PRIMARY RESEARCH ARTICLE

Asynchronous range shifts drive alpine plant–pollinator interactions and reduce plant fitness

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Abstract

Climate change is driving species' range shifts, which are in turn disrupting species interactions due to species-specific differences in their abilities to migrate in response to climate. We evaluated the consequences of asynchronous range shifts in an alpine plant–pollinator community by transplanting replicated alpine meadow turfs downslope along an elevational gradient thereby introducing them to warmer climates and novel plant and pollinator communities. We asked how these novel plant–pollinator interactions affect plant reproduction. We found that pollinator communities differed substantially across the elevation/temperature gradient, suggesting that these plants will likely interact with different pollinator communities with warming climate. Contrary to the expectation that floral visitation would increase monotonically with warmer temperatures at lower elevations, visitation rate to the transplanted communities peaked under intermediate warming at midelevation sites. In contrast, visitation rate generally increased with temperature for the local, lower elevation plant communities surrounding the experimental alpine turfs. For two of three focal plant species in the transplanted high-elevation community, reproduction declined at warmer sites. For these species, reproduction appears to be dependent on pollinator identity such that reduced reproduction may be attributable to decreased visitation from key pollinator species, such as bumble bees, at warmer sites. Reproduction in the third focal species appears to be primarily driven by overall pollinator visitation rate, regardless of pollinator identity. Taken together, the results suggest climate warming can indirectly affect plant reproduction via changes in plant–pollinator interactions. More broadly, the experiment provides a case study for predicting the outcome of novel species interactions formed under changing climates.

KEYWORDS
alpine ecosystems, climate change, community ecology, migration, mutualism, pollination, range shifts

1 | INTRODUCTION

Understanding species' responses to climate change is essential for predicting how ecological communities will change in the future. We now have substantial and mounting data demonstrating the direct effects of climate on species' fitness, demography, and range limits (Miller-rushing, Høye, Inouye, & Post, 2010; Parmesan, 2006; Thuiller, 2004; Walther et al., 2002). However, climate can

also indirectly affect species' performance by altering species interactions (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Suttle, Thomsen, & Power, 2007). We are only just beginning to uncover the mechanisms that drive these indirect effects.

One way in which climate will indirectly affect species' performance is through the emergence of novel interactions resulting from asynchronous range shifts (Alexander, Diez, & Levine, 2015; Urban, Tewksbury, & Sheldon, 2012). In temperate communities, average annual temperatures are expected to increase by between 0.5 and 5°C by the year 2100 (IPCC, 2014). In response to this rapid change in temperature, species are predicted to migrate in the direction of cooler climates, generally poleward or upslope in montane habitats (Forister et al., 2010; Kelly & Goulden, 2008; Parmesan et al., 1999). Because species often differ in their dispersal, motility, and life history, the rate at which they migrate to track changing climates should also differ (Urban et al., 2012). As a result, species will interact with novel competitors, predators/prey, and mutualists in future environments (Alexander et al., 2015; Urban et al., 2012). These novel interactions have the potential to affect species' performance in surprising ways. For example, experimental range expansion of Florida mangrove seedlings into mature mangrove habitat showed species-specific direct effects of canopy microclimate on seedling survival and indirect effects of herbivore damage, driven by microclimate (Chen et al., 2019).

Plant–pollinator communities present a useful study system for investigating how climate-driven range shifts create novel species interactions. Pollinators are thought to be particularly sensitive to climate change, as their persistence depends on abiotic climatic factors as well as close associations with plant species (Hegland, Nielsen, Lazaro, Bjerknes, & Totland, 2009; Memmott, Craze, Waser, & Price, 2007; Rafferty, 2017). As climate warms, pollinators in montane habitats have been shown to rapidly shift their native ranges upslope to accommodate changes in the thermal environment (Forister et al., 2010; Kerr et al., 2015; Konvicka, Maradova, Benes, Fric, & Kepka, 2003, but see Bedford, Whittaker, & Kerr, 2012). Plant species, however, may respond to climate change more slowly than pollinators due to comparatively limited dispersal (Corlett & Westcott, 2013; HilleRisLambers, Theobald, Ettinger, Harsch, & Ford, 2013). Therefore, we might expect plant species that fail to migrate to encounter a completely different pollinator community than the one to which they have adapted. Moreover, these altered interactions can have dramatic effects on reproductive success and subsequent demographic performance. For example, a wealth of studies on the effects of climate on plant–pollinator interactions has shown that warming can temporally offset plants and their pollinators within a season due to changes in their phenology, with subsequent negative consequences for plant reproduction (CaraDonna, Iler, & Inouye, 2014; Gezon, Inouye, & Irwin, 2016; McKinney et al., 2012; Rafferty & Ives, 2011). How climate change spatially offsets plants and their pollinators is far less explored (Potts et al., 2010; Rafferty, 2017) because it is difficult to manipulate today's plant–pollinator communities to simulate the novel interactions of the future, particularly in the field.

There are several approaches to examine the consequences of asynchronous migration between plants and pollinators. Joint species distribution models have proven to be an effective way to predict range shifts under different climate scenarios; however, their ability to accurately capture alterations of species interactions is still in its infancy (Giannini, Chapman, Saraiva, Alves-dos-Santos, & Biesmeijer, 2013). Another approach is to conduct studies in locations where range shifts have already occurred. This generally requires historical datasets to use as a baseline for comparison to present-day communities (Pyke, Thomson, Inouye, & Miller, 2016) While informative, this approach is limited in cases where historical datasets do not exist. Furthermore, it can be difficult to tease apart effects of range shifts from other landscape-scale effects, such as land use change. A complementary approach is to experimentally simulate range shifts using elevational transplants. This approach is not without its own limitations. For instance, simulated range shifts often abruptly translocate species, and thus can fail to capture the effects of longer term processes, such as local adaptation, unfolding during actual range shifts. This approach, however, allows for experimental inference that cannot be achieved through comparisons to historical scenarios and captures altered species interactions that are known to be important, but are currently difficult to study using joint species distribution models. For these reasons, we use experimental range shifts as an approach for studying asynchronous range shifts, while acknowledging its limitations.

We experimentally simulated the effects of future climate change on an alpine plant community by transplanting an alpine (2,000 m) plant community down in elevation in the Swiss Alps (Figure 1). We compared plant–pollinator interactions in biologically realistic future scenarios under climate change, capturing a range of scenarios that would emerge with increasing amounts of warming. Our experiments are specifically designed to simulate the fate of alpine plant species at their trailing (low elevation) range edge under climate change. While the leading range edge of the alpine plants will likely advance upslope, the trailing range edge is expected to be invaded by low elevation pollinators whose mobility allows them to rapidly shift their range to track climate. For the same reasons, low elevation plant competitors will also invade, outcompeting much of the alpine community. Thus, the remnant high-elevation alpine plants, at the trailing edge of their range will interact with novel lower elevation pollinators and plant competitors, all in a warmer climate. The greater the warming, the greater the influx of lower elevation pollinator and plant competitor species.

