



RESEARCH ARTICLE

Herbivory damage but not plant disease under experimental warming is dependent on weather for three subalpine grass species

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Abstract

- Both theory and prior studies predict that climate warming should increase attack rates by herbivores and pathogens on plants. However, past work has often assumed that variation in abiotic conditions other than temperature (e.g. precipitation) do not alter warming responses of plant damage by natural enemies. Studies over short time periods span low variation in weather, and studies over long time-scales often neglect to account for fine-scale weather conditions.
- Here, we used a 20+ year warming experiment to investigate if warming affects on herbivory and pathogen disease are dependent on variation in ambient weather observed over 3 years. We studied three common grass species in a subalpine meadow in the Colorado Rocky Mountains, USA. We visually estimated herbivory and disease every 2 weeks during the growing season and evaluated weather conditions during the previous 2- or 4-week time interval (2-week average air temperature, 2- and 4-week cumulative precipitation) as predictors of the probability and amount of damage.
- Herbivore attack was 13% more likely and damage amount was 29% greater in warmed plots than controls across the focal species but warming treatment had little affect on plant disease. Herbivory presence and damage increased the most with experimental warming when preceded by wetter, rather than drier, fine-scale weather, but preceding ambient temperature did not strongly interact with elevated warming to influence herbivory.
- Disease presence and amount increased, on average, with warmer weather and more precipitation regardless of warming.

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5. *Synthesis.* The effect of warming over reference climate on herbivore damage is dependent on and amplified by fine-scale weather variation, suggesting more boom-and-bust damage dynamics with increasing climate variability. However, the mean effect of regional climate change is likely reduced monsoon rainfall, for which we predict a reduction in insect herbivore damage. Plant disease was generally unresponsive to warming, which may be a consequence of our coarse disease estimates that did not track specific pathogen species or guilds. The results point towards temperature as an important but not sufficient determinant and regulator of species interactions, where precipitation and other constraints may determine the affect of warming.

KEYWORDS

climate change, graminoids, infrared heating, intraannual weather variation, natural enemies, Poaceae, repeated sampling, subalpine meadow

1 | INTRODUCTION

Climate change is expected to alter species interactions in a complex and often context-dependent manner (Tylianakis et al., 2008; Vázquez et al., 2017). The direct effects of climate change on organisms are physiological, including increases in desiccation and heat stress that can increase mortality (Mech et al., 2018; Peñuelas et al., 2011). Climate change can also indirectly alter the interactions between species. For example, earlier snowmelt caused by climate warming reduced floral abundance in a subalpine meadow that consequently decreased the abundance of pollinating bees (Ogilvie et al., 2017). Understanding the indirect effects of climate change on species interactions can improve our ability to preserve ecosystem services and functions in future climates (Montoya & Raffaelli, 2010).

Climate warming is expected to shift plant communities towards more resource competitive species (Alexander et al., 2016). Field-based warming experiments have repeatedly supported this hypothesis. For instance, in situ winter warming increased the abundance of taller, more competitive species by extending the growing season, thus increasing plant biomass production in a northern England grassland (Fridley et al., 2016). Twenty-three years of warming in a subalpine grassland of the Colorado Rockies increased shrub biomass over ambient plots and caused sharp initial decreases in soil organic carbon associated with declines in forbs (Harte et al., 2015). On top of this swing from forbs to shrubs, warming also decreased grass abundance while promoting sedges (Rudgers et al., 2014).

Warming may also shift the composition of plant–herbivore and pathogen communities because plant–enemies have species-specific responses to warming depending on their thermal optima. For instance, warming reduced insect community richness and evenness relative to controls in an old field in the Eastern USA mainly through increased abundance of already dominant morphospecies and declines in both a co-dominant species and in rare species (Villalpando et al., 2009). Warming can similarly increase the relative abundance of bacterial leaf pathogens (Aydogan et al., 2018), while foliar endophytes that are beneficial or neutral to plants did not respond strongly to in situ warming

(Kazeneel et al., 2019). Taken together, current work suggests that climate warming can cause large changes in insect and microbial community composition that increase damage to plants.

Past theoretical work generally predicts that warming, all else being equal, should lead to increased insect and pathogen damage to plants via increased metabolic rates (Brown et al., 2004; Burnside et al., 2014; Gilbert et al., 2014, but see O'Connor et al., 2011), but field experiments that have evaluated experimental warming effects on plant–herbivore or plant–pathogen interactions have provided mixed evidence. In line with theoretical predictions, total herbivore and pathogen leaf damage for six common forb species increased with warming/early snowmelt (Roy et al., 2004) and three alpine-restricted grass species had increased insect herbivory when transplanted to warmer, low elevation sites with earlier snowmelt (Lynn et al., 2021). In contrast with theory, experimentally increased temperature led to lower herbivory in *Quercus alba* seedlings (Burt et al., 2014). Fungal pathogen loads both within species and across the plant community increased with warming in a Tibetan alpine meadow (Liu et al., 2019). In contrast, snow additions caused outbreaks of a fungal pathogen, *Arwidssonia empetri*, that killed much of the dominant shrub, *Empetrum hermaphroditum* (Olofsson et al., 2011). The causes behind these deviations from theoretical predictions are required to accurately forecast how the indirect effects of plant–enemies will drive community and ecosystem change.

This context dependence in how warming affects plant–herbivore and plant–pathogen interactions is mechanistic (Catford et al., 2022) and suggests that other, unconsidered factors may promote or limit damage under warming. For instance, recent theoretical work points out that increases in herbivory rates with temperature are dependent on other limiting resources, such as precipitation (Lynn et al., in press). To this point, many of these past single year studies may not adequately account for the role of climatic/weather variation that occurs outside of treatment effects, such as inter- or intraannual variation in temperature and precipitation (Ward et al., 2019). This has several consequences for interpreting results from warming experiments: (i) at time of sampling, warming has the potential to push plant–enemies past

their thermal optima (Stoks et al., 2017), causing reductions in damage compared to controls that may not hold throughout the season; and (ii) given experimental warming exerts greater evaporative demand and earlier snowmelt, observed damage may be more sensitive and limited by ambient rainfall than in control plots. Such fine-scale weather conditions may be particularly important in monsoonal systems, where postsnowmelt droughts occur until late summer rainfall.

