gathered from the Ephraim garden. Seeds collected in 2013 for measurements of seed mass were stored in paper envelopes in a lab environment (~22 °C with no humidity control) and processed in 2021 for determination of oil content and composition. Although these seeds experienced substantial time in storage, they remained undisturbed and intact prior to derivatization and analysis. The oxidative stability of intact seeds tends to be high ([Priestley et al. 1985](#); [Goffman and Möllers 2000](#)).

For the analysis of oil content, each sample was subjected to nuclear magnetic resonance (NMR) on an Oxford MQC NMR fitted with an 18-mm probe (Oxford Instruments, Abingdon, UK). A calibration curve for Lewis flax was developed from a collection of samples with different oil contents quantified with the AOAC method 2003.05 analysis with petroleum ether as solvent (Minnesota Valley Testing Laboratories, New Ulm, MN, USA; J. Sieh, pers. comm., Minnesota Valley Testing Laboratories, 2021).

Fatty acid composition was analysed according to a scale-modified method used for sunflowers, as previously described ([Hulke et al. 2010, 2017](#)). Individual samples consisted of seeds harvested from each plot (plants within plots were pooled) in replications (blocks) 1–4 from the Ephraim location. The gas chromatography conditions are described in [Supporting Information—Methods](#).

Statistical analysis

We analysed data from the Millville and Ephraim gardens separately. All analyses were performed using R version 4.1 ([R Core Team 2021](#)). Code for all analyses is available at github.com/peterinnes/LILE_common_garden.

Estimating accession-level means trait values. In order to estimate and compare mean trait values of each accession, we fit linear mixed models for each trait using the R package *lme4* ([Bates et al. 2014](#)), with accession as a fixed effect, and block, plot and plant as random effects. The plant random effect was only included for traits that were based on multiple measures from the same plant (e.g. forks per stem and capsules per stem in the Ephraim garden). For each model, if a random effect term had a variance component estimated as zero, we dropped that term ([Pasch et al. 2013](#)). We assessed model fit using diagnostic plots, and transformed data to improve homoscedasticity and normality of residuals. For Millville, we natural log-transformed capsules per stem, and square root-transformed capsules per plot, biomass per plot (both years) and stems per plot. For Ephraim, we natural log-transformed yield, fecundity, capsules per stem and stem diameter, while indeterminacy index and forks per stem were square root-transformed.

To identify top-performing accessions, we compared estimated marginal means of each accession using Tukey's HSD, implemented in the R package *emmeans* ([Lenth 2021](#)). These tests were performed on transformed data, and resulting marginal means were back-transformed to their original scale for visualization purposes. We also used back-transformed

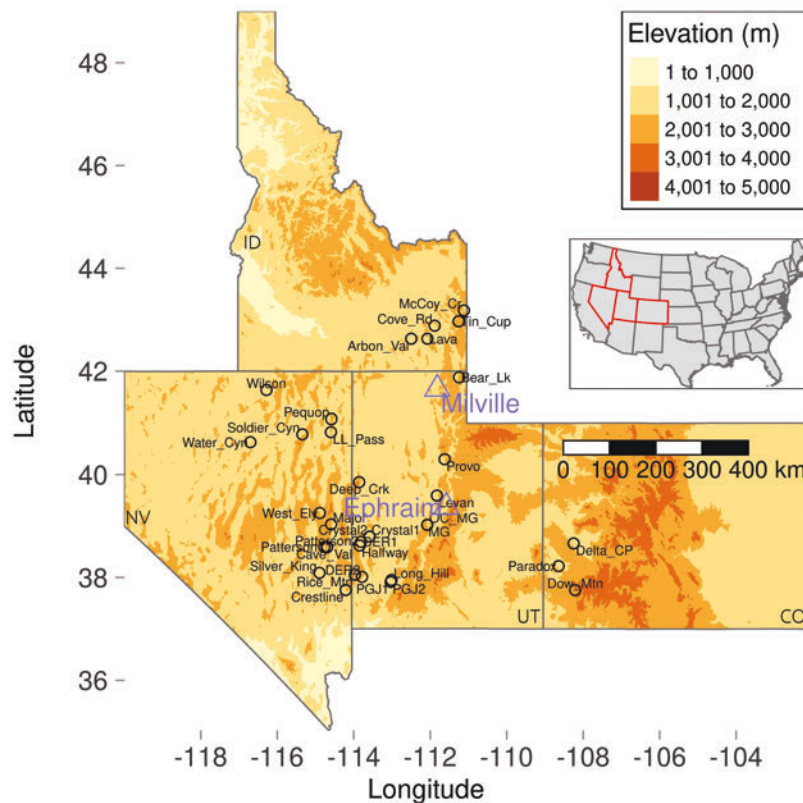


Figure 1. Map of sampling locations (circles) and common garden sites (triangles). Inset shows location within contiguous USA.

means to calculate pairwise Pearson correlations between traits. Lastly, we calculated the error coefficient of variation (CV) for each trait by dividing the root mean squared error of the mixed model by the overall mean, as implemented in *sjstats* (Lüdecke 2021).

