



Common camas (*Camassia quamash*) response across an urban–rural gradient in coastal oak meadows in Greater Victoria, Canada

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Abstract

Coastal oak meadows are fragmented across an increasingly urbanized landscape in Greater Victoria with implications for common camas (*q^włəł/KŁO,EL/Camassia quamash*) fitness. Common camas, frequently present in coastal oak meadows, is an ecologically important cultural keystone species that forms the foundation of one of the most important Indigenous food systems in the region. Previous research has examined how the pressures associated with urbanization shape plant community composition and structure, but how these pressures influence individual plant fitness remains unclear. To improve our understanding, we assessed environmental conditions and common camas growth and reproductive traits across an urban-rural gradient in Greater Victoria. We found that urbanization on this landscape alters several key environmental variables (namely increased trampling and soil compaction, and decreased soil depth, canopy cover, and soil phosphorus) and that common camas appears to be responding to these altered conditions with a reduction in growth and reproductive trait values. By targeting the identified pressures, management can work towards supporting more successful urban camas populations into the future.

Keywords *Camassia quamash* · Functional responses · Intraspecific variation · Plant functional traits · Urban ecology

Introduction

In 2022, 55% of the global population resided in urban areas and the United Nations (2019) predicts that this percentage will increase to 68% by 2050. In Canada, population growth in urban centers is outpacing nation-wide growth, urban areas are becoming more densely populated, and urban sprawl continues to expand into surrounding rural areas (Statistics Canada 2022). Urbanization is associated with a range of altered environmental conditions, including the loss and/or degradation of natural areas, altered local

hydrology (due to vast expanses of impermeable surfaces), modified nutrient cycling, increased introductions of invasive species, air and water pollution, among others (Grimm et al. 2008; Kowarik 2011; Parris 2016; Pickett et al. 2001). Urban land use can have direct effects on plant communities by altering site conditions (e.g., soil temperature) and indirect effects through modifying habitat availability and spatial configuration (Albrecht and Haider 2013; Vallet et al. 2010). It is well understood that these direct and indirect effects of urbanization shape plant community composition and structure (Albrecht and Haider 2013; Knapp et al. 2009; Williams et al. 2015).

Altered environmental conditions and disturbance regimes associated with urban land use act as filters that control community composition through the selection of plants with a particular set of attributes or functional traits (Knapp et al. 2009; Palma et al. 2017; Vallet et al. 2010; Williams et al. 2015). Plant functional traits are a useful framework for examining the attributes of plants and the patterns of their response to different environmental pressures (Kattge et al. 2020; Pérez-Harguindeguy et al. 2013; Williams et al. 2005). Urban areas tend to favour the same set of plant traits, often leading to biotic homogenization whereby species

Positionality statement The author team is composed of settlers writing from the traditional territories of the *lək^wəŋən* (Songhees and Esquimalt) and *W̱SÁNEĆ* Nations. We acknowledge that this research has taken place on a landscape where, for millennia, Indigenous peoples learned and applied extensive ecological knowledge to steward the coastal oak meadows we work in today. This is a responsibility and relationship that continues to this day.

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and functional diversity decrease (de Ruas Barros et al. 2022; Thompson and McCarthy 2008). This understanding of the environment filtering for specific plant traits enables the prediction of species frequency and distribution across an urban-rural gradient, particularly of interest for species not well adapted to urban environments (Knapp et al. 2009; Vallet et al. 2010). However, how individual plants of a single species vary in their response to these changes in their environment remains unclear, with implications for plant success and persistence in urban areas.

Intraspecific trait variation is the trait variation within a species (Violle et al. 2012). It varies less than the trait variation among species (interspecific trait variation), but it is not negligible and has the capacity to contribute to a significant proportion of trait variation in plant communities (Siefert et al. 2015; Westerband et al. 2021). Only a handful of studies globally have examined how individuals within a species vary in their response to the complex, often interacting environmental pressures associated with urbanization (Borowy and Swan 2020; Cochard et al. 2019; Pisman et al. 2020; Zhu and Xu 2021). Exploring variation in traits in individual species across an urban-rural gradient will provide insight into the drivers of reproductive and fitness response (and potential adaptability) of these species to urbanization (Pisman et al. 2020; Weston et al. 2021). This is particularly important for ecologically and culturally important species that only exist in largely urban areas.

The objective of this study was to address this knowledge gap by investigating how common camas ($q^w\text{t}\text{ə}\text{t}$ in $l\text{ə}k^w\text{ə}n\text{ij}\text{t}\text{ə}n\text{ə}j$ and $K\text{ŁO,EL}$ in SENCOTEN, *Camassia quamash*) is responding to increasing urbanization in Greater Victoria. Common camas is an ecologically important cultural keystone species (Beckwith 2004; Garibaldi and Turner 2004; Gritzner 1994; Proctor 2013) that exists almost entirely in urban areas across its Canadian range (GOERT 2011). Present in oak meadows from northern California to southern British Columbia, common camas is a perennial forb species in the Asparagaceae family with an inflorescence of striking blue-purple flowers that bloom into a showy floral display in oak meadows each spring (Hitchcock and Cronquist 2018). Across Coast Salish territories, camas was, and continues to be, actively stewarded by Coast Salish First Nations and is a significant component of their traditional foods system (Proctor 2013; Turner and Kuhnlein 1983). Prior to European colonization and the dispossession of Indigenous peoples from their lands, camas was extensively cultivated across this region (Beckwith 2004; Garibaldi and Turner 2004; Proctor 2013). Today, the distribution of common camas in this region, particularly on southern Vancouver Island, is limited to small, fragmented oak meadows across an increasingly urbanized landscape (GOERT 2011). Understanding that this region is experiencing some of the greatest urban population growth in the country (Statistics Canada 2022), it is paramount to

understand how this species is responding to the pressures associated with urbanization to support its success and persistence into the future.

To assess how common camas growth and reproduction is impacted by increasing urbanization in the Greater Victoria region, the objectives of this study were twofold. First, we sought to examine whether urbanization is associated with shifts in the environmental conditions found in remnant oak meadows in Greater Victoria. Second, we sought to investigate how common camas individuals are responding to these altered conditions. An improved understanding of how urbanization affects local site conditions in oak meadows across Greater Victoria, and how common camas individuals may be responding to these altered conditions, will contribute to local and regional planning and initiatives that seek to target specific urban pressures and support more successful urban camas populations into the future. At a broader scale, examining how individual plants respond to environmental change can contribute to global efforts that aim to better understand how plant species may respond to urbanization, a pressure that is largely increasing in vulnerable ecosystems worldwide.

Methods

Study area

The project area is within the traditional territory of the $l\text{ə}k^w\text{ə}n\text{ə}n$, $W\text{S}\text{ÁNEC}$, $M\text{ÁLEXEŁ$, $Sc'\text{ianew}$, and $T'Souke$ peoples. Located on the southern tip of Vancouver Island, off the west coast of British Columbia, Canada (Fig. 1), this region experiences a Mediterranean climate characterized by mild, wet winters and warm, dry summers (GOERT 2011). In the rain shadow of the Olympic and Vancouver Island mountain ranges, this region is the driest part of the Coastal Douglas fir biogeoclimatic zone and supports coastal oak meadow ecosystems (Barlow et al. 2021; GOERT 2011). Ranging from northern California to southwestern BC, oak meadows in Canada represent the northernmost extent of these ecosystems, with most of their Canadian range limited to southeastern Vancouver Island and the southern Gulf Islands (GOERT 2011).