Here, we measured herbivory and pathogen caused plant disease on three dominant grass species for 3 years in a warming experiment that has been running for more than 25 years. We used data from a local weather station to investigate if the effects of warming on damage accumulation were dependent on within-season temperature and precipitation fluctuations. We asked (1) How does long-term experimental warming affect the presence and amount of herbivore and disease damage? (2) Does the affect of long-term experimental warming on natural enemy damage depend on fine-scale weather patterns in temperature and/or precipitation? We expected that long-term experimental warming would increase both the presence and amount of herbivore and disease damage, damage would increase with fine-scale increases in temperature and precipitation, and experimental warming would exacerbate increased damage over controls more so under warmer and wetter weather periods. Furthermore, we predicted that greater ambient precipitation would increase herbivore and disease damage more than fine-scale temperature if early season droughts are a primary constraint on both herbivore and disease activity, as precipitation is considered a primary constraint of productivity for the region (Seddon et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Warming experiment

In the fall of 1990 at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA, 10 permanent 10 × 3 m plots were established oriented lengthwise along the ridge of a moraine. Five treatment plots were warmed year-round by overhead electric heaters (~22 W/m² infrared radiation). The treatment warmed the soil surface (top 15 cm) by ~2°C, dried the soil by ~10%–20% gravimetric, and increased growing season length by ~12 days through warming effects on snowmelt (Harte et al., 1995; Harte & Shaw, 1995; Saleska et al., 2002). Treatments were designed to reflect a warming scenario of doubled atmospheric CO₂ based on conditions at the onset of the experiment (Harte & Shaw, 1995). Control plots without mock heaters were alternated between warmed plots. Each plot was split into three blocks from top to bottom of the ridge, and warming effects on the abiotic environment were greatest in the top (driest) block, where we concentrated our sampling effort. Additional detail on experiment design and upkeep can be found in Harte et al., 2015, Harte & Shaw, 1995, and Rudgers et al., 2014. Other effects of long-term experimental warming included declines in soil carbon (Harte et al., 2015), increased dominance of the shrub sagebrush (Perfors et al., 2003), and increased representation of sedges over grasses

without much change in total graminoid cover (Rudgers et al., 2014). On average across plots and years of this study (2015–2017), warmed plots melted out 38 days before the control plots (Julian day of 86 vs. 124). All fieldwork was performed on RMBL land with full permission.

2.2 | Focal plant species

We studied three dominant perennial grasses (Poaceae): *Achnatherum lettermanii*, *Festuca thurberi* and *Poa pratensis*. Both *A. lettermanii* and *F. thurberi* are bunchgrasses, while *P. pratensis* is rhizomatous. Prior work on herbivory in the warming meadow had not included grasses (Roy et al., 2004), leaving a large portion of the plant community unstudied. *Poa pratensis* has significantly declined in the warmed plots compared to controls, and both *A. lettermanii* and *F. thurberi* trended towards declines in warmed plots (Rudgers et al., 2014). We focused on herbivore and disease damage to these three most common grass species to gain further insight into a potential indirect mechanism of their decline in response to warming.

2.3 | Herbivory and pathogen disease measurements

In the beginning of each growing season (early to mid-June, depending on snowmelt), we used plastic zip ties to mark three randomly chosen individual tillers on each of six individuals per species per plot. Six individuals per species per the 3 × 3 m upper zone made up between 60 and 100% of individuals of the focal species in the plots, anecdotally. This enabled us to track accumulation of damage on tillers throughout the growing season. If zip ties fell off the tillers, we randomly selected another tiller to track (~5% of observations). We sampled individuals at the top of the ridge in the first block, but for *F. thurberi*, we could not find the desired six individuals per plant species in plots 7–10. In this case we included individuals in the lower blocks until the desired number was achieved (see Figures S1 and S2 - no differences in the plots where this occurred).

Herbivory and, likely pathogen caused, disease damage was visually estimated by an observer, to the nearest 1% of leaf area damaged. Visual estimates of percentage damage were calibrated between two observers (one student and one expert—J.S. Lynn) by consensus. After 1 to 2 days of training, one-student observer carried out the rest of the observations for the season. In total, four observers recorded herbivory (N. Abo-Sido - 2015, I. McCowen -2016, S. Villanueva -2017 and J.S. Lynn—across years). These and similar methods of plant-enemy damage estimation are standard practice for the field (e.g. protocols from herbvar.org; Baskett & Schemske, 2018; Roy et al., 2004). Each grass tiller contained two-three leaves. Additionally, we noted the type of herbivore damage among the following classes: cell sucking damage (aphids, leaf hoppers, etc.), chewing damage (caterpillar, grasshopper) or leaf-miner damage (flies, moths). Disease was classified by symptom rather than species due to lack of funds for sequencing. We used the following classes with descriptions: powdery

mildew (white powdery damage), rust (reddish-coloured dusty damage), black (bulbous black pocks), brown (brown, oozy lesions) or yellow (yellowy discoloured lesions) disease. We only counted disease if we could identify pathogen caused disease symptoms (e.g. spores, hyphae, moulds, ooze) and no other factors (e.g. discoloration from abiotic stress or mechanical damage).

2.4 | Climate data and manipulation

We used climate data from the National Atmospheric Deposition Program (<http://nadp.slh.wisc.edu/siteOps/ppt/default.aspx>) at the CO-10 site ID, which was approximately 50m from the warming meadow. We investigated how fine-scale weather patterns correlated with the presence and amount of damage. We focused on temperature (°C) and precipitation (mm) as the key climatic variables. We calculated average daily temperature as the midpoint between daily minimum and maximum temperatures. Then, because we observed damage every 2 weeks, we averaged daily temperature values over the 2 weeks prior to each sampling date to obtain average conditions leading up to sampling. We summed the amount of precipitation over the 2 and 4 weeks prior to sampling. The 2-week weather windows were chosen to cover weather variation between samplings. The 4-week precipitation window was added because of the long 'moisture memory' of the soil in the experiment (takes ~4 weeks of no precipitation to reach below plant wilting point; Harte et al., 1995).