To mimic these warming scenarios, we transplanted replicate turfs containing high-elevation plant communities to progressively warmer climates at lower elevations, and into the plant and pollinator communities found in these climates/elevations. Turfs transplanted to lower elevations thus experience climatic conditions broadly consistent with expected future climate change as well as novel plant and pollinator communities that may arrive with warming were they to track climate. We manipulate the severity of climate and community change by transplanting high-elevation turfs to three elevations downslope: 1,800 m (minor warming), 1,600 m (moderate warming),

Experimental manipulations   Climate change scenarios
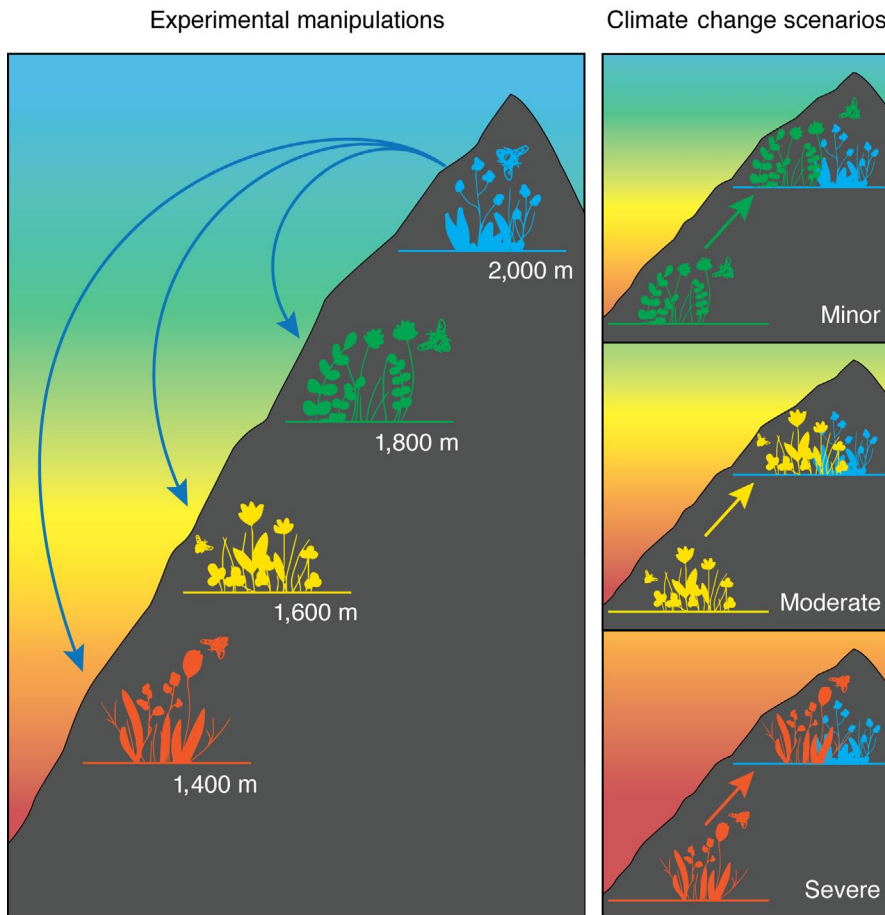
FIGURE 1 Schematics illustrating the climate change scenarios investigated here and the experimental manipulations to create them. The panel on the left shows plant and pollinator communities in their current climate, depicted by the bee and flower cartoons, respectively and color-coded by elevation. The experimental manipulations show scenarios in which high-elevation plants fail to migrate and therefore experience both warming climate and novel, low-elevation plant and pollinator communities that have migraged upslope to track their current climate. The panel on the right shows the severity of climate change in the different scenarios varying from minor to moderate to extreme. Illustration by Julie Johnson

and 1,400 m (more severe warming). The associated increases in average daytime temperature capture much of the range of predicted warming (0.5–5°C) expected globally under climate change (IPCC, 2014). The fate of the alpine plants under these future climate scenarios were compared to their fate under no climate or pollinator community change, by also transplanting replicate turfs of the alpine plant community within the same elevation. Prior work has examined the direct competitive effects of the low elevation plant competitors on the focal alpine species (Alexander et al., 2015). Here, local plant competitors at each elevation only affect focal plants indirectly via their effects on the local pollinator community.

We investigated three key questions. (a) How does plant–pollinator community composition currently differ along the elevational gradient? (b) In the transplanted communities, how does total pollinator visitation and the identity of the visitors to the alpine plants change with elevation? (c) How does female plant fitness (seed production) change after transplantation to warmer sites and novel pollinator communities?

We expected high pollinator community turnover along the temperature gradient. Alpine pollinator communities consist of relatively cool-adapted species such as bumble bees and flies (Mizunaga & Kudo, 2017). Under warming, the abundance of more warm-adapted species, such as small-bodied bees, may increase. Cool weather can also hinder physiological processes, such as flight, in ectothermic pollinators (Herrera, 1995). Thus, we predicted that

pollinator activity would be higher at warmer sites, leading to higher floral visitation and increased seed set for plants down the elevation gradient. Alternatively, increased visitation may not translate to increased seed set if visits are made by novel, ineffective pollinators. Additionally, low elevation pollinators may disproportionately visit low-elevation plants to which they are adapted at the expense of the novel alpine plants. In this case, any potential increase in pollinator activity would not necessarily translate to higher visitation to high-elevation plants. By taking a novel experimental approach to conduct large-scale, whole-community manipulations, we highlight the plant fitness consequences of climate-driven asynchronous range shifts.

2 | MATERIALS AND METHODS

2.1 | Study site and plant community transplantation

The study was conducted in the eastern Swiss Alps (Calanda mountain, Canton des Grisons). The landscape is dominated by perennial grasses and herbaceous flowering plants. Plants in the summer growing season experience daytime temperatures ranging from approximately 5 to 25°C, and summer rain is common. Flowering commences following the melting of the winter snowpack; however,

there is little evidence that snow melt per se drives flowering phenology (C. A. Johnson, unpubl. data). This experiment was performed on a subset of a larger experimental manipulation; here, we discuss the treatments relevant to this experiment. At the end of the growing season in 2016, 40 1 m × 1 m turfs containing plant roots and the organic soil layer down to 20 cm were removed intact from sites at 2,000 m in elevation. These turfs contain the focal alpine plant community for this study. Ten turfs were transplanted laterally to another location at 2,000 m (46.887778, 9.489398) roughly 400 m from the source population to control for artifacts associated with transplantation. The remaining 30 turfs were transplanted to progressively lower elevations (hereafter referred to as "sites"): 1,800 m (46.886529, 9.495310), 1,600 m (46.877351, 9.493980), and 1,400 m (46.869208, 9.490178; Figure 1). All sites were on southeast-facing slopes. At each elevation, 10 turfs were placed roughly 0.5 m apart due to space constraints within the fenced experimental sites, and sunk into the ground so that they were flush with the soil surface. As with our prior work with this experimental design (Alexander et al., 2015), the geographic scale of the manipulation and the logistics it entails prevents replication of the elevation gradients. Thus, the differences between the sites are assumed (but not proven) to reveal the effects of temperature and other elevation associated variables. The edges of the transplanted turfs (hereafter referred to as "plots") were lined with a water permeable root barrier to avoid encroachment from neighboring plants. We watered the 1,400 m site with 2.5 L of water three times/week for 4 weeks beginning on June 12, and we commenced the same watering regime at all other sites beginning on June 19 as those sites began to warm. All sites were surrounded by electric fencing to exclude cattle. Two HOBO loggers were deployed at the soil surface at each site to record daily air temperature (°C) at 30 min intervals. Data from the HOBO loggers confirmed the warming gradient from high to low elevation (Figure S1). The differences in temperature across sites were consistent with expectations for future climate change of mean annual temperature increases of 2.8–6.0°C for alpine environments in Central Europe (IPCC, 2014).