Multivariate analysis. We used redundancy analysis (RDA) to analyse trait dimensionality and to examine relationships of trait variation with geography and climate. This analysis was implemented with the R package *vegan* (Oksanen et al. 2020) and was performed with accession-level marginal trait means that were centred and scaled to unit variance. We excluded the accession ‘Appar’ from the RDA, as it is a different species. We extracted 19 bioclimatic variables for each collection site from the CHELSA climate data set, version 1.2 (Karger et al. 2017, 2018). These data consist of 11 temperature and eight precipitation variables from the period 1979–2013 at a resolution of 30 arc-seconds (~1 km) and are derived via statistical downscaling rather than interpolation as in the WORLDCLIM data set (Hijmans et al. 2005). We combined these bioclimatic predictors with latitude, longitude and elevation for a total of 22 environmental predictors. Geographic predictors capture additional information beyond bioclimatic variables. Latitude is a primary predictor of day length, and elevation incorporates factors such as snow cover duration and solar radiation. All environmental variables were scaled to unit variance prior to RDA. Tests of statistical significance of constrained axes were performed via permutation tests (Legendre et al. 2011).

Transfer distance test of local adaptation

We used a transfer function approach to test the hypothesis that Lewis flax exhibits local adaptation to different environments

within the Intermountain region (Wang et al. 2006; Evans et al. 2016). Specifically, we tested the relationship between fitness-related traits—survival (Millville) and estimated fecundity (Ephraim)—and squared transfer distance of an accession’s collection site to the location of the common garden in which the trait was measured. To calculate transfer distance (td), we first conducted a principal component analysis (PCA) of the 22 environmental variables for collection and garden sites, then subtracted PC1 scores of the garden from that of the collection site ($td = \text{accession} - \text{garden}$, in environment PC1 space). We used a quadratic regression model: $\text{trait} \sim td + td^2 + \text{error}$. Under scenarios of local adaptation, the squared term is expected to have a negative effect estimate with an apex at approximately zero.

Results

Trait variation and correlation

In the Millville garden, the accessions West Ely, Lava Hot Springs, Dow Mountain, Patterson Pass 1, Patterson Pass 2 and Rice Mountain (Table 1; Fig. 1) were top performers for both capsules per plot and biomass in 2013 (Fig. 2; see Supporting Information—Table S1). However, for these traits individually, there were broad significance intervals covering top- and mid-performing accessions. Specifically, the six aforementioned accessions had significantly more capsules per plot than only the five lowest accessions, and they had greater 2013 biomass than just the lowest seven accessions (Fig. 2; see Supporting Information—Table S1). In contrast, 2014 biomass showed more differentiation among accessions, though the CV was relatively high (43.3 %; see Supporting Information—Table S1), with