2.5 | Statistical analyses

We constructed models to investigate how warming treatments: question (1) affected the presence and amount of herbivore damage and disease; and question (2) how warming effects on herbivore damage or disease depend on ambient temperature and/or precipitation. Herbivory damage and disease data were highly zero-inflated. Therefore, we used a hurdle-model approach (Martin et al., 2005), in which we first modelled whether an individual received damage as a Bernoulli process (0,1 with logit link), then we removed all observations of zero damage and modelled the amount of damage that occurred conditional on the presence of damage. Damage was averaged across tillers to the individual plant level. We logit transformed the amount of damage because it is a proportion/percentage of the total leaf area (Warton & Hui, 2011). Each grass species was analysed separately. For question (1), we modelled both presence and amount of damage with the following model:

$$y = \text{warm} + \text{days} + \text{year} + N(0, \sigma^2_{\text{plot}}) + N(0, \sigma^2_{\text{ind}}) \quad (1)$$

Where y was either presence or amount of either herbivore or disease damage (four separate models) of an individual and *warm* was the experimental warming treatment. We fit different intercepts with *warm* to determine the mean effect of the treatment on damage. The model fit *days* to account for damage accumulation over time within a year

and *year* intercepts accounted for interannual variation in damage. We did not model the interactive effects of year with warming. Although our experiment is strengthened by its temporal replication, interannual replication was too low to meaningfully interpret temporal patterns in association with interannual climatic variation. Finally, we fit plot (σ^2_{plot}) and individual (σ^2_{ind}) random/group intercept variance effects for the 10 replicate plots that comprised the experiment and for the repeated measures on each individual plant.

For question (2), we used:

$$y = \text{warm} \times x + \text{days} + \text{year} + N(0, \sigma^2_{\text{plot}}) + N(0, \sigma^2_{\text{ind}}) \quad (2)$$

which is the same as (Equation 1), but with the addition of x , which represents either the mean temperature of the 2 weeks before sampling or the summed precipitation of the 2 or 4 weeks prior to sampling. In addition to fitting warming treatment intercepts, this model assessed whether the relationship (slope) between fine-scale temperature/precipitation and damage differed between control and warmed plots to evaluate if the observed effect of warming was dependent on fine-scale weather. Finally, we built models that included the interaction of treatment, temperature and either 2- or 4-week precipitation to investigate if damage increases with one of the weather variables was conditionally dependent on the other.

We used Bayesian estimation in JAGS (Plummer, 2003) with the R2JAGS package (Su & Yajima, 2015). All models were run for at least 30,000 iterations with three chains, thinned by 5, and the first 15,000 iterations used as burn-in. We checked for good mixing and uniquely identified parameters with traceplots and that models had reached convergence with the potential scale reduction parameter ($\hat{R} < 1.01$ means adequate convergence; Gelman & Rubin, 1992). All priors were uninformative with normal priors ($N(0, 1E-6)$) for fixed effects and gamma priors ($\Gamma(1E-3, 1E-3)$) for variance parameters on random/group effects. Amount of damage (logit transformed) was modelled with a normal error distribution and gamma priors ($\Gamma(1E-3, 1E-3)$) for variance.

We checked model fit with two posterior predictive checks. First, we plotted the sum of squared residuals (SSQ) for the observed data versus SSQ for the data simulated by model predictions, where points falling on the 1:1 line indicate the model simulates data with similar error to the observed data. And second, we calculated Bayesian p -values, which assess bias in the SSQ of simulated versus observed data, where values of 0.5 indicate no discrepancy between the two (Gelman et al., 1996). All models passed posterior predictive checks, and we reported Bayesian p -values in Table 1. We estimated a 'Bayesian R^2 ' for each model as the variance in the fixed effect modelled predictive means divided by the addition of the modelled predictive means and residual variance (Gelman et al., 2019).

Models in (Equation 1) fit the main effect of warming on damage while models in (Equation 2) assessed if adding fine-scale weather patterns explained further variation in damage. We used model comparison between main effect and weather models to test if adding weather patterns improved predictive ability based on two information criterion: WAIC and LOOCV (Hooten & Hobbs, 2015). Like other information criteria, smaller WAIC and LOOCV values indicate lower

TABLE 1 Model selection results for weather versus main effect predictions of herbivore and disease damage amount and presence by species. Each row of the table specifies the set of 'Predictors' for a given damage metric and species where 'Main' effect models included warming treatments alone; '2-week precipitation', '4-week precipitation' and 'Temperature' included the interaction of a weather variable with warming treatment; and 'Interaction (2-week)' and 'Interaction (4-week)' included the interaction between precipitation at one of the two time scales, temperature and warming treatments (see methods for further model details). Δ WAIC and Δ LOOCV show the difference between the best and a given model. Bayes R^2 values are Bayesian approximations to the coefficient of determination (see methods). Bayes p -value assess if there is similar residual error in observed versus simulated data by the model, where a value close to 0.5 indicate a properly fitted model. N is the sample size for a model.