Coastal oak meadows are unique ecosystems with distinct flora, often containing Garry oak (*Quercus garryana*) trees, and are frequently associated with Garry oak woodlands, grasslands, vernal wetlands, coastal bluffs, and rocky outcrops (Fairbarns n.d.; GOERT 2011). These ecosystems are among the most endangered ecosystems in Canada, largely due to habitat degradation from human disturbance, habitat fragmentation, exotic species invasions, overgrazing, fire suppression, and the loss of First Nations stewardship (Clements 2013; Dunwiddie and Bakker 2011; GOERT 2011).

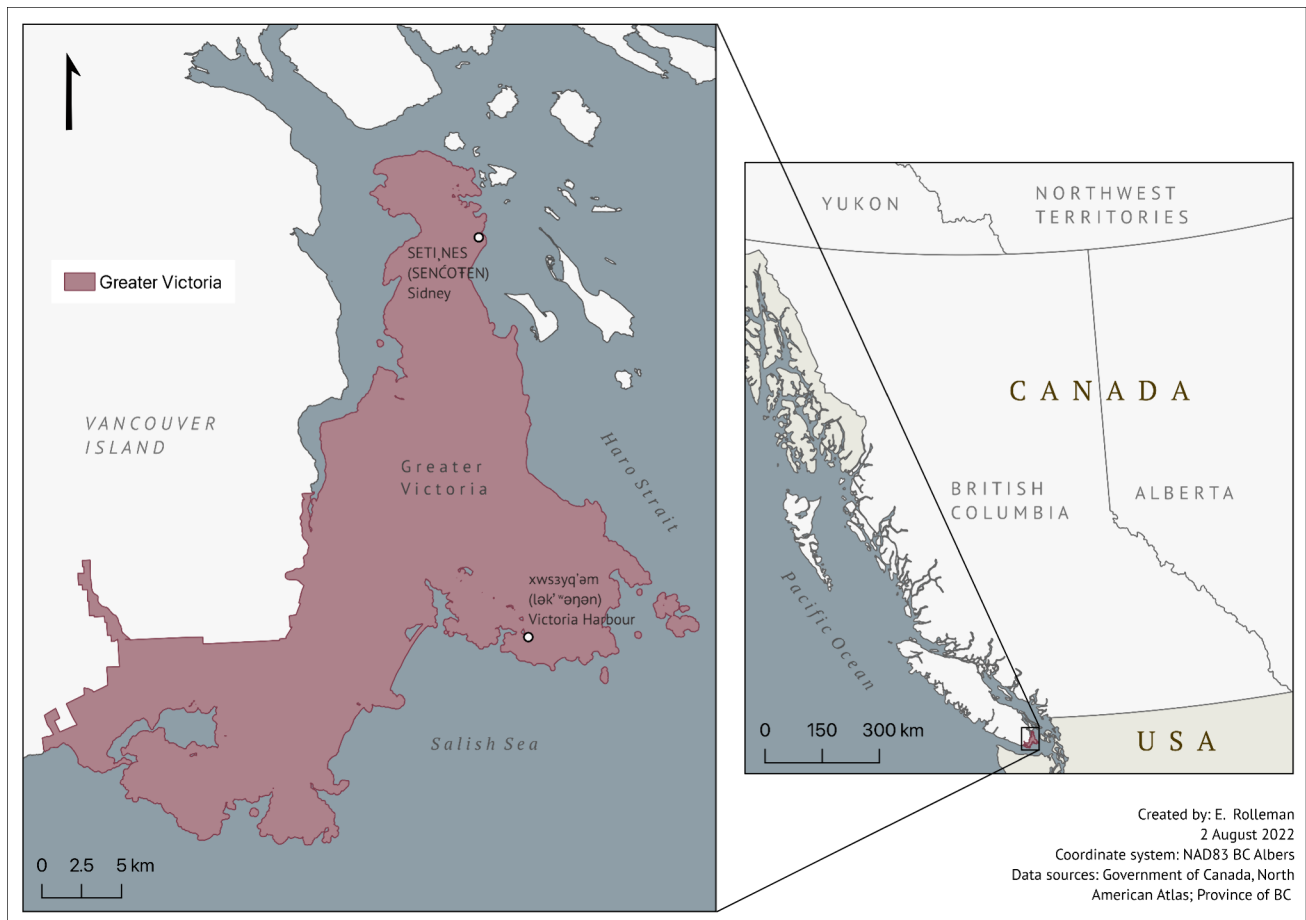


Fig. 1 A map of the Greater Victoria region on Vancouver Island, British Columbia

Indigenous stewardship of these ecosystems to cultivate food, medicine, and other culturally important species led to these ecosystems thriving across much of the Greater Victoria region pre-European colonization (MacDougall et al. 2004). With colonization and the dispossession of Indigenous peoples from their traditional territories, these systems of stewardship were disrupted, and large swaths of oak meadows were converted to agriculture or residential areas. The meadows were targeted for settlement and agriculture because in the eyes of the European settlers they appeared as open, cleared tracts of park-like land absent of human occupation or cultivation (Deur 2002; MacDougall 2008). In stark contrast to this assumption, however, was the reality that these meadows had been actively stewarded by local First Nations for millennia to sustain a highly productive food system (Beckwith 2004; Turner and Kuhnlein 1983). Fire stewardship, soil building, weeding, tilling, and rock removal, among other practices over centuries, sustained the presence of these vast meadows and prevented the encroachment of what would otherwise be late succession Douglas-fir forests (Turner 1999; Turner and Kuhnlein 1983). Ongoing habitat loss and degradation has led

to the remaining patches of oak meadows being fragmented across an increasingly urbanized landscape, with implications for species migration, dispersal, and persistence (Evju et al. 2015; GOERT 2011).

Ecology and history of camas

Common camas (*Camassia quamash* (Pursh) Greene) is one of the six species in the North American genus *Camassia* (POWO 2023) (Fig. 2). Common camas is the most widespread of the five species across the Pacific Northwest and can be found from northern California to southern British Columbia. Common camas is a bulbous geophyte, a perennial plant with an underground storage structure (Hitchcock and Cronquist 2018). In early spring, long basal leaves emerge from the underground bulbs. A few weeks later, a terminal raceme blooms with pale to deep blue-purple flowers, putting on a showy display across oak meadows from early April to early May, and attracting a diversity of pollinator insects (Hitchcock and Cronquist 2018; Rammell et al. 2019). Each flower that matures into a capsule produces several shiny



Fig. 2 Common camas (*Camassia quamash*)

black seeds (Hitchcock and Cronquist 2018). From seed, common camas have a lengthy maturation period that can take 5 or more years for the seeds to grow into mature, flowering plants (Carney et al. 2021; Proctor 2013). Common camas reproduce both from seed and asexually through bulb division (Beckwith 2004; Carney et al. 2021). The resources stored in their bulbs can also enable camas plants to remain dormant during the growing season in response to harsh environmental pressures such as drought or resource limitations (Beckwith 2004).