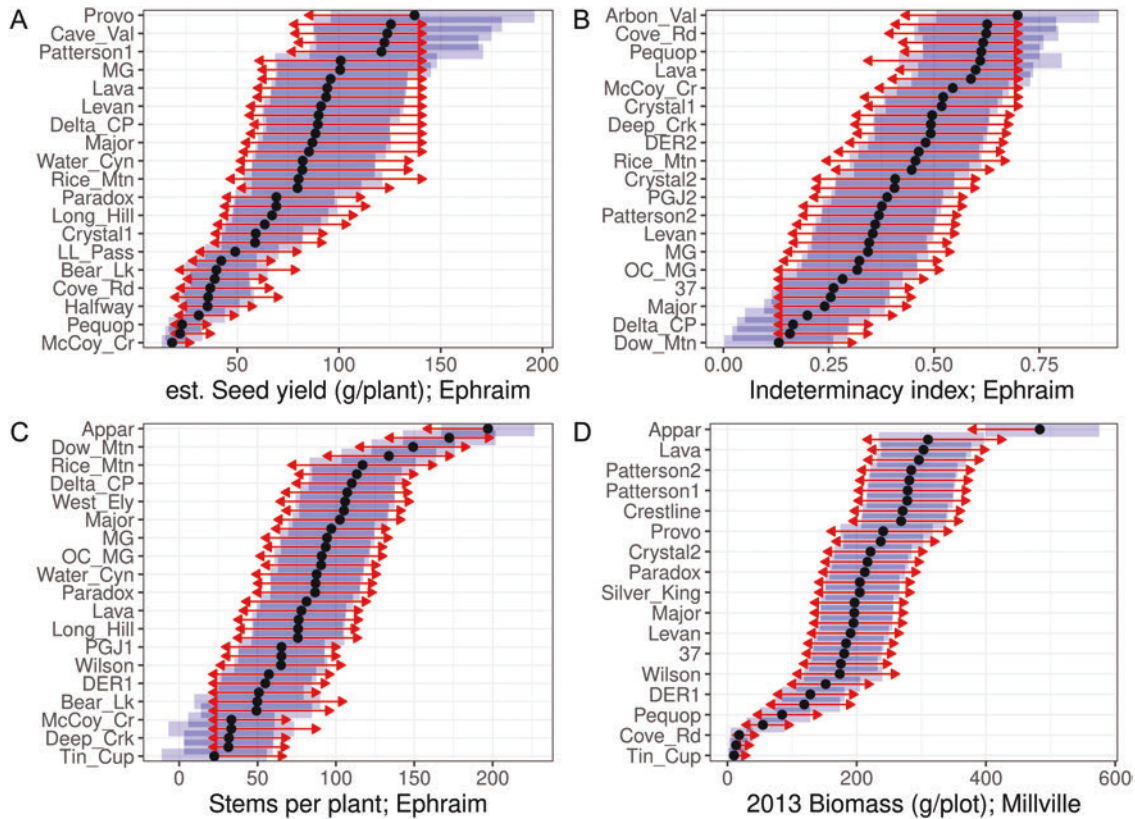


Figure 2. Accession-level mean trait values for (A) seed yield, (B) indeterminacy index, (C) stems per plant and (D) 2013 biomass. The first three traits were measured in the Ephraim garden, the latter is from Millville garden. For indeterminacy index, larger values indicate more delayed or prolonged flowering. All accessions are Lewis flax (*L. lewisii*) except for 'Appar' (*L. perenne*). Black dots show accession-level means estimated from linear mixed models. Blue bars depict 95 % confidence intervals, and red arrows represent Tukey's HSD pairwise comparisons ($\alpha = 0.05$). If arrows overlap, accessions are not significantly different. For visualization purposes, accession labels on y-axis are only shown for every-other accession. Plots were made with R package *emmeans*. See Methods for statistical approach; see [Supporting Information—Tables S1–S3](#) for accession-level means of all traits from both gardens.

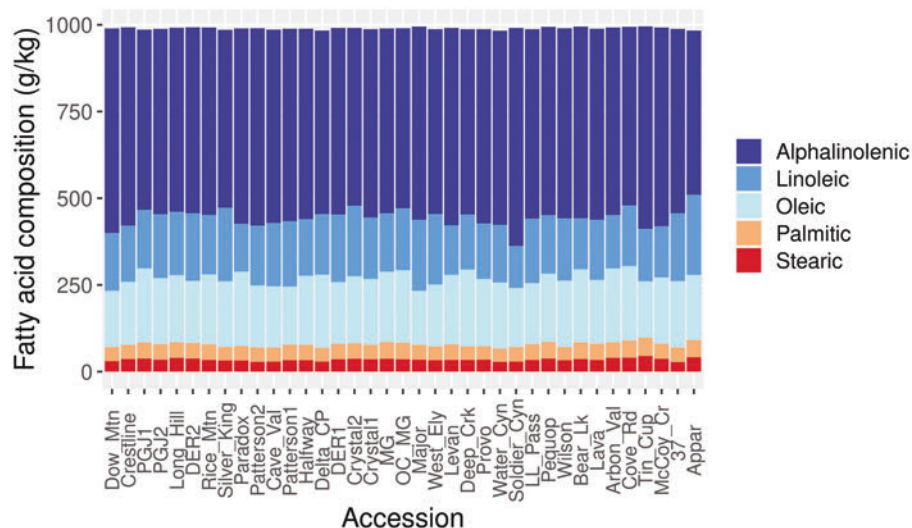


Figure 3. Variation in oil composition among accessions, arranged by latitude. Poly- and monounsaturated fatty acids (alpha-linolenic, linoleic, oleic) are shaded blue and are the upper three stacked bars. Saturated fatty acids (palmitic and stearic) are in shades of red and are the two lower bars.

Dow Mountain, Levan, Lava Hot Springs and Crestline having significantly greater biomass than the bottom 20 accessions. West Ely, a top performer in 2013 biomass, declined in biomass in 2014 by 45 %, from 310 to 142 g per plot [see [Supporting Information—Table S1](#)].

In the Ephraim garden, average 50-count seed mass ranged from 75.4 mg (Tin Cup) to 171.6 mg (Silver King) [see [Supporting Information—Table S2](#)]. Cave Valley and Accession 37 also had among the heaviest seeds. Appar had the second smallest seed mass (76.6 mg per seed) after Tin Cup, while also having the

Table 2. RDA trait loadings, eigenvalues, proportion variance explained by successive RDA axes for Millville garden. Loadings are in bold when greater than $\sqrt{1/m}$, where m = number of traits, 7.

	RDA1	RDA2
Biomass_per_plot_2013	0.46	0.11
Capsules_per_plot	0.44	-0.12
Stems_per_plot	0.44	-0.05
Biomass_per_plot_2014	0.37	-0.51
Plant_diameter	0.35	-0.25
Capsules_per_stem	-0.28	-0.39
Plant_height	0.26	0.71
Eigenvalue	3.65	0.93
Proportion explained	0.29	0.07
Cumulative proportion	0.29	0.36

Table 3. RDA trait loadings, eigenvalues, proportion variance explained by successive RDA axes for Ephraim garden. Loadings are in bold when greater than $\sqrt{1/m}$, where m = number of traits, 18.