Damage metric	Species	Predictor	WAIC	Δ WAIC	LOOCV	Δ LOOCV	Bayes R^2	Bayes p -value	N
Herbivory presence	<i>Achnatherum lettermanii</i>	2-week precipitation	1117.5	0.0	1117.6	0.0	0.119	0.664	900
		Interaction (2-week)	1117.8	0.3	1117.9	0.3	0.128	0.755	900
		Interaction (4-week)	1123.3	5.8	1123.4	5.8	0.123	0.739	900
		4-week precipitation	1130.5	13.0	1130.6	13.0	0.105	0.667	900
		Temperature	1140.2	22.7	1140.3	22.7	0.100	0.691	900
		Main	1144.6	27.1	1144.7	27.1	0.088	0.635	900
	<i>Festuca thurberii</i>	Interaction (2-week)	995.7	0.0	995.9	0.0	0.151	0.673	897
		Temperature	995.9	0.2	996.0	0.1	0.137	0.573	897
		2-week precipitation	996.7	1.0	996.9	1.0	0.140	0.632	897
		Interaction (4-week)	1001.0	5.3	1001.2	5.3	0.145	0.674	897
		Main	1001.9	6.2	1002.0	6.1	0.127	0.567	897
		4-week precipitation	1005.3	9.6	1005.5	9.6	0.129	0.621	897
	<i>Poa pratensis</i>	4-week precipitation	996.1	0.0	996.3	0.0	0.228	0.646	896
		Interaction (2-week)	997.5	1.4	997.8	1.5	0.237	0.721	896
		Interaction (4-week)	1000.6	4.5	1000.9	4.6	0.234	0.724	896
		2-week precipitation	1001.7	5.6	1001.9	5.6	0.225	0.654	896
		Main	1043.0	46.9	1043.2	46.9	0.177	0.604	896
		Temperature	1044.3	48.2	1044.5	48.2	0.181	0.645	896
Disease presence	<i>Achnatherum lettermanii</i>	Interaction (4-week)	800.1	0.0	800.3	0.0	0.290	0.754	900
		Interaction (2-week)	812.3	12.2	812.5	12.2	0.278	0.764	900
		4-week precipitation	816.6	16.5	816.7	16.4	0.270	0.622	900
		Temperature	816.7	16.6	816.8	16.5	0.265	0.668	900
		2-week precipitation	827.6	27.5	827.7	27.4	0.264	0.653	900
		Main	832.9	32.8	832.9	32.6	0.249	0.542	900
	<i>Festuca thurberii</i>	4-week precipitation	792.6	0.0	792.7	0.0	0.361	0.529	897
		Main	796.2	3.6	796.4	3.7	0.348	0.393	897
		Interaction (4-week)	796.9	4.3	797.1	4.4	0.367	0.652	897
		2-week precipitation	797.4	4.8	797.6	4.9	0.354	0.498	897
		Temperature	798.4	5.8	798.6	5.9	0.351	0.477	897
		Interaction (2-week)	802.7	10.1	802.9	10.2	0.359	0.589	897
	<i>Poa pratensis</i>	Interaction (4-week)	867.0	0.0	867.2	0.0	0.332	0.673	896
		4-week precipitation	880.3	13.3	880.5	13.3	0.321	0.600	896
		2-week precipitation	890.2	23.2	890.3	23.1	0.314	0.524	896
		Interaction (2-week)	892.0	25.0	892.2	25.0	0.319	0.606	896
		Temperature	895.2	28.2	895.3	28.1	0.307	0.527	896
		Main	901.0	34.0	901.1	33.9	0.302	0.455	896
Herbivory amount	<i>Achnatherum lettermanii</i>	4-week precipitation	989.7	0.0	989.7	0.0	0.174	0.503	369
		2-week precipitation	995.0	5.3	995.4	5.7	0.170	0.498	369
		Interaction (4-week)	995.1	5.4	995.6	5.9	0.184	0.496	369
		Main	996.5	6.8	996.7	7.0	0.158	0.499	369
		Interaction (2-week)	997.4	7.7	998.0	8.3	0.181	0.504	369
		Temperature	997.6	7.9	998.1	8.4	0.166	0.496	369

Damage metric	Species	Predictor	WAIC	Δ WAIC	LOOCV	Δ LOOCV	Bayes R^2	Bayes p -value	N
	<i>Festuca thurberi</i>	4-week precipitation	1631.0	0.0	1631.3	0.0	0.157	0.493	618
		2-week precipitation	1632.0	1.0	1632.3	1.0	0.156	0.506	618
		Interaction (2-week)	1633.3	2.3	1633.6	2.3	0.168	0.503	618
		Interaction (4-week)	1633.5	2.5	1633.9	2.6	0.167	0.494	618
		Main	1634.8	3.8	1635.0	3.7	0.146	0.499	618
	<i>Poa pratensis</i>	Temperature	1637.9	6.9	1638.1	6.8	0.150	0.497	618
		4-week precipitation	1421.0	0.0	1421.4	0.0	0.187	0.501	526
		2-week precipitation	1425.8	4.8	1426.1	4.7	0.181	0.500	526
		Interaction (4-week)	1426.3	5.3	1426.8	5.4	0.195	0.498	526
		Interaction (2-week)	1431.0	10.0	1431.5	10.1	0.188	0.503	526
Disease amount	<i>Achnatherum lettermanii</i>	Main	1431.2	10.2	1431.5	10.1	0.167	0.494	526
		Temperature	1434.5	13.5	1434.8	13.4	0.170	0.494	526
		Interaction (4-week)	2179.5	0.0	2179.8	0.0	0.381	0.506	659
		4-week precipitation	2197.3	17.8	2197.5	17.7	0.359	0.498	659
		2-week precipitation	2202.1	22.6	2202.3	22.5	0.346	0.500	659
	<i>Festuca thurberi</i>	Interaction (2-week)	2202.6	23.1	2202.8	23.0	0.362	0.505	659
		Temperature	2205.9	26.4	2206.1	26.3	0.344	0.500	659
		Main	2206.5	27.0	2206.5	26.7	0.340	0.497	659
		Interaction (4-week)	1996.9	0.0	1997.1	0.0	0.323	0.503	622
		4-week precipitation	1998.2	1.3	1998.4	1.3	0.312	0.502	622
<i>Poa pratensis</i>	Interaction (2-week)	2002.4	5.5	2002.6	5.5	0.316	0.497	622	
	Main	2002.7	5.8	2002.8	5.7	0.302	0.501	622	
	2-week precipitation	2003.7	6.8	2003.9	6.8	0.305	0.496	622	
	Temperature	2005.5	8.6	2005.6	8.5	0.305	0.497	622	
	Interaction (4-week)	1887.6	0.0	1888.0	0.0	0.257	0.507	543	
	<i>Poa pratensis</i>	4-week precipitation	1899.8	12.2	1900.1	12.1	0.228	0.504	543
		Interaction (2-week)	1899.8	12.2	1900.2	12.2	0.242	0.504	543
		Temperature	1903.3	15.7	1903.6	15.6	0.224	0.504	543
		Main	1904.1	16.5	1904.3	16.3	0.216	0.506	543
		2-week precipitation	1907.3	19.7	1907.6	19.6	0.218	0.496	543

within sample predictive error compared to models with higher values, and, unlike DIC, WAIC and LOOCV are valid for comparing hierarchical models (Hooten & Hobbs, 2015). We discuss the effects of treatment and weather in terms of 95% credibility intervals (hereafter, 95% CIs) of their parameters in the model. Credibility intervals should generally be interpreted as probability density functions of possible parameter values (Hobbs & Hooten, 2015), but setting cut-offs like the oft used 95% CI aids interpretation of the uncertainty or 'significance' of a parameter.

In 2016 and 2017, we additionally estimated herbivore and disease damage for the entire, whole-plant leaf area of the individuals. We provide an additional analysis of the main effects of warming for this whole-plant data in the supplement Figure S3. General patterns described in the main text applied to the whole-plant results. We did not further investigate the effect of within-year weather on whole-plant damage because of limited replication. Also, we provided

figures of herbivory and disease by category of damage in the supplement (Figures S4 and S5).