Common camas and great camas (*Camassia leichtlini*) (another species of camas frequently present in coastal oak meadows) were extensively cultivated across Coast Salish territories prior to European colonization (Garibaldi and Turner 2004; GOERT 2011; Proctor 2013). Camas bulbs were a dietary staple providing a key source of carbohydrate and vegetable protein in an otherwise largely animal-based diet (Gritzner 1994; Turner and Kuhnlein 1983). The bulbs are usually prepared by steaming or roasting in

earth ovens, where hot temperatures for sustained periods of time convert the complex carbohydrates into easier to digest forms (Carney et al. 2021; Turner and Kuhnlein 1983). Evidence of camas consumption dates back over 8000 years in the Pacific Northwest (Carney et al. 2021; Kramer 2000), and trade moved these bulbs extensively around the region (Lutz 2008). Sophisticated land management practices regulated camas production in family-run plots, and cultivation practices based on extensive knowledge of camas and its habitat enabled tremendous bulb harvests (Beckwith 2004; Gritzner 1994; Lyons and Ritchie 2017; Turner 1999). Today camas is still cultivated and harvested by local First Nations (Penn 2006), but a mere fraction of pre-colonization camas habitat exists.

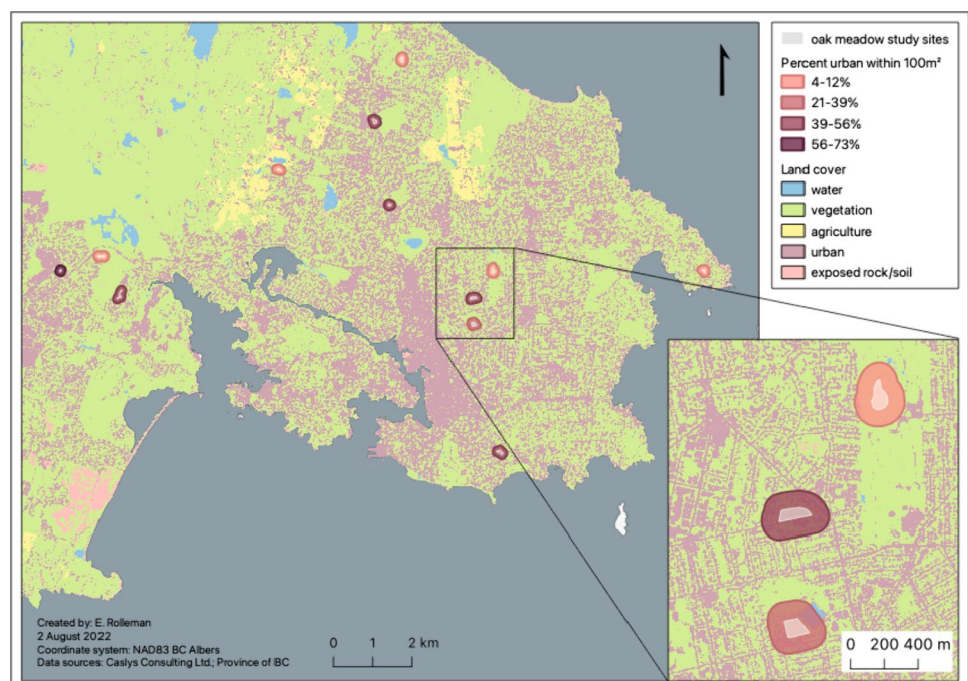
The remaining oak meadows in this region have become important sites of eco-cultural revitalization centered on camas. Local First Nations are engaging in a resurgence of cultural practices within the *q̓w̓təł/KŁO,EL* food system to revitalize stewardship practices and regenerate community roles and responsibilities (Corntassel and Bryce 2012). The same forces that threaten the biodiversity of coastal oak meadows also threaten Indigenous peoples' relationships with their homelands and the health and well-being of their communities (Corntassel and Bryce 2012). Through land-based learning, youth education, and broader public education (e.g., community pit cooks and invasive species removals), local First Nations are reinstating traditional roles and practicing everyday acts of resurgence within coastal oak meadows.

Sample site selection

We characterized the urban-rural gradient across Greater Victoria using a 1m² land cover classification raster layer obtained from Habitat Acquisition Trust (prepared by Caslys Consulting Ltd. 2013) for the study area based on aerial imagery from 2011. Using a preliminary dataset previously developed which combines the best-known oak meadow distributions in the region (Supplementary Material 1.2), 100 m buffers were drawn around each oak meadow patch and used to calculate the number of 1m² pixels of each land cover type surrounding each oak meadow (Fig. 3). The number of urban land cover pixels (defined as all impervious surfaces including buildings and roads) per 100 m buffer was converted to a percentage to generate a gradient across the landscape. All oak meadow patches surrounded by > 60% urban land cover were less than 13km² in size, so all meadow patches larger than 13km² were removed from the analysis to control for habitat patch size. The number of study sites was further reduced to twelve sites by restricting the scope to four municipalities (the Capital Regional District, City of Langford, City of Victoria, and District of Saanich). The twelve study sites were reviewed by archaeologist Dr. Darcy Mathews to ensure the study sites did not conflict with any recorded archeological sites. See Fig. 3 for a map of the twelve sites where field data were collected.

Within the twelve study sites, a stratified-random sampling design was implemented to select four 1m² data collection plots. Data collection was limited to four plots at

Fig. 3 A map of the twelve oak meadow study sites ranging from 4-73% urban land cover in the surrounding 100 m²



each site due to the seasonal constraints of a short blooming window for common camas. Each study site was divided into four equal area quadrants and ten points were randomly located within each and labelled 1-10. In the field, data were collected at one point location per quadrant, starting at the point labelled 1. If there were not five common camas individuals in bloom at point 1, data were collected at point 2, and so on. If five common camas individuals were not present at any of the ten point locations in a quadrant, a location within the quadrant was visually selected. If that was not possible due to a lack of five blooming camas individuals within 1m², a location within one of the other three quadrants was selected that was not spatially proximate to the other data collection plots at the site.

Data collection

Data were collected at two scales, at the 1m² plot-level and at the individual plant-level and occurred in two phases. The first phase took place April 20-May 12, 2022 when common camas was in peak bloom, and the second phase took place July 4-11, 2022 when the camas had gone to seed (Table 1).

Plot-level measurements were recorded in each of the 1m² data collection plots. Canopy cover readings using a Forest Suppliers spherical concave densiometer were taken from the four compass directions and averaged for a more accurate estimate. Soil compaction (using a Durham Geo Pocket penetrometer) and soil depth were measured five times in each quadrat (once in each corner and once at the center) and averaged. One soil core was taken per plot using a 1-inch diameter soil auger, and the sample was air-dried and sieved to < 2 mm before being sent to the BC Analytical Laboratory for nutrient (nitrogen, carbon, sulphur, and available phosphorus) and pH testing. Trampling and herbivory were estimated using a 5 × 5 grid within each 1m² quadrat with the number of grid squares that exhibited trampling or herbivory counted and converted to a percentage. Graminoid cover in each plot was estimated using seven cover classes: A < 1%, B 1-5%, C 6-25%, D 26-50%, E 51-75%, F 76-95%, G > 95% (Daubenmire 1959). Graminoids were not identified to family due to the challenges of identification pre-bloom. Camas abundance was calculated by counting the number of camas plants in bloom, bud, or neither (juvenile plants lacking an inflorescence or adult plants whose inflorescence was absent) per quadrat.