	RDA1	RDA2
Seed_mass	0.32	-0.02
Capsule_diam	0.31	0.06
Est_Capsules_per_stem	-0.30	0.03
Indeterminacy_index	-0.30	0.08
Est_yield	0.30	-0.21
Stems_per_plant	0.29	-0.27
Stearic	-0.28	0.13
Height	0.27	0.27
Forks_per_stem	-0.26	-0.04
Palmitic	-0.25	0.01
Est_fecundity	0.23	-0.25
Rust_presence	0.21	0.31
Stem_diam	0.16	0.19
Capsule_fill	0.15	0.21
Linoleic	0.13	0.42
Oleic	-0.09	0.14
Oil_content	-0.04	-0.32
ALA	0.01	-0.49
Eigenvalue	7.15	2.65
Proportion explained	0.25	0.09
Cumulative proportion	0.25	0.35

most stems per plant and the highest estimated fecundity (see [Supporting Information—Table S2](#); [Fig. 2](#)). However, Appar was not significantly different for fecundity from approximately the top 55 % of accessions. Given this, and the relatively low CV of this trait (2.9 %; see [Supporting Information—Table S2](#)), it seems that overall variation in fecundity among accessions is limited. Provo, Soldier Canyon, Maple Grove and Dow Mountain

had among the highest estimated fecundity for Lewis flax [see [Supporting Information—Table S2](#)]. Within Lewis flax, we did not find a trade-off between seed mass and estimated fecundity—these traits were in fact positively correlated ($r = 0.46$, $P = 0.004$; see [Supporting Information—Fig. S1](#)). In terms of estimated seed yield in the Ephraim garden, Provo had the highest mean (137.1 g per plant), even above Appar (125.5 g per plant), although this specific comparison was not statistically significant ([Fig. 2](#); see [Supporting Information—Table S2](#)). Cave Valley, Dow Mountain, Patterson1, West Ely and Maple Grove were also among the statistically top-performing accessions for estimated seed yield ([Fig. 2](#); see [Supporting Information—Table S2](#)).

Average seed oil content in Lewis flax accessions ranged from 218 to 341 g kg⁻¹, for Arbon Valley and Soldier Canyon accessions, respectively [see [Supporting Information—Table S3](#)]. Levan, Pequop and Halfway were also among the accessions with the highest seed oil content. Interestingly, ‘Appar’ had numerically lower seed oil content than all Lewis flax accessions, at 211 g kg⁻¹. We also measured oil content of the domesticated annual flax ‘ND Hammond’ cultivar (*L. usitatissimum*; [Rahman et al. 2019](#)), though this cultivar was not included in the original experimental gardens. On the same NMR instrument, ND Hammond had 459 g kg⁻¹ oil, which is 35 % greater than the maximum oil content measured in Lewis flax.

Lewis flax accessions also varied in their seed oil composition, although they were generally marked by high percentages of poly- and monounsaturated fatty acids ([Fig. 3](#); see [Supporting Information—Table S3](#)). Alpha-linolenic acid (ALA) varied from 512 to 628 g kg⁻¹ total fatty acid in Silver King and Soldier Canyon, respectively. Linoleic acid was negatively correlated with ALA and varied from 138 to 212 g kg⁻¹. Oleic acid, a monounsaturated fat, was found at similar levels to linoleic acid and varied from 156 to 221 g kg⁻¹. Saturated fat levels in Lewis flax were comparatively much lower, with palmitic and stearic fatty acids ranging from 38.4 to 53.2 g kg⁻¹ and 27.8 to 44.8 g kg⁻¹, respectively. By comparison, the ‘ND Hammond’ annual flax cultivar had 542 g kg⁻¹ ALA, 161 g kg⁻¹ linoleic, 203 g kg⁻¹ oleic, 49.5 g kg⁻¹ palmitic and 41.1 g kg⁻¹ stearic, which are all in agreement with existing data on linseed oil composition ([Muir and Westcott 2003](#)). This makes Lewis flax and annual flax virtually indistinguishable in terms of oil composition.

Tincup, McCoy Creek, Cove Road, Arbon Valley and Appar had the lowest recorded rust presence in the Ephraim garden [see [Supporting Information—Table S2](#); [Supporting Information—Fig. S2](#)]. These accessions had close to zero rust recorded across the entire garden, indicating rust failed to establish on these accessions despite infecting neighbouring plants of other accessions. Rust presence was otherwise statistically indistinguishable across accessions and the CV was very high (116 %) [see [Supporting Information—Table S2](#); [Supporting Information—Fig. S2](#)], indicating our experiment did not generate a particularly powerful rust phenotype for differentiating genotypes.

Correlations among traits are reflected in RDA results below ([Tables 2 and 3](#); [Fig. 4](#)), but are also described in Pearson correlation matrices [see [Supporting Information—Fig. S3](#)]. Notably, in the Millville garden, both second- and third-year biomass were positively correlated with capsules per plot in the second year (second-year: $r = 0.93$, $P < 0.05$; third-year: $r = 0.64$, $P < 0.05$; see [Supporting Information—Fig. S3a](#)). This pattern was consistent in the Ephraim garden, with stems per plant (indicative of overall size/biomass) being moderately to strongly correlated with seed mass and overall reproductive output (seed