3 | RESULTS

3.1 | Main effects of experimental warming on plant damage

Generally, herbivory was greater in warmed versus control plots, while there was little evidence that warming affected disease. Herbivory presence was 11% more likely in warmed plots for *F. thurberi* and 28% more likely for *P. pratensis*, while there was little increase with warming for *A. lettermanii* (Figure 1). Herbivory amount was also larger in warmed than control plots by 9% for *A. lettermanii*, 26% for *F. thurberi*, and 52% for *P. pratensis* (Figure 1). However, herbivory

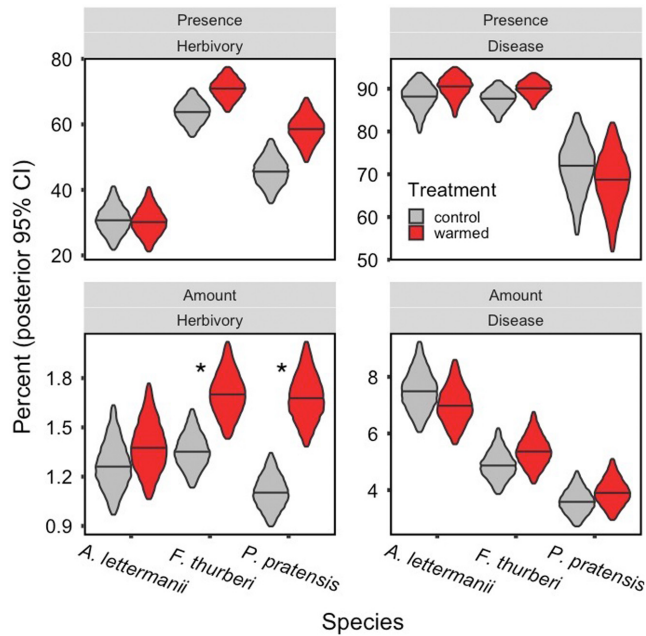


FIGURE 1 Main effect results for herbivory or disease presence or amounts of damage. Panels are arranged by columns left to right for herbivory and disease damage metrics, and top to bottom for presence and amount of damage. Presence panels are percent of individuals with damage and amount panels are in percentage leaf area damaged. The legend in the top-right panel applies to all panels. Violins represent the posterior 95% credibility intervals from models for the year 2015 at the centre of the sampling period (standardized time = 0; full parameter estimates in Table S1). Figures with data points are in the supplement Figure S6. Asterisks (*) indicate differences in treatment (95% CIs not including 0). Note, herbivory presences were different between treatments for *F. thurberi* and *P. pratensis* at the 90% CI cutoff.

amounts were generally low across species and treatments using our tiller-level methods, with mean herbivory amounts generally <2.5%. Models provided little support for warming effects on disease presence or amount of damage for any grass species (Figure 1).

3.2 | Warming effects on herbivory are dependent on precipitation

For all three species, the presence of herbivory on an individual plant was better predicted by either 2- or 4-week precipitation windows or their interaction with temperature than by the main effect of the warming treatment alone. Fine-scale precipitation was the best predictor for two of the three grasses based on WAIC and LOOCV model selection (Table 1). The best model for *A. lettermanii* and *P. pratensis* suggested that herbivory presence increased with increasing precipitation, and this relationship was much stronger in the experimentally warmed plots than in control plots (Figure 2a,c). Herbivory presence was best predicted by 2-week precipitation interacting with temperature for *F. thurberi* and increased with warmer

ambient air temperatures in addition to higher precipitation during the 2 weeks prior to census, but there was little evidence that this relationship was altered by experimental warming (interaction term 95% CI includes zero; Figure 2b).

The 4-week precipitation window was the best predictor of herbivory amount for all three grasses compared to the main effect of the warming treatment or fine-scale air temperature (Table 1). For *A. lettermanii*, in controls, herbivory amount decreased with precipitation amount during the 4 weeks prior to each census, but in warmed plots, was positively correlated with precipitation. However, both relationship 95% CIs included zero (Figure 3a). Herbivory amount increased with 4-week precipitation for *F. thurberi* with a steeper slope in warmed plots than controls, but both 95% CIs included zero (Figure 3b). Finally, there was no relationship between herbivory amount and 4-week precipitation for *P. pratensis* in control plots (95% CI includes 0), but herbivory amount increased with precipitation in warmed plots (95% CI >0; Figure 3c).

3.3 | Pathogen disease presence increases with fine-scale temperature and precipitation but not with long-term experimental warming

The best predictors of the disease presences on a plant, based on model selection, were the interaction of temperature and 4-week precipitation for *A. lettermanii* and *P. pratensis* and 4-week precipitation alone for *F. thurberi* (Table 1). Disease presence on *A. lettermanii* increased with both 4-week precipitation and temperature in control plots (95% CI >0), but the positive relationship between 4-week precipitation and disease presence was weaker in the warmed plots (warm x precipitation slope 95% CI <0; Figure 2d). Disease damage on *F. thurberi* increased with 4-week precipitation in both control and warm plots (95% CI >0), but there was no difference between warming treatments (Figure 2e). Disease presence increased with 4-week precipitation and temperature with a negative interaction term that dampened the additive predictions of both weather variables for *P. pratensis* (95% CI did not include zero; Figure 2f). However, there was no evidence that these predictions for *P. pratensis* differed between warming treatments (Figure 2f).

3.4 | Disease damage amount increases with precipitation dependent on temperature

Consistently for all three focal species, disease amount was best predicted by the interaction between temperature and 4-week precipitation (Table 1). Disease amount on *A. lettermanii*, *F. thurberi* and *P. pratensis* increased with 4-week precipitation with no difference between warmed and control treatments, and a negative temperature x precipitation interaction that predicted decreased disease as both temperature and precipitation increased (other model term 95% CIs included zero; Figure 3d-f).