Table 1 Definitions of all measurements, at what scale they were measured, and during which phase (phase 1 being April 20 – May 12, 2022, and phase 2 July 4 – 11, 2022)

Measurement	Definition (units)	Method of measurement	Scale	Date
Disturbance	The percentage of the plot affected by trampling (flattened foliage) and/or herbivory (%)	Visual estimation	Plot	April/May
Canopy cover	The percentage of ground covered by the vertical projection of surrounding vegetation (%)	Forest Suppliers spherical concave densiometer (Model-C)	Plot	April/May
Soil pH	(0 – 14 from acidic to alkaline)	Soil sample tested at the Province of BC's Analytical Laboratory	Plot	July
Soil compaction	The extent and depth of subsurface compaction (kg/cm ²)	Durham Geo Pocket Penetrometer (S-170)	Plot	July
Soil nutrient content	The amount of total carbon, nitrogen, and sulphur (%), and available phosphorus (mg/kg) present in the soil	Soil sample tested at the Province of BC's Analytical Laboratory	Plot	July
Soil depth	The vertical distance from the soil surface to bedrock, parent material, or other physical barrier to plant root growth (cm)	Metal skewer and ruler	Plot	July
Graminoid cover	Estimated percentage cover of graminoids (%)	Visual estimation	Plot	April/May
Camas abundance	The number of <i>Camassia quamash</i> in bloom, and the number <i>Camassia quamash/leichtlinii</i> in bud or lacking an inflorescence (count)		Plot	April/May
Height (Hmax)	Distance between base of a plant at the soil surface and highest photosynthetic tissues (cm)	Ruler	Plant	April/May
Specific leaf area (SLA)	The ratio of fresh leaf area to dry leaf mass (mm ² /mg)	WinFOLIA	Plant	April/May
Longest leaf	Length of the longest leaf per individual (cm)	Ruler	Plant	April/May
Leaf count	Number of leaves per individual (count)		Plant	April/May
Flower count	Number of flowers per inflorescence (count)		Plant	April/May
Capsule count	Number of fruit capsules per individual (count)		Plant	July
Seed mass	The average air-dried mass of one seed per individual (mg)	VWR high precision scale (VWR-205AC)	Plant	July
Seed count	Number of seeds produced per individual and average number of seeds per capsule (count)		Plant	July

Differentiating *Camassia quamash* from *Camassia leichtlinii* is easiest when in bloom (based on the symmetry of their petal arrangement); therefore, the number of camas plants in bud and the number lacking an inflorescence may include *Camassia leichtlinii* individuals. Slope, aspect, and elevation were similar across the gradient and therefore were excluded from the site condition assessment.

Plant trait data were collected from five common camas plants in each of the 1m² data collection plots using a stratified random sampling design. The common camas plants selected for measurement were all in peak bloom to control for differences in phenology and to confirm species identification. The plant traits selected relate to the competitive vigor and reproductive capacity of plants (Borowy and Swan 2020; Pérez-Harguindeguy et al. 2013).

Two leaves were collected from the five selected plants per 1m² quadrat. The outer leaves were more often affected by herbivory and the inner leaves were often smaller than the outer, therefore, one outer and one inner leaf were collected. When possible, leaves not affected by herbivory were collected. The leaves were cut as close to the soil surface as possible and stored in sealed plastic bags with damp paper towel. A breath was added into the bags to enhance CO₂ concentration and air humidity, which minimizes transpiration and water loss (Pérez-Harguindeguy et al. 2013). Samples were stored in a cooler until scanned for leaf area later in the same day using a flatbed scanner and WinFOLIA software (Regent Instruments Canada Inc.). Both leaves were scanned at the same time for a total leaf area measurement. Some leaves were curled, wilted, or were visibly chewed. We quantified the magnitude of this error by estimating the percent of leaf that was curled or wilted and thus not captured in the area measurement. Leaves that were visibly chewed were recorded as one, both, or neither sample leaves chewed. Once scanned, the leaves were placed in a drying oven at 70 °C for 72 h and weighed for dry mass. Specific leaf area (SLA) was calculated by dividing fresh leaf area by dry leaf mass.

All seeds were counted by hand and weighed using a high-precision scale (VWR-205AC). The number of seeds per capsule was calculated by dividing the total number of seeds per individual by the number of capsules. The average mass of a single seed was calculated by dividing the total mass of all seeds per individual by the number of seeds per individual. Due to the inability to count fruit capsules and collect seeds across all sites at the same time, some stems had desiccated capsules and/or seeds missing when sampled. This error was estimated by visually assessing whether seeds were likely missing to dispersion (yes or no), and another error estimate captured whether herbivory of the inflorescence since the previous measurements (flower count) was likely (yes or no).

Statistical analysis

Plot-level analysis

An analysis of plot-level measurements was conducted to examine how urbanization in Greater Victoria is altering local site conditions. All analyses were performed using R statistical software (version 4.2.1, R Core Team 2022). An analysis of plot-level measurements was performed by fitting a linear regression between each plot-level measurement (the response) and the percent of urban land cover in the surrounding 100m² (the predictor). The disturbance measurement was separated into its two component parts, trampling and herbivory. In each model, sample size was $n = 48$ (one value per plot, with four plots in each of the twelve sites), and study site was included as a random effect in all models to account for non-independence in observations within each study site (Zuur et al. 2009).

To determine whether each response variable should be fit with a linear mixed model (LMM) or a generalized linear mixed model (GLMM), the normality of each response variable was assessed. If the data satisfied the assumptions of a normal (Gaussian) distribution, a LMM was fit using the `lmer()` function from the *lme4* package (Bates et al. 2015) in R. If positive skew was present in the histogram of residuals, the response was log-transformed, and normality assessed. If the log-transformed data satisfied the assumptions of a Gaussian distribution, a LMM was fit using the log-transformed data. Otherwise, a GLMM was fit using the `glmmTMB()` function from the *glmmTMB* package (Brooks et al. 2017) in R, with the family of distribution selected based on an understanding of the general characteristics of each distribution and the best fit (via model checking). Response variables fit with a LMM include canopy cover, soil compaction (log-transformed), soil depth (log-transformed), soil phosphorus (log-transformed), soil carbon, and soil sulphur. Response variables fit with a GLMM with a beta distribution (logit link function) include soil nitrogen and soil pH. Response variables fit with a GLMM with a beta distribution (logit link function) and zero-inflation term include trampling (23% zeros), herbivory (29% zeros), and graminoid cover (2% zeros). For each response, residuals were plotted against fitted values, a histogram of residuals was visually examined, the normality of a quantile-quantile plot was assessed, and a Shapiro-Wilk test was run (a p -value ≥ 0.05 satisfies a normal distribution). All models were checked and validated using the *performance* package (Lüdtke et al. 2021) and the *DHARMA* package (Hartig 2022) in R (Supplementary Material 2.1.2).