2.2 | Pollinator community composition and visitation to local plant communities

We performed twice weekly floral visitor observations over the course of the growing season from June 30, 2017 to September 8, 2017. Observations were made between 09:00 and 18:00 hr on days without rain and average temperature at least 15°C. We made observations at all four sites on all days, randomizing the order in which we visited sites.

To quantify how the background pollinator community varies with temperature, we cordoned off one 20 m × 1 m band transect at each site, which contained the local, low-elevation plants. We used transects instead of individual replicate plots as this was the most efficient way to characterize the pollinator community visiting local plants within the physical constraints of the fenced experimental

sites. Transects were located 1–3 m away from the experimental plots. Twice weekly at each site, two observers would simultaneously walk along different directions of the transect for 20 min each at a consistent pace until a floral visitor entered the transect, at which point an observer would follow the floral visitor over its foraging bout until it left the transect. Visits outside of the transect but within a floral bout were noted but excluded from the analyses. A total of 20 person-hours of observation per site was performed over the course of the growing season. The visitor was identified in situ to the lowest taxonomic unit possible, based on a reference collection of visitors caught at each site over the course of the growing season. Bee species were identified at least to genus; butterflies were identified to family; and flies were identified to family only in the case of Syrphid flies (family Syrphidae). See Table S1 for a complete taxonomic list of floral visitors. Observers counted each floral visit and recorded the plant genus visited using a handheld digital voice recorder (Trustin). On each observation day, we also counted all flowers within each transect, identified to genus (Table S3; Figure S5). We opted to identify to genus as a conservative measure because some plant species were difficult to distinguish at the species level.

2.3 | Pollinator community composition and visitation to the alpine plants

We performed floral visitor observations, similar to those described above, in the 10 experimental plots of transplanted alpine community at each site. Observations were made over the growing season, from June 30, 2017 to September 8, 2017. Twice weekly at each site, two observers would watch two to three plots each for 15 min increments until all 10 plots were observed. A total of 30 person-hours of observation was performed at each site over the course of the growing season. We randomized the order in which we visited sites on each day. Because of the spatial placement of the plots, we could not completely randomize the order in which we observed plots, but did randomize which observer watched which section of the plots as well as whether they watched two or three plots at a time. Using this method, each plot at each site was observed for 30 min/week.

During each 15 min observation period, the observer would be stationary and within 1 m of all plots being observed. When a floral visitor began visiting flowers in a focal plot, the observer recorded each visit, including plant visited (identified to species) using a handheld digital voice recorder, until the visitor left the area of the focal plots. Floral visitors were identified in situ as described above. See Table S2 for a complete taxonomic list of floral visitors. On each observation day, we also counted all flowers in all plots, identifying flowers to species (Table S4; Figures S2 and S3).

2.4 | Quantifying plant female fitness

During the growing season, we marked at least 36 individual plants across the transplanted turfs at each site of the following

focal species: *Trifolium pratense* (Fabaceae), *Campanula scheuchzeri* (Campanulaecae), and *Euphrasia minima* (Orobanchaceae) using a small wooden stake and white or green lab tape. These species were selected because they were sufficiently abundant at all sites during the period of observation and were different enough in floral morphology to possibly interact with different pollinator species.

Trifolium has a wide distribution (native to Europe and Asia, and introduced in meadow habitats across the globe), and produces compact inflorescences (approx. 15 cm high) of deep pink flowers (Rosso & Pagano, 2005). *Campanula* is native to montane regions of central Europe, and produces single, deep purple, or blue radially symmetrical flowers, approximately 10 cm high (Pohl, Stroude, Buttler, & Rixen, 2011). The distribution of *Euphrasia* is restricted to the Swiss and Italian Alps, and produces flowering talks (up to 15 cm high) containing approximately 5–10 small (approx. 5 mm), white, bilaterally symmetrical flowers (Liebst & Schneller, 2005). *Trifolium* and *Campanula* are perennial, outcrossing species, while *Euphrasia* is an annual species with some degree of self-compatibility (Liebst & Schneller, 2005; Palmer-Jones, Forster, & Clinch, 1966; Trunschke & Stöcklin, 2016). While these are primarily high elevation species, *Trifolium* and *Campanula* were observed in the low-elevation plant communities surrounding the replicate alpine turfs at all sites, although *Campanula* was found only at low densities in all sites except for 2,000 m (Figure S4). *Trifolium* density varied across the season at each site, with the exception of the 1,400 m site, where it was consistently found at low density (Figure S4). *Euphrasia* was only observed in the surrounding plant community at 2,000 m. We collected all viable fruits as they matured. At the end of the growing season, when all fruits were collected, we counted the total number of mature seeds per plant from each focal species at each site. It is important to note that, due to constraints associated with the transplant design and its long-term use by several research groups, we were unable to quantify the efficacy of distinct pollinator groups (e.g., by conducting pollinator exclusion or hand pollination experiments) or test for direct effects of elevation on plant fitness. Instead, our study captures broad patterns of pollinator community change with elevation, and the association between these patterns and plant reproductive consequences.

2.5 | Statistical analyses

All analyses were performed in R version 3.5.0 (R Core Team, 2018); all models, model selection for seed set analyses, and outputs are included in Tables S5 and S6. We visualized among-site differences in pollinator community composition and plant community composition using linear discriminant analysis (MASS package, Venables & Ripley, 2002). To quantify differences among sites, we used permANOVA (vegan package, Oksanen et al., 2018), which partitions differences in composition within and among sites, assessed using Euclidian distance. We used plot as the within-site replicate.

We evaluated among-site differences in visitation rate to the transplanted alpine turfs using generalized linear models. We performed four models: one testing for differences in visitation to all plant species and one testing for differences in visitation to each of the three focal species from which we obtained seed set information. In all models, the response variable was the number of visits/0.25 hr/plot, and was averaged across the number of observation days. Because the response variable data were averaged counts, we used a quasipoisson error structure to account for non-integers. This also accounted for any overdispersion in the data. Site was used as the explanatory variable. The average floral density (flowers/m^2) was included as a covariate to all models, with fit determined using AIC. We tested for overall treatment (site) effects with a likelihood ratio test using the car package (Fox & Weisberg, 2011), and tested for pairwise differences between sites with a Holm test using the phia package (De Rosario-Martinez, 2015).