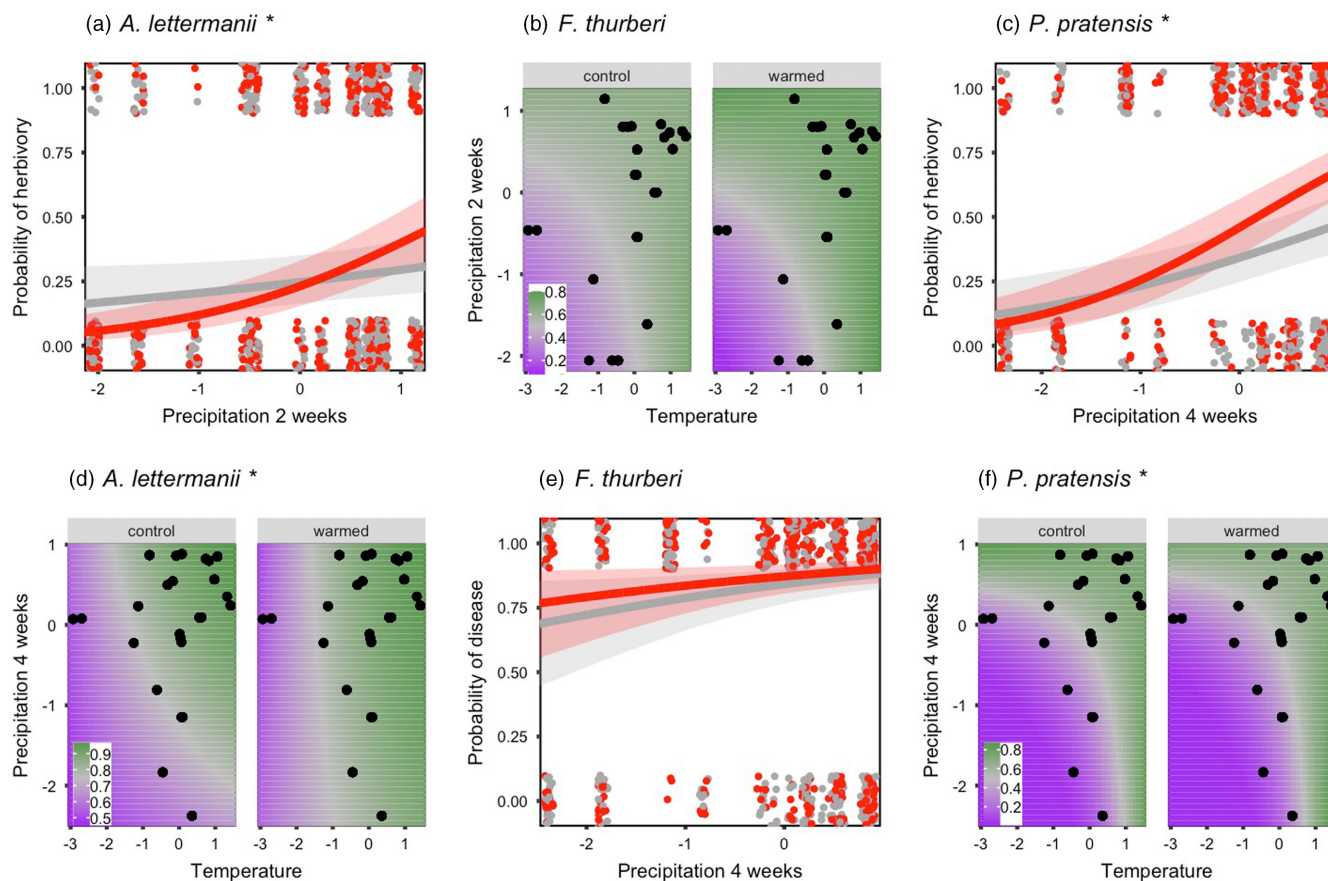


FIGURE 2 Herbivory and disease damage presence predicted by either standardized (unitless) precipitation, temperature or their interaction based on model selection (Table 1). Red represents warmed while grey represents control treatments. Thick lines represent posterior means while the shaded region is the 95% credible interval. Points are the observed data from all years and were jittered to ease visualization. Panels (d) and (f) show the predictions from the interaction model where colour (purple shading to green, scale legend in lower left-hand corner of panels) represents increasing predicted disease presence and the points represent the environmental coverage (temperature and precipitation) in the data. Note, modelled predictions are for 2015 at the standardized day midpoint (0) with all the raw data (see Table S1 for full parameter estimates). Asterisks (*) indicate differences in slopes by warming treatment (interaction terms with 95% CIs not including 0).

4 | DISCUSSION

Experimental warming effects on herbivory, but not disease, were dependent on fine-scale weather patterns. Specifically, the probability and amount of insect damage on common subalpine grasses increased in experimental warming with warmer air temperatures and more precipitation. Importantly, experimental warming effects on the probability or amount of herbivory were amplified by local weather conditions, both precipitation (*A. lettermanii*, *P. pratensis*) and temperature (*F. thurberi*). Across species, precipitation was a key predictor of the presence and amount of herbivore damage. In contrast, there was little evidence that disease was sensitive to experimental warming, but it did correlate with fine-scale weather patterns.

The dependence of herbivory presence and amount on fine-scale ambient precipitation is a novel finding suggesting that the effect of warming can be dependent on rainfall pulses. The result is especially important given that high latitude systems in North America are expected to have more precipitation in the future (Trenberth, 2011),

even as monsoon rains are expected to weaken (Wang et al., 2021). Past theoretical (O'Connor et al., 2011), experimental (Barrio et al., 2016; Birkmoe et al., 2016; Li et al., 2019) and observational (Ebeling et al., 2022; Lynn et al., in press) work suggests warming as well as spatial gradients in temperature can increase overall rates of herbivory, but our work fine-tunes this result by demonstrating that herbivory on dominant grasses is not simply energy (temperature) limited but also depends on precipitation. This conclusion is supported by the observation that herbivory presence and amount was lower in warmed plots compared to controls during low precipitation periods but flipped and was higher in warmed plots than controls during periods with more precipitation. Increases in within season rainfall may release water limitations of insect communities (Prather et al., 2020), driving higher rates of consumption. This result also aligns with past work that demonstrated simultaneous increases in both temperature and precipitation increased herbivory on *Argentina anserina* (Pepi & Karban, 2021) and that standing herbivory on plants is often greater in warm regions with high precipitation over large spatial scales (Kent et al., 2020; Moreira et al., 2015).