Table 2 Definitions of individual plant level response variables including units and the corresponding sample size

Response variable	Definition (units)	Sample size
Foliar biomass	(Dry mass of two leaves / 2) * number of leaves per individual (g)	240
Specific leaf area (SLA)	Area of two leaves / dry mass of two leaves per individual (mm ² /mg)	240
Stem height	Distance from soil surface to highest photosynthetic tissues (cm)	240
Number of flowers per inflorescence	Number of flowers per inflorescence (count)	240
Ratio of flowers to capsules	Number of capsules / number of flowers per individual (%)	203
Average number of seeds per capsule	Number of seeds / number of capsules per individual (count)	153
Average mass of a single seed	Mass of seeds / number of seeds per individual (g)	153

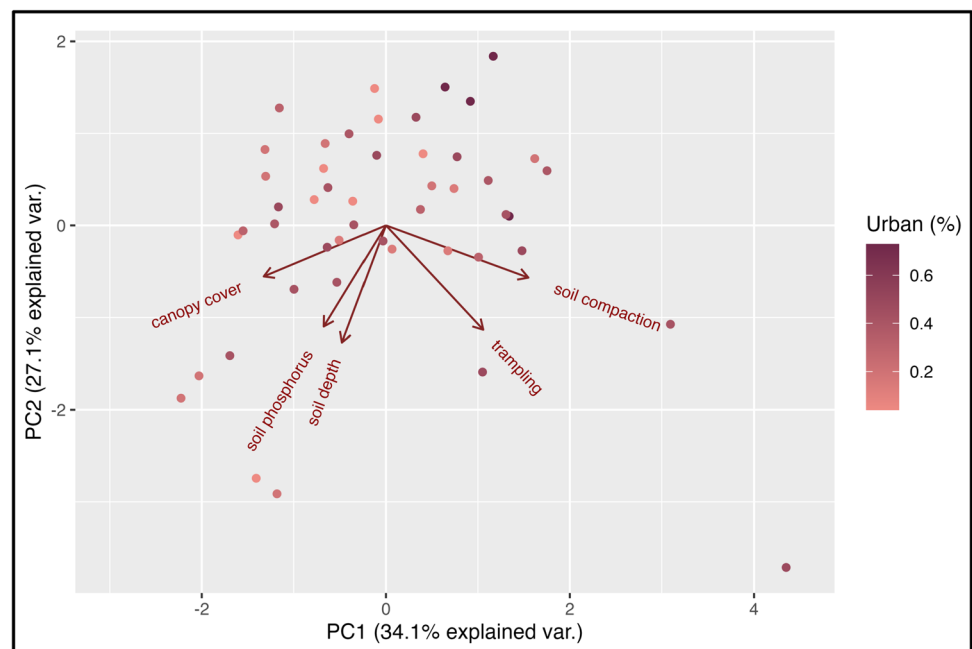
Individual plant-level analysis

An analysis of individual plant-level measurements was performed to investigate how individual common camas plants are responding to the local site parameters associated with urbanization on this landscape. Table 2 outlines the plant-level response variables and the associated sample size. Longest leaf was the only trait not included in the statistical analysis as herbivory was so prevalent across the landscape that this measurement did not provide useful information on plant growth or resource allocation. Five individuals were measured per plot (48 plots total, $n=240$); however, by the second phase of data collection some of the previously measured individuals were no longer present, likely due to herbivory or human disturbance, resulting in smaller sample sizes.

To investigate how each plant trait was responding to the pressures associated with urbanization on this landscape, a Principal Component Analysis (PCA) was performed. A PCA enabled an investigation into how the different local site parameters most associated with urbanization on this landscape were influencing common camas growth and reproductive traits. A

linear model (with the percent of urban land cover within 100m² as the predictor) was used for exploration in the analysis but a PCA provided additional insight (Supplementary Material 2.2.3). The principal components identified in the PCA were used as the predictors (fixed effects) in a linear mixed model for each response trait. A PCA enabled a reduction in the number of fixed effects included in each mixed model. The inputs for the PCA were the variables most closely related to the urbanization gradient in the plot-level analysis, and included trampling, canopy cover, soil compaction, soil depth, and soil phosphorus. Graminoid cover and herbivory had a weak relationship to the percent of urban land cover in the surrounding 100m² and therefore were not included in the PCA. The first two principal components (PC1 [34.15%], PC2 [27.12%]) explained 61% of the variance and thus were the two components selected to be included in the linear mixed models (henceforth referred to as ‘urbanization stress index (USI) 1’ and ‘urbanization stress index (USI) 2’). USI 1 is largely associated with an increase in soil compaction and trampling, and a decrease in canopy cover and USI 2 is largely associated with a decrease in soil depth, trampling, and soil phosphorus (Fig. 4).

Fig. 4 The first two principal components in the PCA ordination plot explain 61% of the variance. Principal component 1 is associated with increased trampling and soil compaction, and decreased canopy cover, soil depth, and soil phosphorus. Principal component 2 is associated with decreased trampling, canopy cover, soil compaction, soil depth, and soil phosphorus



A linear mixed model was run for each of the seven plant trait measurements outlined in Table 2. The response variable was the plant trait measurement, the three predictors (fixed effects) were USI 1, USI 2, and herbivory, and the random effect was a nested random effect of plot within study site to account for non-independence in observations within each of the four plots within each study site (Zuur et al. 2009). The ratio of flowers to capsules model had a study site random effect near equal to zero and the conditional r-squared could not be computed, therefore, the model was run with plot as the only random effect with each plot containing a unique code to avoid the grouping of plots across different sites. The model outputs were the same as those from the model that included study site as a random effect. To determine whether each response variable should be fit with a LMM or a GLMM, the same model structure fitting process was used as outlined in the plot-level analysis. Response variables fit with a LMM include specific leaf area, foliar biomass (log-transformed), stem height (log-transformed), and flower count (log-transformed). Response variables fit with a GLMM include the ratio of flowers to capsules (beta distribution (logit link function) and zero-inflation term), the average number of seeds per capsule (tweedie distribution), and the average mass of a single seed (tweedie distribution).

Certain plant trait measurements had errors associated with them: SLA (curled and/or chewed leaves), capsules per flowers (herbivory of the inflorescence between flower count and capsule count), and seeds per capsules (seeds missing due to dispersal prior to collection). The errors were plotted against the model residuals to determine whether any pattern existed. If there was a pattern, the model was run including the error variable(s) as fixed effect(s) and the significance examined. If the errors as fixed effects returned a p-value of < 0.05, the error variable(s) were left in the model. All models were checked and validated using the same methods as applied to previous models (Supplementary Material 2.2.2). To check the validity of the PCA axes, the model results were also compared to models using percent of urban land cover as the urbanization fixed effect (Supplementary Material 2.2.3).

The individual plant level mixed models were visualized using the `ggpredict()` function from the `ggeffects` package (Lüdtke 2018). The `ggeffects` package computes estimated predicted values for the response by holding the non-focal variables constant (Lüdtke 2018). Specifying the `ggpredict()` function as either “fixed” or “random” returns the same population-level predictions, however, “fixed” returns confidence intervals and “random” returns prediction intervals (taking into consideration the uncertainty in the variance parameters (the mean random effect variance)),

therefore the visualizations were specified as “fixed” to return confidence intervals.

Results

Plot-level

None of the plot-level measurements indicated a significant relationship to the percent of urban land cover in the surrounding 100m² (Fig. 5). There was a change in these local site parameters across the landscape (except for soil carbon, sulphur, and pH) however, they were not strongly associated to urbanization as defined for this study. The two variables with the strongest relationship to urbanization were soil compaction (p-value = 0.096) and trampling (p-value = 0.079).