We tested whether visitation rate varied across the growing season using quasipoisson GLM (one model for each focal species). In these models, the average number of visits across plots was the response variable and Julian Day was the explanatory variable. Finally, we tested whether the floral density of each focal species in the plots differed by site and across the growing season using quasipoisson GLM. A test of overall differences in floral density across sites was performed using a likelihood ratio test, and pairwise differences between sites were evaluated using a Holm test. Floral density (flowers/1 m^2, averaged across plots) was the response variable, and site and Julian Day were explanatory variables. There was a significant interaction between site and Julian Day in the *Campanula* and *Euphrasia* models; thus, the interaction term was retained for these models.

To test for among-site differences in female plant fitness (seed production) in the focal plant species, we performed separate generalized linear models for each species. To account for overdispersion in the data, we used a negative binomial error structure (MASS package, Venables & Ripley, 2002). Seed production in *Campanula* was low overall, with many plants producing no seeds. Because of this, we used a zero-inflated model for *Campanula* only (pscl package, Zeileis, Kleiber, & Jackman, 2008); model selection using AIC determined this model to be the best fit (Table S6). In all models, average seeds/plant, replicated across plots, was used as the response variable, and site was included as a fixed effect. Plant height (cm) was included as a covariate in the *Euphrasia* model, because we observed variation in *Euphrasia* plant height that we did not observe in the other two species. Evaluation of the overall site/elevation effect was performed using a likelihood ratio test for all models (car package, Fox & Weisberg, 2011), and pairwise differences between sites were evaluated using a Holm test (lsmeans and phia packages, Lenth, 2016; De Rosario-Martinez, 2015). Finally, we evaluated whether mean seed production was correlated with mean visitation across sites using a separate linear model for each focal species.

3 | RESULTS

### 3.1 | How do plant and pollinator community composition currently differ along the elevational gradient?

Hymenopteran and/or dipteran insects were dominant flower visitors to local plants across the sites. Bumble bees were common visitors at every elevation but most common at the 1,400 m site, while solitary and small-bodied bees were common only at lower elevations—the 1,400 and 1,600 m sites (Figure 2). Non–Syrphid flies were common at the 2,000 m site and less common at the other site, particularly 1,800 m (Figure 2). Syrphid flies were most common at the 2,000 m site (Figure 2). Flowering plants included a broad diversity of genera at each site (Figure S5). A qualitative assessment of the flowering plant community suggests that composition differed across sites, although we did not perform a statistical analysis of the compositional differences due to a lack of replication within site (Figure S5).

3.2 | How do total pollinator visitation and the identity of the visitors to the transplanted alpine plants change with elevation?