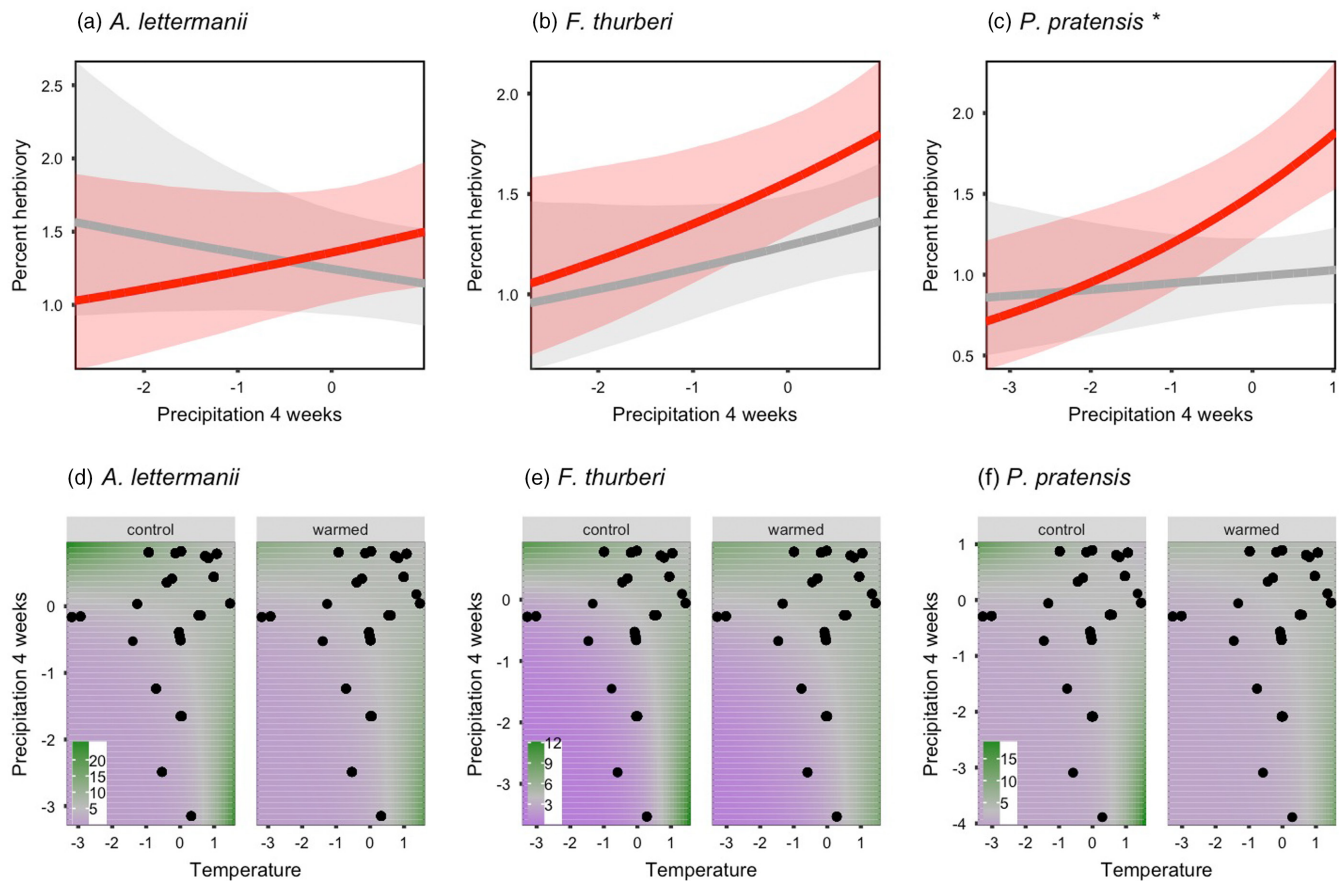


FIGURE 3 Herbivory and disease damage amount (% leaf area damaged) predicted by either standardized (unitless) precipitation, temperature or their interaction based on model selection (Table 1). In (a–c), red represents warmed while grey represents control treatments. Thick lines represent posterior means while the shaded region is the 95% credible interval. Points were excluded to visualize modelled patterns. Figures with data points are in the Figure S7. Panels (d–f) show the predictions from the interaction model where colour (purple shading to green, scale legend in lower left-hand corner of panels) represents increasing predicted disease amounts and the points represent the environmental coverage (temperature and precipitation) of the data. Note, modelled predictions are for 2015 at the standardized day midpoint (0; see Table S1 for full parameter estimates). Asterisks (*) indicate differences in slopes by warming treatment (interaction terms with 95% CIs not including 0).

Our finding highlights the need to understand the complex, interacting abiotic contexts in which species interactions respond to climate change (Lynn et al., *in press*).

Contrary to our hypotheses, plant disease was not more likely or greater in amount under experimental warming, and there was less evidence that disease tracked within-season weather patterns. Past work in the system had also found that pathogen damage was generally less responsive to warming than herbivore damage (Roy et al., 2004). Thus, climate-induced changes in damage by plant pathogens may be more difficult to predict than for insect herbivory, possibly due to high specialization and opposite responses of different pathogen types (and genotypes) to a given climatic change (Branco, 2019; Burdon et al., 2006). For instance, snow-blight pathogens will likely decrease with warming because snow will melt earlier in the season (Olofsson et al., 2011). In contrast, increased precipitation accelerates transmission of some bacterial (Hirano & Upper, 1983) and fungal (Fisher et al., 2012) pathogens. Therefore, it is possible that overall climate warming along with fine-scale weather patterns may increase the abundance of one type of

pathogen and disease symptoms while decreasing another type, re-ordering relative abundances of plant enemies. Our study was not able to assess reordering due to the coarse level of disease measurement. Future work may benefit from disentangling how weather and climate manipulations interact to influence plant enemies with different life-history strategies and niche dimensions.

One consequence of warming in many mountain systems is earlier snowmelt (Rixen et al., 2022) and, therefore, a longer period before late summer monsoons relieve early summer drought, which may amplify plant drought stress. Drought stress has typically been hypothesized to increase herbivory on plants, but prolonged drought stress can alternatively reduce herbivory (Huberty & Denno, 2004). The early snowmelt date in warmed plots may have caused a prolonged drought stress period in the focal plants, leading to lower amounts of herbivory (Figure 3a–c) in warmed compared to control plots during low precipitation periods of the early growing season. However, longer monitoring (more postsnowmelt drought periods observed) and explicit estimation of drought length/severity need to be considered to further assess this hypothesis. Depressed

herbivory due to chronic early season drought aligns with past experimental work that demonstrated less consumption and reduced survival of a mining insect on increasingly drought-stressed individuals of the grass species *Holcus lanatus* (Scheirs & De Bruyn, 2005). More work is needed to understand how drought-stressed graminoids resist versus tolerate herbivory (Strauss et al., 2002) through altered physiology or defensive chemistry. Additionally, the abundance and diversity of insect herbivores may respond directly to abiotic drivers such as low soil moisture or warm temperature (Adler et al., 2007; Prather et al., 2020).