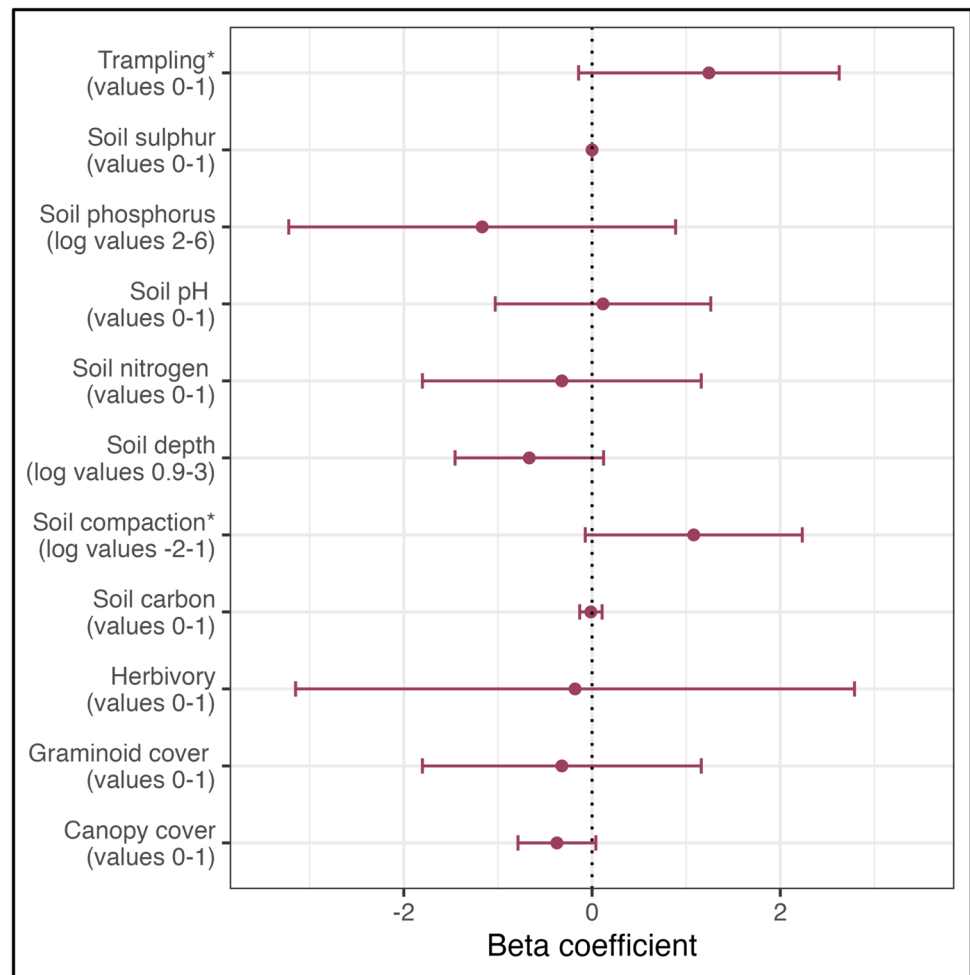
Individual plant-level

Six out of the seven plant trait responses were significantly related to one or both urbanization stress indexes (a p-value < 0.05) (Table 3). Seeds per capsule was the only response variable that was not significantly related to either urbanization stress index. Foliar biomass, specific leaf area, plant height, flower count, and seed mass all decreased with USI 1. The ratio of capsules per flowers increased with USI 1; however, this trait was strongly driven by measurements at two urban sites and was significantly influenced by the error associated with herbivory of the inflorescence. Foliar biomass and plant height decreased with USI 2. The three response variables with errors associated (specific leaf area, capsules per flowers, and seeds per capsule), all displayed significant relationships with the error measurements. Herbivory was not significantly related to any of the plant trait responses on this landscape.

Along the urbanization stress gradient represented by our lowest stress sites to our highest stress sites (as depicted by USI 1), foliar biomass was predicted to decrease on average 80% from 1.27 g [CI 0.96, 1.68] to 0.25 g [CI 0.16, 0.38], specific leaf area 20% from 4.1mm²/mg [CI 3.81, 4.38] to 3.3mm²/mg [CI 2.84, 3.75], plant height 63% from 67.05 cm [CI 59.84, 75.14] to 25.15 cm [CI 21.08, 30.00], flower count 63% from 16.34 flowers [CI 13.41, 19.90] to 6.01 flowers [CI 4.35, 8.30], and seed mass 58% from 8.15 g per thousand seeds [CI 6.84, 9.70] to 3.45 g per thousand seeds [CI 2.55, 4.66] (Fig. 6). The ratio of flowers to capsules was predicted to increase on average 125% from 32% of flowers producing capsules [CI 0.24, 0.41] to 72% producing capsules [CI 0.57, 0.83] (Fig. 6).

Along the urbanization stress gradient represented by our lowest stress sites to our highest stress sites (as depicted by USI 2), foliar biomass was predicted to decrease on average

Fig. 5 Urbanization had a weak to absent relationship with the environmental variables measured in each quadrat as indicated in the beta coefficient plot where all 95% confidence intervals cross zero. A positive coefficient indicates an increase in the plot-level measurement with greater urbanization and a negative coefficient indicates a decrease. Response variables with an asterisk were significant at the $\alpha=0.1$ level



62% from 1.34 g [0.84, 2.15] to 0.51 g [0.39, 0.67] and plant height was predicted to decrease on average 24% from 56.65 cm [46.87, 68.46] to 43.14 cm [38.56, 48.27] (Fig. 7).

Discussion

Common camas growth and reproductive trait values exhibit a decrease in urban oak meadows in Greater Victoria, indicating that common camas individuals have decreased fitness in highly urbanized environments. Urbanization does not have consistent effects on the local environment in this landscape but does seem weakly related to key variables, namely trampling, soil compaction, canopy cover, soil depth, and soil phosphorus (Supplementary Material 2.1.1). These key variables are not strongly related to urbanization on their own, however, when combined into two axes (via the PCA) they explain a large proportion of the variation across the gradient and drive trait responses in common camas individuals.

The weak relationship between the environmental variables measured and the percent of urban land cover in the surrounding 100m² may be due to the oversimplified way

the urban-rural gradient was defined and the absence of a temporal perspective (Foster et al. 2003; Ramalho and Hobbs 2012). Urban growth and intensification are not linear processes but instead occur in patchy and complex spatial patterns across the landscape, resulting in natural areas transitioning to urban areas at different rates, with implications for the state and processes of remnant ecosystems (Ramalho and Hobbs 2012). Interacting with the patchy growth and intensification of cities is the lagged ecological responses to urbanization, whereby the impact on the environment is not immediate and the biotic responses being currently observed can be masked by ongoing fragmentation and environmental change that is not yet reflected in the ecosystem (Ramalho and Hobbs 2012). The oak meadows across Greater Victoria were urbanized at different times and have unique land-use legacies that are likely still influencing the plant communities that exist (Armstrong et al. 2021; Perring et al. 2016). Land-use legacies associated with agriculture have been observed to affect urban remnant soils (through soil inputs, grazing, and tilling) (Foster et al. 2003; Ramalho and Hobbs 2012) and Indigenous land-use legacies have been observed to

Table 3 Summary of the plant-level mixed-effects models. β is the beta coefficient, and CI is the confidence interval. Predictors with a significant relationship to the response variable are in bold (p-value < 0.05). The marginal r-squared considers only the variance of the fixed effects,

while the conditional r-squared takes both the fixed and random effects into account (Nakagawa and Schielzeth 2013)