Community composition of pollinator visitors to the transplanted turfs differed significantly across sites, with the 1,400 and 1,800 m sites being the most different ($F_{3,34}$ = 5.44, p < .001; Figure 3a). Overall pollinator visitation to the transplanted alpine meadow turfs (Figure 3) did not follow the elevational trend in the visitation for the local plant communities observed in the transects (Figure 2). In contrast to peak visitation of the local communities at the lower elevation sites, visitation (mean visits/0.25 hr) to the alpine transplants
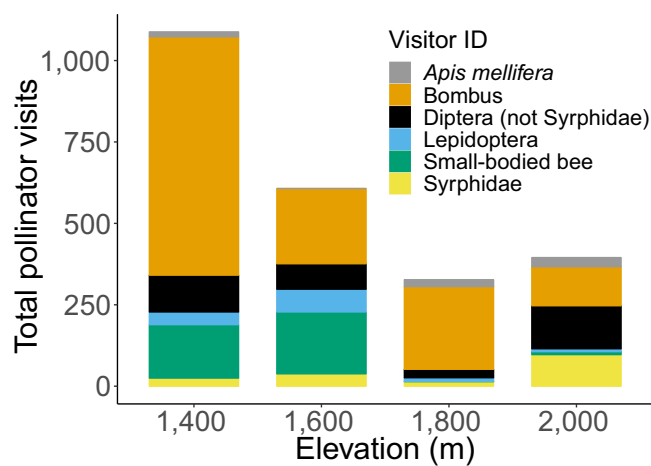
FIGURE 2 Total floral visits to all plant species in the local communities at each elevation, determined via transect observations. Color blocks of bars represent the proportion of visits by each visitor taxonomic group. For ease of interpretation, taxonomic groups have been broadly defined in this figure. See Table S1 for complete taxonomic list
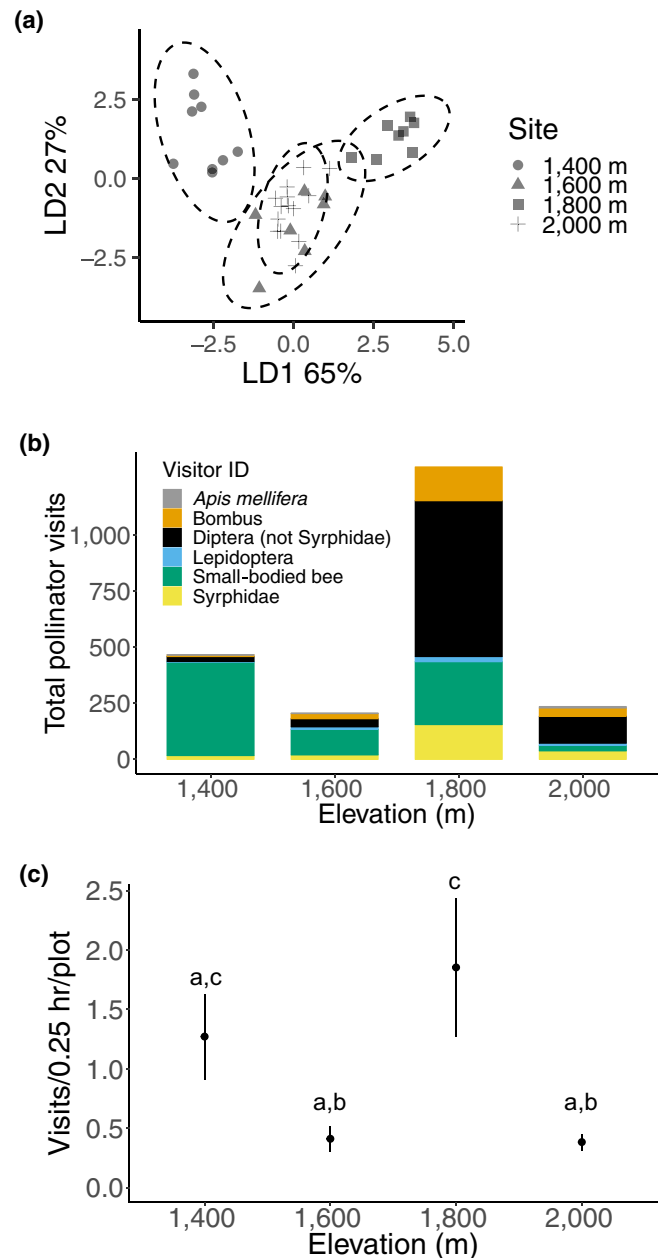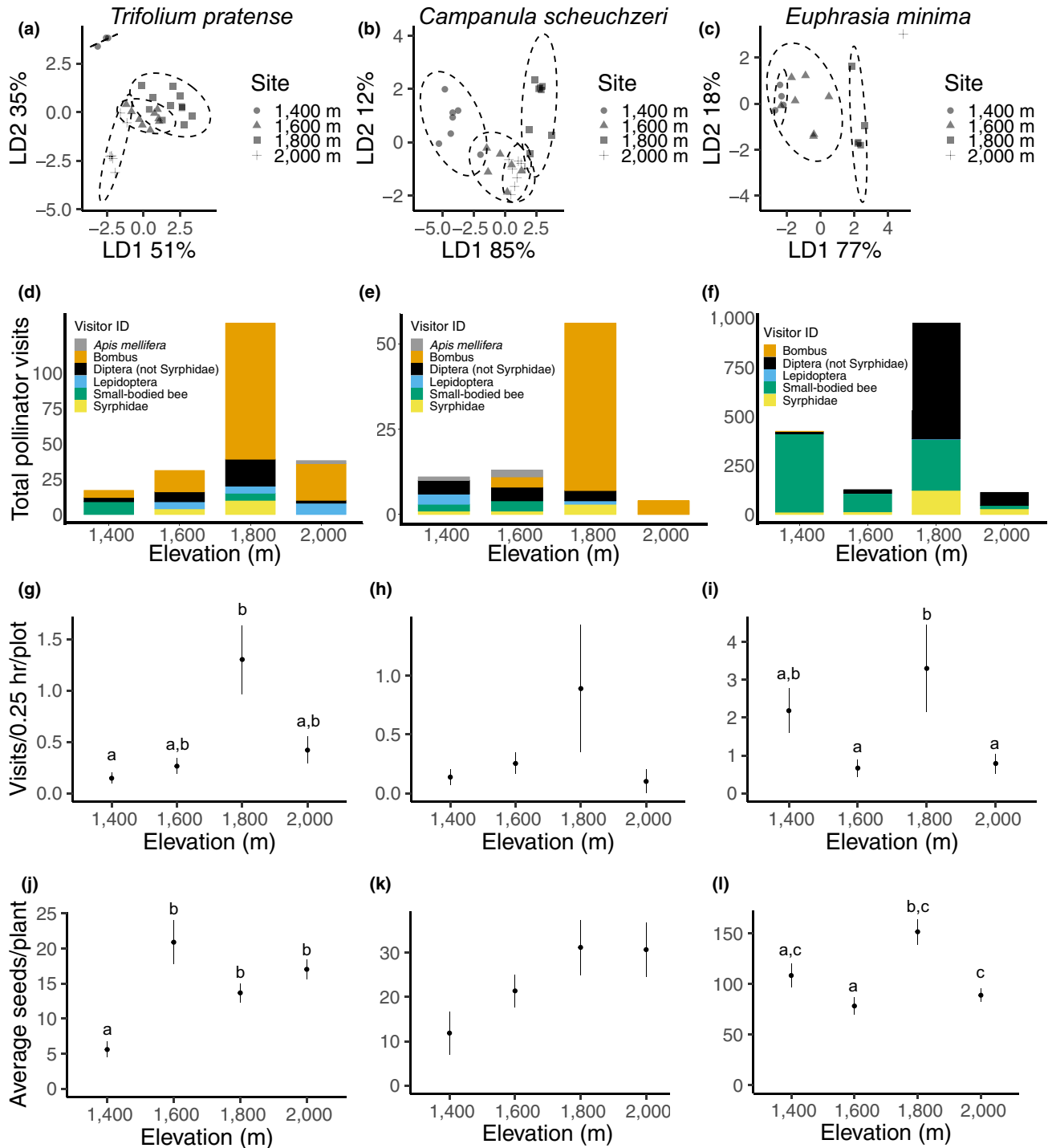

FIGURE 3 Pollinator community and floral visitation to all plant species in the experimental plots. Panel (a) shows the pollinator community in ordination space, organized using linear discriminant analysis. Each point represents abundance of pollinator species in terms of their floral visits/0.25 hr, and colors of points correspond to each of the four sites. Ellipses represent 95% confidence intervals. Panel (b) shows total floral visits to all plant species. Color blocks of bars represent the number of visits by each visitor taxonomic group. For ease of interpretation, taxonomic groups have been broadly defined in this figure. See Table S2a for complete taxonomic list. Panel (c) shows the average number of floral visits per 0.25 hr observation period. Dots and bars represent means and standard errors, respectively. Letters represent statistically significant (p < .05) differences between treatment groups, based on a Holm test

was highest at 1,800 m (Figure 3b,c), and 31%, 78%, and 79% lower at 1,400, 1,600, and 2,000 m, respectively (χ_3^2 = 12.28, p = .006; Figure 3c). Results are shown both for total visits (Figure 3b) and

visits per 0.25 hr (Figure 3c) in order to clearly present the proportion of total visits performed by different pollinator taxonomic groups. When evaluating all transplanted plant species pooled

across sites, bumble bee visitation was relatively rare, especially in contrast to visitation patterns seen to the local plant communities. Solitary bees were the most common visitors at the two lower


FIGURE 4 Pollinator community and floral visitation to three focal plant species: *Trifolium pratense* (a, d, g, j), *Campanula scheuchzeri* (b, e, h, k), *Euphrasia minima* (c, f, i, l). Panels (a–c) show each pollinator community in ordination space, organized using linear discriminant analysis. Each point represents abundance of pollinator species in terms of their visits/0.25 hr/plot, and colors of points correspond to each of the four sites. Ellipses represent 95% confidence intervals. Panels (d–f) show total floral visits to all plant species. Color blocks of bars represent the proportion of visits by each visitor taxonomic group. For ease of interpretation, taxonomic groups have been broadly defined in this figure. See Table S2b–d for complete taxonomic list. Panels (g–i) show the average number of floral visits per 0.25 hr observation period/plot. Panels (j–l) show average plant reproduction, measured as average seeds per plant. In panels (g–l), dots and bars represent means and standard errors, respectively. Letters represent statistically significant (*p* < .05) differences between treatment groups, based on a Holm test

elevation sites (1,400 and 1,600 m), while non-Syrphid Diptera were the most common visitors at the higher elevation sites (1,800 and 2,000 m). Floral density was positively correlated with visitation rate (model estimate ± SE = 0.035 ± 0.005, t = 6.63, p < .001). Plant community composition in the plots was similar across sites, although there were some marginal differences that emerged even in this first year after transplanting (Figure S2).