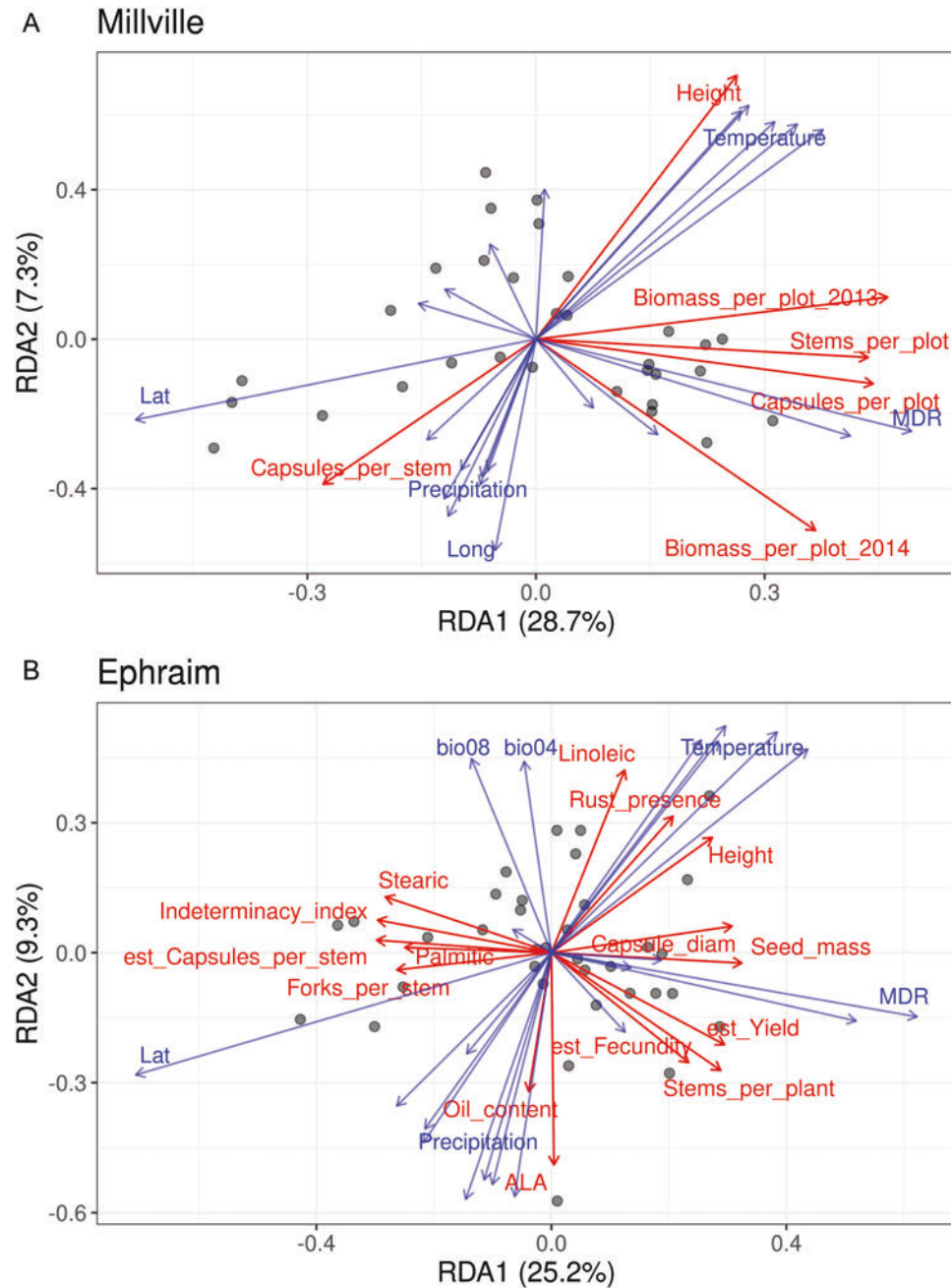


Figure 4. Redundancy analysis of traits and environmental variables for (A) Millville garden and (B) Ephraim garden. Red vectors show trait loadings while blue vectors show environmental predictor loadings. Length of vectors from the origin along either axis indicate the strength of loading on that axis; angles between vectors represent the strength of their correlation, with angles closer to parallel indicating stronger correlation. Loadings are listed in [Tables 2 and 3](#) and [Supporting Information—Tables S4 and S5](#), respectively. For visualization purposes, vectors for traits without strong loadings on RDA1 or RDA2 are excluded, as are labels of predictor variables with weak loadings. ‘Temperature’ includes variables bio01, bio05, bio06, bio10, bio11. ‘Precip’ includes bio12, bio13, bio14, bio16, bio17, bio19. ALA, alpha-linolenic acid; MDR, mean diurnal range (bio02). See [Supporting Information—Figure S4](#) for plots with all vectors and labels shown.

mass: $r = 0.61$, $P < 0.001$; fecundity: $r = 0.89$, $P < 0.001$; seed yield: $r = 0.91$, $P < 0.001$; see [Supporting Information—Fig. S3b](#)).

Trait variation related to climate

In the Millville garden, the 22 spatial and bioclimatic variables together accounted for ~47.3 % of the total trait variation (adjusted R^2) in our RDA. The first RDA axis accounted for 28.7 % of the variation in traits and was primarily associated with latitude, mean diurnal range, isothermality and other

temperature variables ([Fig. 4A](#); see [Supporting Information—Fig. S4a](#); [Table 2](#)). Second-year (2013) biomass, capsules per plot and stems per plot covaried with this RDA axis: plants originating from southern latitudes, with increased temperatures and greater diurnal range, tended to have increased plot-level stem, capsule and biomass production. The second Millville RDA axis accounted for 7.3 % of the variation in traits and was associated most strongly with average and maximum summer temperatures, longitude and various precipitation variables.

Along this axis, overall hotter and drier environments located further west were characterized by taller plants with fewer capsules per stem and reduced third-year biomass (2014). However, RDA2 explained considerably less of the total trait variation than RDA1, and was not statistically significant (RDA1 $P < 0.02$; RDA2 $P = 0.46$).