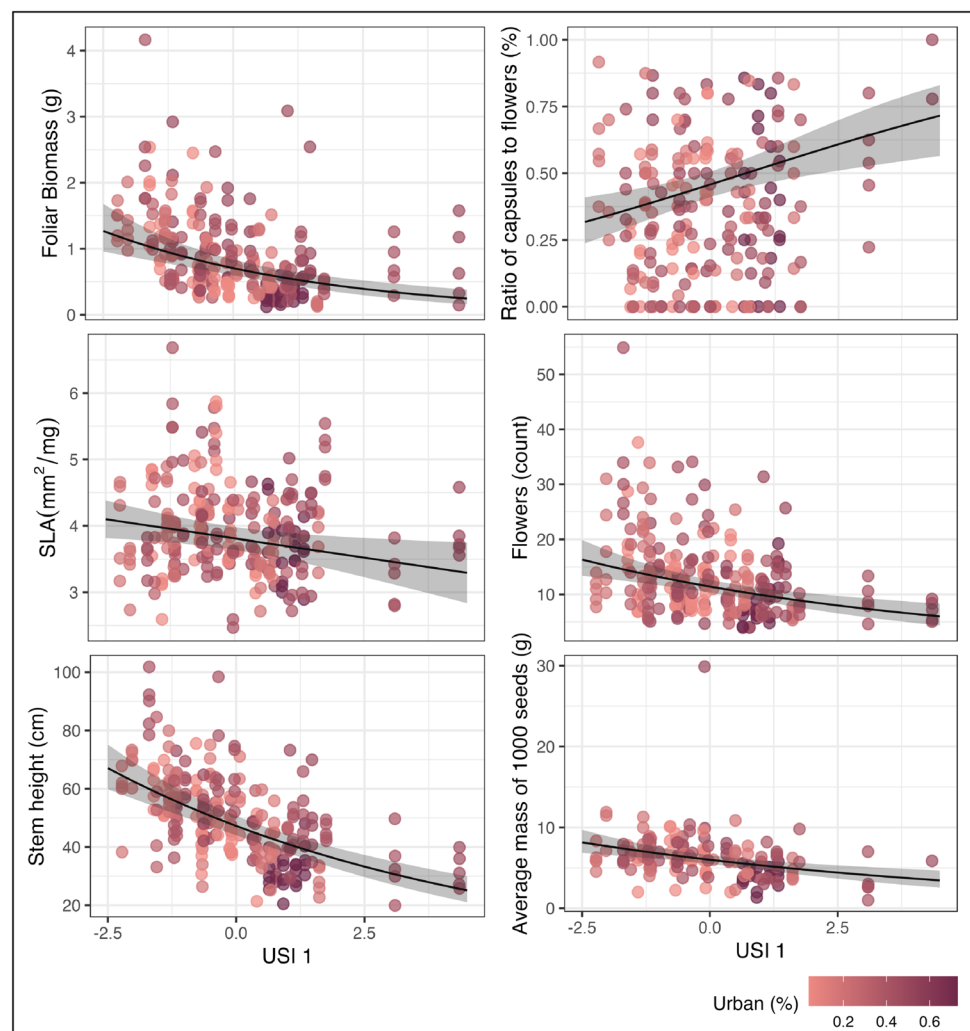
Response	Sample size	Predictor	Distribution	β	95% CI	p-value	Marginal/ conditional R ²
Foliar biomass	240	USI 1	gaussian, log transformed	-0.23	[-0.33, -0.14]	< 0.001	0.26/ 0.58
		USI 2		-0.16	[-0.27, -0.05]	0.006	
SLA	240	herbivory	gaussian	0.24	[-0.20, 0.68]	0.293	0.19/ 0.51
		USI 1		-0.11	[-0.21, -0.02]	0.020	
		USI 2		0.06	[-0.05, 0.17]	0.279	
		herbivory		0.01	[-0.49, 0.51]	0.959	
		curled leaf (y/n)		-1.19	[-1.99, -0.39]	0.004	
Height	240	leaf chewed (y/n)	gaussian, log transformed	0.28	[0.15, 0.41]	< 0.001	0.38/ 0.63
		USI 1		-0.14	[-0.18, -0.10]	< 0.001	
		USI 2		-0.05	[-0.09, 0.00]	0.049	
Flower count	240	herbivory	gaussian, log transformed	0.09	[-0.09, 0.27]	0.328	0.15/ 0.41
		USI 1		-0.14	[-0.21, -0.07]	< 0.001	
		USI 2		-0.05	[-0.13, 0.03]	0.203	
Capsules per flowers	203	herbivory	beta (logit link function), zero inflation term	0.06	[-0.26, 0.38]	0.715	0.38/ 0.90
		USI 1		0.24	[0.10, 0.38]	0.001	
		USI 2		-0.13	[-0.29, 0.03]	0.106	
		herbivory		-0.42	[-1.07, 0.24]	0.210	
Seeds per capsule	153	herbivory likely (y/n)	tweedie	-0.56	[-0.94, -0.18]	0.004	0.08/ 0.38
		USI 1		-0.05	[-0.17, 0.06]	0.352	
		USI 2		0.09	[-0.03, 0.21]	0.147	
		herbivory		0.16	[-0.30, 0.63]	0.488	
Seed mass	153	seeds missing (y/n)	tweedie	-0.22	[-0.43, -0.01]	0.042	0.16/ 0.37
		USI 1		-0.12	[-0.19, -0.06]	< 0.001	
		USI 2		0.01	[-0.06, 0.09]	0.701	
		herbivory		0.20	[-0.07, 0.48]	0.151	

influence present-day soils and leave unique genetic signatures in extant plant communities resulting from millennia of habitat modification (Armstrong et al. 2021; Lowther 2022; McCune et al. 2013). The elevated soil phosphorus levels present in some of the rural oak meadows on this landscape may thus be the result of Indigenous habitation and/or an agricultural past. To strengthen the relationship between local site conditions and urbanization on this landscape, how the urban-rural gradient was defined could be improved upon by incorporating a temporal perspective that integrates the time since each oak meadow was urbanized and the land-use legacies that may continue to influence each patch.

Several past studies show that across an urban-rural gradient, urban soils are more compacted than rural soils, with implications for plant establishment and growth (Bassett et al. 2005; Bejarano et al. 2010; Mariotti et al. 2020). Common camas appears to be responding to increased compaction in this region with a reduction in foliar biomass

and plant height, with implications for resource acquisition, competitive vigor, and fecundity (Borowy and Swan 2020; Pérez-Harguindeguy et al. 2013; Weiher et al. 1999). Compacted soils physically impede root growth and seedling establishment, and alter the oxygen, water, and nutrients available to plants (Alameda and Villar 2012; Kuss and Graefe 1985; Mariotti et al. 2020). In the case of geophytes, soil compaction can also impede bulb development (Beckwith 2004). In response to soil compaction, plants have been observed to exhibit reduced above- and belowground growth traits, including decreased aboveground biomass and plant height (Alameda and Villar 2012; Mariotti et al. 2020). Soil compaction in urban meadows is likely a consequence of the absence of Indigenous cultivation practices as well as the result of the high number of visitors to these parks. Indigenous harvesting and stewardship practices in the q̄w̄əł̄/K̄ŁO,EL food system involved regularly digging up camas bulbs and tilling the soil (Beckwith 2004; Turner and Kuhnlein 1983). These practices frequently aerated the

Fig. 6 Assuming a linear relationship, foliar biomass, specific leaf area, stem height, flower count, and the average mass of 1000 seeds were predicted to decrease with an increase in USI 1. The ratio of capsules to flowers was predicted to increase. Greater urban stress as defined by USI 1 is indicated by increasing values along the x-axis



soil, and in turn facilitated camas growth and development (Beckwith 2004).