Bumble bees were the most common visitors to *T. pratense* at the 1,600, 1,800, and 2,000 m sites; solitary bees were the most common visitors at the 1,400 m site (Figure 4a,d). There was a marginally statistically significant difference in *Trifolium* visitor community composition across sites, with the 1,400 m site qualitatively differing from the other three sites ($F_{3,26}$ = 2.25, p = .08; Figure 4a). Visitation to *Trifolium* was highest at the 1,800 m site; flowers at this site received at least twice as many visits/0.25 hr than at any of the other sites on average (χ^2_3 = 9.53, p = .02; Figure 4g). Visitation rate decreased over the course of the growing season (model estimate ± SE = −0.046 ± 0.015, t = −2.981, p = .004; Figure S3). Floral density was marginally positively correlated with visitation rate (model estimate ± SE = 0.034 ± 0.019, t = 1.79, p = .08). There were significant differences in floral density across sites and across the growing season, with density being highest at the 1,800 m site (site χ^2_3 = 62.113, p < .001; Figure S3; Table S5).

The proportion of taxa visiting *C. scheuchzeri* differed substantially across sites (Figure 4e). Notably, bumble bees were the sole visitor species at the 2,000 m site, and were the most common at 1,800 m, and declined as visitors at lower elevation sites (Figure 4e). Still, there was no statistically significant difference in visitor community composition with site ($F_{3,16}$ = 0.98, p = .21; Figure 5b). Visitation to *Campanula* was highest at the 1,800 m site; flowers at this site received at least 3.5 times as many average visits/0.25 hr than at any other site; however, results of the likelihood ratio test were not statistically significant (χ^2_3 = 3.97, p = .26; Figure 4h). Visitation rate stayed constant over the course of the growing season (model estimate ± SE = −0.010 ± 0.031, t = −0.331, p = .74; Figure S3). Floral density was positively correlated with visitation rate (model estimate ± SE = 0.141 ± 0.022, t = 1.65, p < .001). Floral density was highest at the 1,600 and 1,800 m sites (χ^2_3 = 18.656, p < .001; Figure S3) and overall floral density did not change significantly over the course of the growing season (model estimate ± SE = −0.003 ± 0.042, t = −0.077, p = .93; Figure S3; Table S5).

Solitary bees were the most common visitors to *E. minima* at the lower sites (1,400 and 1,600 m), while flies (Syrphid and non-Syrphid) were the most common visitors at the higher sites (1,800 and 2,000 m; Figure 4f). Visitor community composition was significantly different across sites; the 1,400 and 1,800 m sites were the least similar ($F_{2,29}$ = 3.62, p = .002; Figure 4c). Visitation to *Euphrasia* was highest at the 1,800 m site and second highest at the 1,400 m site. Flowers at the 1,800 m site received 52% more visits/0.25 hr than flowers at the 1,400 m site and at least four times as many visits
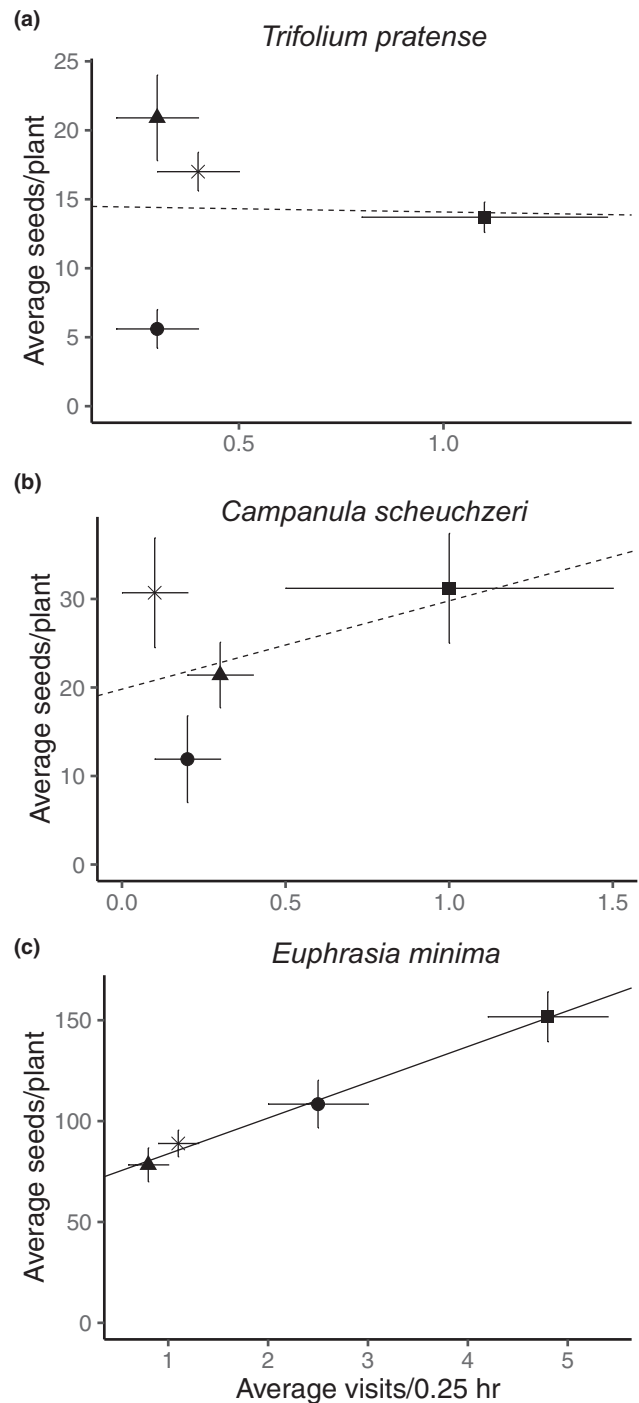
FIGURE 5 Average seed production in response to average visitation for focal species (a) *Trifolium pratense*, (b) *Campanula scheuchzeri*, (c) *Euphrasia minima*. Points represent sites: 1,400 m (circle), 1,600 m (triangle), 1,800 m (square), 2,000 m (cross). Horizontal error bars represent variation in visitation rate across plots within a site; vertical error bars represent variation in seed set across plots within a site. Solid regression line (c) represents statistically significant (p < .05) relationship between visitation rate and seed production; dashed regression lines (a and b) represent statistically insignificant relationship (p > .05) between visitation rate and seed production

than flowers at the 1,600 or 2,000 m sites on average (χ^2_3 = 9.40, p = .02; Figure 4i). Visitation rate stayed constant over the course of the growing season (model estimate ± SE = 0.006 ± 0.010, t = 0.607, p = .55; Figure S3). Plant density was positively correlated with visitation rate (model estimate ± SE = 0.017 ± 0.003, t = 6.34, p < .001). Floral density was highest at the 1,800 m site (χ^2_3 = 19.151, p < .001), and overall floral density did not change significantly over the course of the growing season (model estimate ± SE = 0.004 ± 0.013, t = 0.310, p = .76; Figure S3; Table S5).