The Ephraim garden RDA revealed overall similar patterns of trait–environment associations. The 22 environmental predictors together explained ~53 % of total variation among the 18 traits. Only the first two constrained axes, RDA1 and RDA2, were statistically significant (RDA1 $P < 0.001$; RDA2 $P < 0.01$). The first axis explained 25.2 % of the total trait variation and, similar to the Millville RDA, was mainly associated with latitude, which loaded opposite to mean diurnal range, isothermality, mean winter temperature and mean annual temperature (Fig. 4B; see [Supporting Information—Fig. S4b](#); Table 3). Plants from more southern latitudes experiencing generally hotter temperatures, and increased diurnal range, tended to have increased seed mass, larger capsules, were taller and had higher estimated yield. Conversely along RDA1, accessions from more northern latitudes had, on average, more forks per stem, more estimated capsules per stem, greater indeterminacy index, as well as higher seed oil compositions of saturated fatty acids (stearic and palmitic acid). The second axis explained 9.3 % of the total trait variation and was predominantly associated with precipitation variables, temperature seasonality and to a lesser extent other temperature variables. Along this axis, accessions with higher ALA composition (and lower linoleic composition), along with oil content, were characterized by collection sites with greater precipitation and lower temperature. Rust presence and estimated fecundity also loaded strongly on RDA2, in opposite directions, such that accessions from overall wetter, cooler sites had lower levels of rust infection and higher fecundity. Redundancy analysis loadings and descriptions of environmental predictors are given in [Supporting Information—Tables S4–S6](#).

Tests for local adaptation based on transfer distance

To test for evidence of local adaptation, we tested the effect of transfer distance from collection site to garden site (in units of environment PC1; see [Supporting Information—Fig. S5](#)) on first-year overwinter survival (Millville garden) and estimated fecundity (Ephraim garden). In both models, the effect of *transfer distance*² was not significant [see [Supporting Information—Fig. S6](#)], indicating lower environmental transfer distance did not confer a clear fitness benefit within the controlled environment of our gardens.

Discussion

Ecological significance

We used two common gardens to analyse a variety of seed and plant growth traits among populations of Lewis flax (*L. lewisii*) in the Intermountain region. We identified substantial phenotypic variation among populations for numerous traits, including flowering indeterminacy, forks per stem, number of stems, estimated yield, biomass, seed mass, and seed oil content and composition. This variation was often associated with geographic and climate variables, which is consistent with local adaptation of Lewis flax to different sites as a result of natural selection. Lewis flax appears to have evolved divergent life-history strategies—primarily according to latitude—that are

centred on a trade-off between increased stem biomass and seed yield versus more indeterminate blooming with more flowers.

Although experimental design differed somewhat between our two common gardens, the results are largely consistent with each other. The primary axis of trait–environment association observed in both gardens was increased stem and seed capsule production in accessions from more southern sites that are generally hotter and experience greater ranges in day–night temperature oscillations (Fig. 4). In the Ephraim garden, plants from more southern sites also tended to have larger seeds. On the other hand, plants from more northern sites displayed fewer stems with more branches (forks) and capsules per stem, which corresponds with more indeterminate flowering (Fig. 4). Those more northern sites displayed greater annual fluctuations in temperature relative to daily fluctuations (decreasing isothermality, bio03; Fig. 4; see [Supporting Information—Fig. S4](#); [Supporting Information—Tables S5 and S6](#)).

This result is mostly consistent with previous research on latitudinal adaptation in domesticated flax (*L. usitatissimum*). The gene *LuTFL1* causes delayed flowering and indeterminate growth in domesticated flax, similar to its ortholog in *Arabidopsis thaliana*, *TFL1* (Shannon and Meeks-Wagner 1991; Gutaker et al. 2019). Latitudinal clines in allele frequency of *LuTFL1* were found in populations of *L. usitatissimum* and its wild progenitor, pale flax (*L. bienne*), such that adaptation to more northern climates with greater annual climate variation is suggested to have occurred, at least in part, via indeterminate flowering (Gutaker et al. 2019). The effect of *LuTFL1* on flowering time was also shown to influence plant architecture and stem height, likely resulting in longer-stemmed plants in northern areas, which may have facilitated the use of flax as a fibre source for textiles (Gutaker et al. 2019). In our study with Lewis flax, we essentially found the opposite pattern: greater height was associated with more southern sites, less branching (forks per stem) and greater determinacy (Fig. 4). It is plausible that Lewis flax and domesticated flax/pale flax have evolved divergent degrees of branching, such that comparatively increased branching in Lewis flax offsets any gain in height otherwise provided by indeterminacy. Notably, ‘Appar’ (*L. perenne*) had more forks per stem than every Lewis flax accession except Arbon Valley. This supports the notion that degree of branching is variable within the *Linum* genus. Overall, our data suggest that Lewis flax may have evolved similar latitudinal adaptations to domesticated flax, by which more indeterminate flowering/growth increases fitness in northern latitudes.