Our warming experiment had been running for more than 25 years before our 3-year window of data collection. This long-term press experiment has altered the ecosystem in ways that may indirectly influence herbivore attack and disease, beyond the direct effects of warming on damage. Here, we speculate on a few possible indirect effects (note, this list is not exhaustive). Warming has increased shrub dominance while graminoids, and grasses in particular (Rudgers et al., 2014), have declined (Harte et al., 2015; Harte & Shaw, 1995). Past work suggests that lower focal species relative abundance would lead to less damage (Kim & Underwood, 2015; Mordecai, 2011) because of density-dependent attack rates, a prediction that does not align with our herbivory or disease results. In addition, experimental warming initially increased nitrogen mineralization rates (Shaw & Harte, 2001) and decreased soil organic carbon though these effects were short-lived (e.g. soil carbon slowly accumulated over time after the initial rapid loss; Harte et al., 2015). Short-lived, higher nitrogen mineralization, especially when combined with greater precipitation, may have increased plant nitrogen content and plant quality thereby increasing herbivore and disease damage because plants were more nutritious for enemies (e.g. Halliday et al., 2021; Liu et al., 2019; Lynn & Fridley, 2019; Rúa et al., 2014). Specific to herbivory, increased quality of plant tissues can also reduce damage amounts because each gram of tissue is more nutritious, translating to less consumed mass to obtain the same nutritional benefit (i.e. the nutrient dilution hypothesis; Welte et al., 2020). New data on plant nutrient content and soil nutrient availability would allow us to evaluate these hypotheses. Finally, it is possible that warming altered plant secondary metabolites and defensive chemistry, thereby indirectly influencing enemy damage. However, past work has turned up mixed results for plant secondary metabolites (Orians et al., 2019; Van De Velde et al., 2019), suggesting a need to pair damage estimates with data on secondary metabolites to understand such indirect effects.

A weakness of this study is the lack of plant-fitness data paired with our herbivory and disease estimates. However, we propose the hypothesis that warming driven increases in herbivore damage may have contributed to the decline of focal species abundance, which ultimately requires further experimentation. Past work using ecological niche modelling suggested that the abundance of all three focal species decreases with increasing herbivory only in the warmer end of their elevational range (Lynn et al., 2019). Paired with the current study's experimental data that warming increases herbivore damage, and the direct evidence of declines in grass abundance over the long-term warming treatment (Rudgers et al., 2014), these results

support a scenario in which warming increases herbivory which then reduces plant abundance over time. In our past work, *P. pratensis* was the only species among our focal taxa that had significantly declined in abundance in warming compared to control plots (Rudgers et al., 2014). Given that warming-induced increases in the presence and amount of herbivore damage were greatest for *P. pratensis* compared to the other two grasses, we propose that increased herbivore damage may explain the long-term declines in *P. pratensis* in warmed plots. Alternatively, disease may have been higher on the focal species earlier in the experiment, driving abundance declines which then fed back to reduce disease back to control levels as plant density declined (see similar results by Liu & He, 2019). Testing these hypotheses would require long-term enemy removal treatments (e.g. pesticides, fungicides) crossed with the warming treatment to disentangle these indirect mechanisms given potentially complex feedbacks between plant density and enemy damage (e.g. Liu & He, 2019; Schuldt et al., 2012; Smilanich et al., 2016).

The responsiveness of plant-insect and, to a lesser extent, plant-pathogen interactions to within-season weather highlights the need to study species interactions over both long and finer-grained time-scales (Bale et al., 2002), given the potential responsiveness to fine-scale weather conditions. Insect-herbivore abundance (Calixto et al., 2021), pathogen abundance (Lang-Yona et al., 2018) and plant chemical composition (Cook et al., 2016; Riipi et al., 2002) vary seasonally, but the effect of fine-grained weather patterns on plant-enemy interactions is likely underappreciated. Although calls for multi-year sampling of plant-enemy interactions are abundant (Anstett et al., 2016; Virtanen et al., 2020), even finer-scale observations of within-year variation may be required to accurately predict these interactions in future climate contexts. This call to account for finer-temporal scale weather variation is echoed by calls for a greater appreciation of spatial variation in microclimate (Lembrechts et al., 2022), which is likely important to performance and behaviours (e.g. microclimate refugia) of both herbivores and pathogens (e.g. Pincebourde & Casas, 2015; Stewart et al., 2021; Warren & Mordecai, 2010). Future studies could track microclimate within experimental warming treatments to evaluate whether warming alters fine-scale spatial variation in the microclimate or how temporal variation in weather translates into microclimates within plots. The importance of within-season weather patterns is clear when considering plant-enemy effects during different stages of plant ontogeny. For instance, leaf toughness and chemical defences of *Plantago lanceolata* increased while nutritional quality decreased as individuals progressed from juvenile to fruit-setting stages, such that herbivores performed best on juveniles (Quintero & Bowers, 2018). Our study highlights the importance of fine-grained temporal patterns in weather because the effect of experimental warming on herbivory flipped from negative to positive as fine-scale precipitation increased.

5 | CONCLUSIONS

Experimental warming not only increased insect herbivory but the magnitude of the response was dependent on within-season pulses

of precipitation, which was not observed in plant disease. Herbivory increased more with fine-scale rainfall under field-based infrared heating. Given that monsoon season precipitation is expected to decline regionally, our results suggest that herbivory will decline under warming because of the limits imposed by this reduced precipitation (Wang et al., 2021). In contrast to our results for insect herbivory, we found little evidence that pathogen caused disease was affected by warming, but it did increase with precipitation and temperature. Overall, our results support that fine-scale temporal monitoring paired with weather data can enrich understanding of the complexity and environmental dependence of plant–enemy interactions.

AUTHOR CONTRIBUTIONS

Joshua Lynn and Jennifer Rudgers designed the study. John Harte designed the warming experiment. Joshua Lynn, Nisreen Abo-Sido, Ian McCowen and Shermila Villanueva collected the data. Joshua Lynn analysed the data with input from Jennifer Rudgers and John Harte. Joshua Lynn led the writing with input from all authors.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.14050>.

DATA AVAILABILITY STATEMENT

Data for this article have been deposited at the Environmental Data Initiative (EDI) here (Lynn et al., 2022): <https://doi.org/10.6073/pasta/Occ0072a1d9a32b1fcd6f44b65d0a604>

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