3.3 | How does female plant fitness (seed production) change after transplantation to warmer sites and novel pollinator communities?

Patterns of visitation did not translate simply into patterns of fecundity with elevation. Despite massively greater visitation at 1,800 m, *T. pratense* seed production was similar across the three higher sites (1,600, 1,800, and 2,000 m), and reduced by at least 59% at 1,400 m (χ^2_3 = 45.35, p < .001; Figure 4j). Seed production in *C. scheuchzeri* was roughly equal at the two highest sites (1,800 and 2,000 m) and was reduced by 31% and 62% at the warmer 1,600 and 1,400 m sites, respectively (χ^2_3 = 15.59, p = .01; Figure 4k). However, after controlling for multiple comparisons, we did not detect any pairwise differences in *Campanula* seed set (Figure 4k). *E. minima* was the only species to show seed production patterns with elevation that matched the visitation patterns. Seed production was highest at 1,800 m, and reduced by 29% at the next most fecund site—1,400 m (χ^2_3 = 26.71, p < .001; Figure 4l). Mean seed production at 1,600 and 2,000 m was 49% and 42% lower, respectively, compared to 1,800 m (Figure 4l). Results of linear analyses testing for a correlation between mean visitation rate and mean seed production revealed a significant relationship for *Euphrasia* only (model estimate ± SE = 17.715 ± 0.979, t = 18.09, p = .003, with an adjusted R^2 of .99; Figure 5c). Model estimates, standard errors, t-values, p-values, and adjusted R^2 for *Trifolium* and *Campanula*, respectively, are −0.469 ± 11.90, t = −0.039, p = .972, with an adjusted R^2 of −.50 and 9.980 ± 14.140, t = 0.706, p = .553, with an adjusted R^2 of −.20 (Figure 5a,b).

4 | DISCUSSION

Using a novel field experimental approach, we simulated future climate change scenarios at the trailing range edge of alpine plants. These plants experience warmer climates as well as potentially novel pollinators—and plant competitors for those pollinators—that may migrate upslope to track their current climate. The dynamics under this scenario were compared to a reference scenario in which high-elevation plant and pollinator communities synchronously track their current climate under future climate change. We found that pollinator communities do indeed differ along the climate/elevation gradient (Figure 2) such that transplanted species interacted with

different pollinator communities along the gradient (Figure 3a,b). Visitation rate to the local plant communities at each site increased with warming (at lower elevation, Figure 2). However, contrary to our predictions, this pattern did not hold for transplanted high-elevation communities (Figure 3b,c).

We further found that differences in pollinator community composition and visitation rate corresponded with differences in plant female fitness across climate scenarios (Figure 4). Specifically, *T. pratense* and *C. scheuchzeri* reproduction suffered under the warmest scenario (lowest elevation). For these species, we attribute reductions in fitness to low visitation by effective pollinators, and perhaps also issues related to low floral density at this site. We discuss these points in more detail below. Although the pollinator community visiting *E. minima* differed across elevation, seed set appears to be more dependent on visitation rate than pollinator identity for this species. Plant mating system, discussed below, may also play a role in *Euphrasia* reproductive success. These results highlight the importance of considering both visitation rate and pollinator effectiveness when predicting species' responses to pollinator change associated with climate change.

4.1 | Plant–pollinator community composition in the local and transplanted communities

Across sites, pollinator visitation to the local plant community differed substantially from visitation in the experimental plots (Figures 2 and 3b). Contrary to our expectations, visitation in the experimental plots peaked at 1,800 m, rather than increasing with decreasing elevation (Figure 3b). One factor contributing to high overall visitation at 1,800 m is the abundance of visits by flies (Diptera). Interestingly, there were far fewer (proportionally) Dipteran visits to the local community at 1,800 m. It is possible that plant species that were observed in abundance in the experimental plots at 1,800 m were more attractive to flies than plant species in the local community. *Euphrasia* received a large number of visits by flies at this site, as did a *Ranunculus* species that was commonly observed (Table S4). Indeed, some of the differences in pollinator community visiting the plant community in the experimental plots may be explained by the marginal difference observed in plant community composition across sites (Figure S2).

Another major difference in pollinator community composition between the local plant community and the transplanted alpine community is the proportion of visits made by bumble bees (Figures 2 and 3b). Bumble bee visits were proportionally much higher in the local community compared to the experimental plots. The same possible mechanism may be at play here: plants in the local community were more attractive to bumble bees than plants in the experimental plots. As discussed below, these patterns suggest that competition for some pollinators may intensify as lower elevation plants invade higher elevation communities with warming climate. Support for the competition for pollinators mechanism for the visitation differences between local and transplanted alpine plants is provided by the fact that local flowers in the transects were proportionally

more abundant than flowers in the transplanted plots at low elevation. These low elevation plants were thus easier for bumble bees to identify against the background vegetation, as bees use visual cues on a broad spatial scale to identify suitable patches (Dafni, Lehrer, & Kevan, 1996).

Similar to visit abundance in the experimental plots, visitation rate to the transplanted communities and each focal species peaked at the 1,800 m site. For the focal species, floral density appears to be a strong driver behind this pattern. Floral density was also highest at the 1,800 m site for all three focal species (Figure S3; Table S5). High floral density encourages pollinator visitation to single and mixed species patches (Ghazoul, 2006; Kunin, 1993). It is unclear what allowed for such high floral abundance at 1,800 m relative to the rest of the sites. It could be that the climate at this elevation was conducive to vegetative growth and floral production, whereas the 2,000 m site was too cold and the two lower sites were too warm to produce flowers at the same density. Future studies that are able to replicate communities at the site level (i.e., multiple sites at each elevation, each containing replicate plots), would provide insight into this possibility.

4.2 | Mechanisms connecting visitation patterns to plant fitness

Visitation to *Trifolium* and *Campanula* was higher at 1,800 m than at any of the other sites (Figure 4g,h); however, this increase in visitation did not translate to higher reproduction (Figures 4j,k and 5a,b). Conversely, visitation rate at the warmest (lowest) site was not significantly lower than at other sites, but resulted in significantly lower reproduction for both species (Figure 4j,k). We propose low visitation by effective pollinators at the 1,400 m site as a possible mechanism. Specifically, bumble bee visits to *Trifolium* decreased with elevation, particularly at the lowest elevation site, and seed production broadly follows the same pattern (Figure 4d,j). Similarly, 100% of pollinator visits to *Campanula* at 2,000 m were made by bumble bees, and bumble bee visitation to *Campanula* in transplanted turfs decreased with elevation; indeed, there were no observed bumble bee visits to *Campanula* at the lowest elevation site (Figure 4e). Bumble bees may be more efficient at transferring conspecific pollen than the visitor taxa that visited more frequently at the warmer sites, such as small-bodied bees. A recent study of a North American *Campanula* species describes this exact mechanism: Smaller bodied solitary bees exacerbated pollen limitation and reduced seed set in *Campanula americana*, while larger bodied solitary bees and bumble bees reduced pollen limitation and increased seed set (Koski, Ison, Padilla, Pham, & Galloway, 2018). We were not logistically able to manipulate individual flowers, and therefore did not test for pollen limitation. Future studies of pollen limitation and effective pollination (i.e., pollinator exclusion studies) are warranted to uncover the mechanism behind observed patterns of reproductive success.