Seed traits often have direct fitness consequences and as a result display important biogeographic variation both across and within species (Meyer and Kitchen 1994; Moles and Westoby 2003; Kattge et al. 2011; Ostevik et al. 2016; Reinert et al. 2019). This was reflected to some degree in the Lewis flax accessions presented here. Out of all the seed traits we measured (mass, oil content, oil composition), seed mass had the strongest loading on the first RDA axis, indicating heavier seeds are associated with more southern accessions (Fig. 4B). Seed mass influences germination and seedling survival such that larger seeds provide improved survival under a variety of hazards (Leishman et al. 2000). The advantage of larger seeds is classically predicted to have a trade-off in fecundity (Smith and Fretwell 1974; Venable and Brown 1988). Interestingly, we found the opposite pattern among Lewis flax accessions, with seed mass and estimated fecundity being positively correlated [see [Supporting Information—Figs S1 and S3b](#)]. Additionally, seed mass and fecundity had a moderate to strong positive correlation with stem number ($r = 0.61$, $P < 0.001$;

$r = 0.89, P < 0.001$; see [Supporting Information—Fig. S3b](#)), suggestive of allometric scaling between plant size and reproductive output. This pattern is not uncommon in perennials (e.g. [Samson and Werk 1986](#); [Piper and Kulakow 1994](#)), and in Lewis flax it could relate to environmental factors at the collection sites, with more favourable sites supporting larger plants with both more and heavier seeds.

Alternatively, as a perennial, Lewis flax may counteract poor survival (i.e. short lifespans) in harsh climates with increases in both seed mass and number (i.e. a more acquisitive or ruderal strategy). Third-year (2014) biomass at our Millville garden provides an indirect measure of longevity, and this trait showed a moderate positive correlation with capsule production the previous year. Thus, if there is a trade-off between vegetative growth/longevity and reproductive output, it is not clearly apparent in the first 3 years of growth. More testing would be useful to validate one or all of these possible hypotheses. However, in agreement with our results, a study of the perennial forb *Physaria mendocina* (Brassicaceae), another oilseed domestication candidate, found no trade-off between current reproductive output and future biomass ([González-Paleo et al. 2016](#)). It is clear from our study and others (e.g. [Herron et al. 2021](#)) that even within perennial species, there is important intraspecific variation in life-history strategies/longevity.

Seed germination in Lewis flax has been previously shown to vary as a function of habitat. In a study of 21 collections of Lewis flax from the Intermountain region—some of which are also included here—seed dormancy was found to generally increase with elevation, such that populations from prairie and pinyon-juniper habitats at lower elevations showed very little dormancy, while collections from upper montane habitats displayed near-complete dormancy and required a chill treatment to germinate ([Meyer and Kitchen 1994](#)). Similar clines in dormancy have been found in other Intermountain forb species ([Meyer et al. 1995](#)). In the present study, we did not find associations between seed traits and elevation, which makes it difficult to directly connect patterns of germination control with seed mass or oil characteristics in Lewis flax.

We did not find obvious evidence for local adaptation when we tested for effects of transfer distance on fitness traits [see [Supporting Information—Fig. S6](#)]. Local adaptation is generally thought to be frequent, but results in the literature have overall been equivocal ([Leimu and Fischer 2008](#); [Hereford 2009](#); [Jones 2013, 2017](#)). As a widely distributed species, populations of Lewis flax may be sufficiently adapted to a wide range of conditions, at least within the Intermountain West. It is possible that demographic processes, such as those related to range expansion and/or contraction, have resulted in patterns of genetic variation that explain most of the variation in phenotypes described here ([McKown et al. 2014](#)). Without genetic data we are unable to conclusively determine whether or not these clines represent adaptive variation or simply the results of benign population genetic forces, such as drift. Alternatively, our transfer distance results could be explained in part by the fact plants were germinated and nursed indoors, weeds were controlled for the duration of the study and the Ephraim garden (but not Millville) received supplemental water in the first year. Benefits to establishment conferred by traits such as increased seed mass or oil content would have been largely unrealized as a result. A pattern of local adaptation may also have been obscured by the fact our transfer distance test was based on historical climate averages for the two garden sites, rather than conditions during the 3 years of the experiment. We conclude the geographic and climatic clines in various Lewis flax traits reported here remain consistent with underlying adaptive processes. This evidence is

intriguing but warrants future experimental and genomic work that more directly tests adaptive hypotheses.

Implications for restoration and domestication

Recent studies have stressed the need for collection and banking of diverse germplasm for species important in restoration, and the same is true for CWRs ([Havens et al. 2015](#); [Prober et al. 2015](#); [Khouri et al. 2020](#); [Zhang and Batley 2020](#)). The trait variation observed among wild Lewis flax accessions in this study is promising for its continued use in ecological restoration and development as a perennial oilseed crop. Lewis flax seems not to be confined to a single life-history strategy, which bodes well for its ability to track a changing climate and its amenability to selective breeding.

Maple Grove is currently the only commercially available variety of Lewis flax. Several of the wild accessions showed promise for being just as productive, if not more so, compared to Maple Grove. Based on capsules per plot and third-year (2014) biomass from the Millville garden, in combination with estimated fecundity from Ephraim garden, we suggest that Dow Mountain, Lava Hot Springs, Levan, Provo, Rice Mountain and Crestline are deserving of further consideration for a new USDA germplasm release, though we caution that our results are preliminary, given that results from the two gardens are not completely comparable.