Urban meadows exhibited a more open canopy on this landscape, potentially benefitting common camas populations despite their growth appearing greater in the more shaded, rural sites. Plant species that thrive in open habitats (such as common camas) may allocate more resources into acquiring sunlight when partially shaded, resulting in greater aboveground growth (e.g., increased plant height and aboveground biomass); however, this often occurs at the cost of decreased flowering and fruiting (Arenas-Corraliza et al. 2021; Kutschera and Briggs 2013). Thus, individuals growing under partial canopy may appear to have more vegetative competitive vigor, but if shaded over the long term, these species can be replaced with more shade-tolerant species (GOERT 2011; McCune et al. 2013). The common camas populations observed on this landscape appeared to be experiencing this phenomenon where individuals exhibited increased height, specific leaf area, and foliar biomass in the more shaded, rural meadows, but greater seedling

production as evidenced by increased abundance in the more open canopy, urban meadows (Supplementary Material 3.0). The increased canopy cover observed in rural areas may be associated with the ongoing encroachment of conifers and other woody species into coastal oak meadows from surrounding forested areas (GOERT 2011; Gedalof et al. 2006; McCune et al. 2013). Coastal oak meadows are a fire-dependent system and have been shaped by the Indigenous stewardship practice of controlled burning (Turner 1999). Prior to European settlement and the suppression of fire, low-intensity fires maintained the open canopy habitat necessary for the shade-intolerant species of coastal oak meadows to thrive (Gedalof et al. 2006; Turner 1999).

Herbivory (grazing) was hypothesized to stimulate a response in camas growth and reproduction across the urban-rural gradient, however, no response was detected potentially because the observed grazing pressure across this landscape was universally so high (Supplementary Material 2.1.1). This region is characterized by high ungulate densities, primarily of black-tailed deer (*Odocoileus*

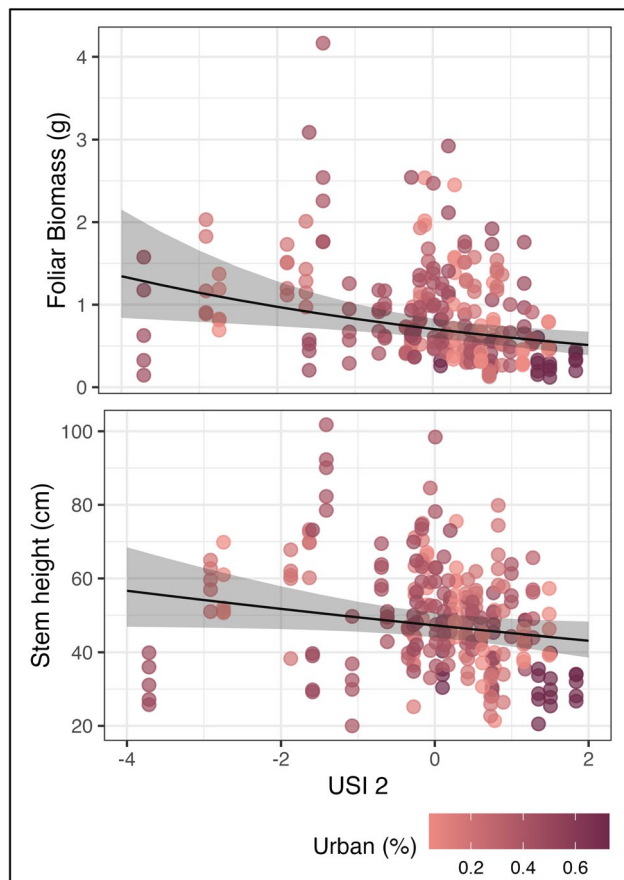


Fig. 7 Assuming a linear relationship, foliar biomass and stem height were predicted to decrease with an increase in USI 2. Greater urban stress as defined by USI 2 is indicated by increasing values along the x-axis

hemionus) (MacDougall 2008). Over the past 100 years, black-tailed deer abundance has increased dramatically due to habitat fragmentation, declines in hunting pressure, and the eradication of predators (Gonzales and Arcese 2008; MacDougall 2008). This grazing pressure on the landscape was expected to stimulate a reduction in common camas growth and reproduction based on literature that associates the herbivory of plants, especially during the early growing season, with reduced plant fitness (Gonzales and Arcese 2008; Hawkes and Sullivan 2001; Stephan et al. 2017; Thompson and Johnson 2016). However, common camas traits on this landscape show no detectable response to herbivory. Geophytes have been observed to be resilient to frequent, severe summer defoliation owing to the resources stored in their underground storage organs (Schmiedel et al. 2021); however, carry-over effects into the next growing season have been reflected in reduced aboveground biomass and inflorescence production (Morris 2021). Restricted to one field season, it is unknown how common camas individuals may be responding year

after year to the persistent, heavy grazing pressure on this landscape; they may be exhibiting tolerance or be universally struggling.

The overall reduction in growth and reproductive trait values in common camas in urban oak meadows indicates a potential reduction in overall fitness, with implications for the future success and persistence of this species in urban spaces (Borowy and Swan 2020; Pérez-Harguindeguy et al. 2013). It is important to note that the findings of this study likely affirm what First Nation land stewards have long understood about what conditions support thriving camas populations. The knowledge of how different site conditions (e.g., aerated soil, open canopy) influence common camas growth and reproduction is reflected in the Indigenous land management practices that led to tremendous camas productivity in this region (Lyons and Ritchie 2017; Proctor 2013; Turner 1999; Turner and Kuhnlein 1983). Co-led management with Indigenous partners could be vital to supporting the persistence and success of camas on this landscape.

Conclusion

Our results illustrate that common camas appears to be responding to a handful of key variables frequently associated with urbanization, namely increased trampling and soil compaction, and decreased canopy cover, soil depth, and soil phosphorus. To support remnant urban camas populations, management and planning initiatives should target these key pressures specifically. Trampling, soil compaction and canopy cover are all conditions that can be managed at small or large scales. Delineating formal trail networks through oak meadow parklands could help reduce trampling, and aerating the soil through weeding, invasive species removal, and local Nations harvesting camas bulbs would likely increase camas fitness. The removal of shrubs and other woody species encroaching into oak meadows could prove effective at reducing canopy cover and encouraging camas abundance. Meaningfully involving Indigenous communities in the restoration of these ecosystems would provide benefits that extend beyond the ecological. As important sites of eco-cultural revitalization, these meadows provide opportunities for reinstating traditional roles and practices, and for Indigenous youth to learn alongside their knowledge holders and scientists (Corntassel and Bryce 2012). Understanding that Coast Salish stewardship practices have never been static, past practices can be adapted to assist in addressing present-day challenges (Grenz 2020).

Further research to build upon this work could examine how common camas populations respond to the restoration actions outlined or extend the analysis to camas populations in other geographical regions. As urbanization continues to shape ecosystems and plant communities around the world, it is critical that we understand how individual

plants respond to these pressures to support the persistence of ecologically and culturally important plant species across urban landscapes for generations to come.

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Data availability The field data collected that support the findings of this study are available in Figshare with the following identifier: <https://doi.org/10.6084/m9.figshare.25436956.v1>.

Declarations

Competing interests The authors declare no competing interests.

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