It is possible that differences in reproduction across sites were driven by a lack of potential mates where high-elevation plant species were rare. Therefore, patterns of floral density observed in the plots and in the local environment may explain reproductive success in the focal species. As floral patches become denser, the sensory cues delivered to pollinators become stronger, therefore making patches more attractive (Dafni et al., 1996). Indeed, floral density in the experimental plots (flowers/m^2) was a significant predictor of visitation rate in *Campanula* and *Euphrasia*, and was a marginally significant predictor of visitation rate in *Trifolium*. However, it is unclear whether floral density played a role in reproductive success. Although there was a relationship between floral density and visitation rate for all three species, there was no relationship between visitation rate and seed production for *Trifolium* or *Campanula* (Figure 5a,b). Invasion by lower elevation plant species is a consequence for high-elevation plant species of failing to migrate in response to climate. Our experiment captures an extreme case in which warming has led to substantial invasion by lower elevation plant species and made high-elevation plant species rare on the landscape. Reproduction in *Trifolium* appears to be consistent with abundance of conspecifics in the local environment; however, a lack of conspecifics in the local environment did not appear to be correlated with reproduction in *Campanula* or *Euphrasia* (Figure 4j–l; Figure S4).

We cannot eliminate the possibility that physiological stress caused by warming may have indirectly or directly reduced seed set. Under experimental warming, plants may flower earlier, losing synchrony with their pollinators (e.g., Rafferty & Ives, 2011). Similarly, investment in floral abundance or flowering duration may limit interaction with pollinators. A study of nine *Campanula* species occurring along an elevation gradient in Greece reports shorter flowering duration at lower elevations, indicating a reduction in investment in reproduction (Blionis, Halley, & Vokou, 2001). There is mixed evidence for warming directly affecting seed production in other systems, including studies reporting increased reproductive output as a direct result of warming (Hovenden et al., 2007; Lambrecht, Loik, Inouye, & Harte, 2007; Price & Waser, 1998). In *Arabidopsis*, maternal environment and increases in temperature during floral development had different consequences for seed production in summer and winter annual varieties (Huang, Footitt, & Finch-Savage, 2013). Future experiments testing physiological performance and reproduction, including hand-pollination along with direct manipulation of the abiotic environment, would be helpful to discern the extent to which temperature directly affects reproductive performance.

In contrast to *Trifolium* and *Campanula*, reproductive success in *Euphrasia* appears to be driven by pollinator visitation rate more than pollinator identity. This contrast may be due to the functional similarities within the *Euphrasia* pollinator community relative to the communities visiting *Trifolium* and *Campanula*. At high elevations, *Euphrasia* was mainly visited by Syrphid and non-Syrphid flies, while small-bodied bees were responsible for the majority of the visits at low elevations (Figure 4f). These groups were generally similar in

body size, and would therefore provide a similar morphological fit to floral reproductive structures (Stang, Klinkhamer, Waser, Stang, & van der Meijden, 2009; Vivarelle, Petanidou, Nielsen, & Cristofolini, 2011). *Euphrasia* is also unique compared to the other two species in that is self-compatible to some extent (Liebst & Schneller, 2005; Palmer-Jones et al., 1966; Trunschke & Stöcklin, 2016). Therefore, it may have experienced seed production due to selfing, which could explain its success compared to the two other species at the lower elevation sites.

Additionally, in circumstances where few mates were available, pollinator deposition of self-pollen may also have contributed to *Euphrasia*'s reproductive success. Certainly, visitation rate played a strong role in seed production (Figure 5c), but it would still be interesting to know whether *Euphrasia* experienced different degrees of selfing at different sites, and if so, what was driving it. Previous work has shown shifts from outcross pollination to selfing as plants expand their ranges into pollinator-limited habitat (Moeller, 2006). For *Euphrasia*, the dynamics may be slightly different: rather than investing in selfing as a result of migration, this species may invest in selfing as a result of failure to migrate. Evaluating differences or plasticity in plant mating systems as a predictor of species' ability to respond to a changing climate is an exciting area of plant reproductive ecology. Our work suggests plant mating systems may play a role in shaping novel plant communities under climate change.

4.3 | Possible role of competition for pollinators

Our results indicate that climate change could impact plant species' reproductive fitness. One potential driver for this pattern, which we did not directly test but our data allude to, is competition for pollination. Pollinator functional groups (large-bodied bees) that correlated with increased seed production at high elevations rarely visited experimental plants at low elevations, where they instead abundantly visited plants in the local communities at each site (Figures 2 and 3b). In our experiment, these local plant species mimic a scenario where low-elevation plant species have migrated upslope to track their climate and now compete with high-elevation plant species for low-elevation pollinators that have also migrated upslope (Figure 1). For plant species that rely on specific pollinator taxa, as may be the case for *Campanula* and *Trifolium*, competition with novel species may become increasingly important under climate change. Indeed, the majority of visits to other *Campanula* species native at low elevation sites were made by bumble bees, which rarely visited the transplanted *C. scheuchzeri* at these sites.

It is important to note that we did not directly measure competition for pollination between plants in the experimental and local communities, and we were not able to control for floral diversity in the transects. Whether plant species that can more easily migrate in response to climate change are dominant competitors for pollinators remains an intriguing and open question. However, the invasive species literature offers compelling examples of pollinator preference switching from native species in favor of invasive congener species, or species with similar floral morphologies (Morales & Traveset, 2009; Yang, Ferrari, & Shea, 2011). For example, experimental additions of invasive purple loosestrife (*Lythrum salicaria*) reduced floral visitation and seed set in its native congener *Lythrum alatum* (Brown, Mitchell, & Graham, 2002). We advocate for community-transplant studies similar to ours that directly evaluate competition for pollinators through the use of pollen supplementation and competitor removal manipulations.

5 | CONCLUSIONS

Our work highlights how climate change can indirectly affect species' performance by modifying species interactions. Under the simulated climate change scenarios, changes in pollinator identity or visitation rate were correlated with differences in plant reproductive success. Pollinator communities—and to some extent plant communities—differed at different elevations; these community-level differences may play a role in how individual plant species are able to respond to climate change. Our results point to several, potentially interconnected, factors that may influence plant fitness. Additionally, our results suggest ways in which competition for pollinators may play an important role in shaping plant–pollinator communities in response to climate-mediated migration. Although our study focuses on climate-mediated shifts in a plant–pollinator interaction, the questions they raise about specificity and indirect competitive interactions are likely applicable to other types of changing species interactions under climate change (e.g., predation). Indeed, how climate alters species interactions is emerging as a major theme in global change biology, and future studies of this kind will be critical for identifying community-level consequences of climate change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.