The Lewis flax accessions which ultimately had the lowest amount of rust infection also had among the lowest seed yield and fecundity: these were Tincup, McCoy Creek, Cove Road and Arbon Valley. Although rust presence and fecundity were loosely associated in RDA space, lack of significant Pearson correlations precludes a clear trade-off between disease resistance and reproductive output [see [Supporting Information—Fig. S3b](#)]. Rust presence results should be interpreted cautiously because pathogen races can vary from year to year, and we did not control for this: we took only descriptive measurements of rust presence, following natural emergence and spread of the pathogen. Ultimately, our primary goal was not a study of rust pathology, but the aforementioned accessions could be screened for beneficial rust-resistance alleles in the future. Additional studies on rust resistance and dynamics in Lewis flax would benefit greatly from more controlled characterization of this pathogen.

Oil quality and quantity are among the primary interests for agricultural applications of Lewis flax as an oilseed. We have shown that oil composition is essentially indistinguishable from that of cultivated flax. Although this has been previously reported ([Yermanos 1966](#)), we have assessed a much broader sample of Lewis flax here. Despite some intraspecific variation, Lewis flax seed has consistently high proportions of ALA and other unsaturated fatty acids that are desirable for human consumption. We observed that the ALA fraction was generally as high or higher than cultivated flax. This should allow oilseed breeding programmes to proceed with inclusion of diverse germplasm. Although total oil content of Lewis flax seed was markedly lower compared to cultivated flax, variation among accessions grown in a common garden suggests a genetic component to this trait that should make it amenable to selective breeding.

Variation found in overall seed yield and longevity—the latter being inferred via third-year plot-level biomass in our study—are additional factors to consider in the establishment of breeding lines moving forward. Decoupling the trade-off between longevity and reproductive output is a fundamental challenge of developing viable perennial oilseed and grain crops ([DeHaan and Van Tassel 2014](#); [Vico et al. 2016](#)). Although we did

not find a trade-off between longevity (third-year biomass) and reproductive output for Lewis flax in this study, we hypothesize such a trade-off might be apparent if observed beyond 3 years. This seems plausible given that we also did not find a trade-off between fecundity and seed mass, nor fecundity and rust presence. Life-history theory would predict that increased reproductive output must come at some cost.

Conclusion

Lewis flax harbours substantial, potentially adaptive, phenotypic variation in the Intermountain region, but much remains to be understood about this widespread species. Collections from populations beyond this region would be particularly valuable in determining whether patterns of trait–climate covariation described here are maintained over broader geographic scales. A study of its population genetic structure across North America could link patterns of genetic diversity to the phenotypic clines described here, and also unveil its frequency of selfing versus outcrossing. Closer investigation of environmental factors and plant traits not included here (e.g. soil characteristics, resource allocation to roots) may shed additional light on the trade-off between acquisitive and conservative life-history strategies in Lewis flax. Although we suggest further screening of top-performing accessions before any public germplasm release or selection of breeding lines, the knowledge of intraspecific variation described here is a clear benefit for both ecosystem restoration and sustainable agriculture.

During the Lewis and Clark expedition in 1805, near the Dearborn River in central Montana, Meriwether Lewis made observations of Lewis flax: ‘I have observed for several days a species of flax growing in the river bottoms... the root appears to be perennial...the seed are not yet ripe but I hope to have an opportunity of collecting some of them after they are so. If it should on experiment prove to yeald [sic] good flax and at the same time admit of being cut without injuring the perennial root it will be a most valuable plant’ (Lewis et al. 2003). Over two centuries later, his words (likely influenced by Indigenous knowledge) continue to shape applied ecological research priorities.

Supporting Information

The following additional information is available in the online version of this article—

Methods. Millville garden phenotyping, Ephraim phenotyping, Gas chromatography conditions.

Table S1. Millville garden accession-level trait means and coefficients of variation.

Table S2. Ephraim garden accession-level trait means and coefficients of variation (non-oil traits).

Table S3. Ephraim garden accession-level trait means and coefficients of variation (oil traits).

Table S4. Millville garden redundancy analysis (RDA) environmental predictor loadings.

Table S5. Ephraim garden redundancy analysis (RDA) environmental predictor loadings.

Table S6. Description of bioclimatic variables.

Figure S1. Estimated fecundity versus seed mass (Ephraim garden).

Figure S2. Rust presence scores (Ephraim garden).

Figure S3. Pairwise Pearson correlation matrices of accession-level trait means.

Figure S4. Trait–environment redundancy analysis (RDA) plots with all vectors displayed and labelled.

Figure S5. PCA plot of all 22 environmental variables.

Figure S6. Transfer distance plots.

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Contributions by the Authors

S.K., T.J., S.J., L.S.J., and D.T. collected seed, designed, and implemented the common garden experiments. AG and BSH carried out seed oil analyses. P.I., A.G., and B.S.H. analysed the data. P.I. wrote the original draft; B.S.H., S.K., T.J., A.G., L.S.J., S.J., and D.T. contributed review and editing.

Conflict of Interest

None declared.

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Data Availability

All data from this study have been deposited in an accompanying Dryad repository: doi:10.5061/dryad.tdz08kq1n. Code to reproduce all results from the data is available at: https://github.com/peterinnes/Lile_common_garden.

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