# Shrub shading moderates the effects of weather on arthropod activity in arctic tundra

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## Abstract

1. Rapid warming has facilitated an increase in deciduous shrub cover in arctic tundra. Because shrubs create a cooler microclimate during the growing season, shrub cover could modulate the effects of global warming on the phenology and activity of ectotherms, including arthropods. We explored this possibility using two dominant arthropod groups (flies and wolf spiders) in Alaskan tundra.
2. We monitored arthropods with pitfall traps over five summers at four sites that differed in shrub abundance, and used generalized additive models (GAMs) to separate the two underlying components of pitfall trap catch: the seasonal trend in arthropod density and the effects of short-term weather variation (air temperature, wind speed, rain fall, solar radiation) on arthropod activity.
3. We found that shrub cover significantly altered the seasonal trend in the abundance of flies by reducing early-season pitfall catch, in line with observed later snowmelt in shrub-dominated plots at these sites.
4. Additionally, shrub cover modulated the effects of many weather variables on arthropod activity: shrub cover shifted wolf spiders' temperature-activity relationship, dampened the positive effect of solar radiation on the activity of arthropods in total, and ameliorated the negative effect of wind on the activity of flies.
5. Thus, our results indicate that shrub encroachment will likely be accompanied by altered arthropod responses to warming and other key weather variables. Because the rate of key ecological processes—herbivory, decomposition, predation – are controlled by activity at the organismal level, these effects on arthropods will have long-term ecosystem-level consequences.

**Keywords**

Phenology, ectotherms, microhabitat, pitfall trap, climate change

## Introduction

Arctic surface temperatures have increased by 2°C in the last 50 years, more than double the global average rate of warming (IPCC 2014). In tundra plant communities, one consequence of rapid warming has been an increase in deciduous shrub cover (Myers-Smith *et al.* 2011). Relative to open tundra—which typically supports a mix of low-stature plants including mosses, graminoids and dwarf shrubs—shrub tundra experiences less solar radiation and reduced air circulation near the soil surface during the growing season (Myers-Smith *et al.* 2011), which could in some cases reduce ground surface temperatures. By modifying their microenvironment, shrubs could moderate the effects of global warming on temperature-dependent ecological processes like decomposition, a possible negative feedback effect that has generated significant interest in recent years (Myers-Smith *et al.* 2011). By the same reasoning, it seems likely that shrub encroachment could moderate the effects of warming on arctic animals, especially arthropods (insects, spiders and relatives) (Kearney *et al.* 2009). As ectotherms, arthropods rely on their external environment to regulate their body temperature; and they interact with their thermal environment at the level of microhabitats, where the abiotic consequences of shrub cover are most acute (Kearney *et al.* 2009). Arthropods represent a substantial component of tundra biodiversity and play important ecological functions as pollinators, herbivores, decomposers and pests (CAFF 2013). They also serve as food for migratory birds (Wirta *et al.* 2015). Arthropods – and animals in general – have rarely been considered in the context of arctic shrub encroachment, but understanding how they will respond to altered climate and microhabitats could help predict changes to other parts of the arctic food web (Boelman *et al.* 2015; Tape *et al.* 2016).

Unlike ectotherms at lower latitudes, arctic arthropods are generally expected to respond positively to global warming—not with symptoms of physiological stress, but rather with enhanced fitness (Deutsch *et al.* 2008). This prediction derives from the skewed shape of their thermal performance curves: ectotherm performance gradually increases from a critical minimum, peaks at a thermal optimum and declines sharply at a critical maximum temperature (Huey and Kingsolver 1989). For most ectotherms regardless of latitude or species, the thermal optimum hovers around 30-35°C, and the critical maximum internal temperature is even more constrained around 40°C (Kearney *et al.* 2009). In contrast, critical minimum temperatures vary widely across latitude and species owing to an arsenal of cold-tolerance strategies employed by temperate and arctic species (Danks 2004; Deutsch *et al.* 2008). As a result, arctic arthropods generally tolerate a wider range of temperatures than their lower-latitude counterparts. Because arctic summers are relatively mild, arthropods probably experience air temperatures that are lower than their thermal optimum and well below their critical maximum temperatures (Deutsch *et al.* 2008).

A few pieces of empirical evidence support the general prediction that warming will release arctic arthropods from the constraints of cold temperatures. First, capture rates of arthropods in pitfall and window traps are positively correlated with temperature in the Arctic, indicating that arthropods are more constrained by cold temperatures than they are hampered by heat (Høye & Forchhammer 2008; Tulp & Schekkerman 2008; Bolduc *et al.* 2013). Second, experimental warming in tundra ecosystems on the order of 2-4°C increases per-capita insect herbivory rates (Barrio *et al.* 2016), accelerates mosquito development (Culler *et al.* 2015), and amplifies arthropod-mediated decomposition (Sistla *et al.* 2013). Third, decades of global warming at one high arctic site has advanced arctic arthropod phenology (Høye *et al.* 2007), triggering phenological mismatches between insect pollinators and flowers (Høye *et al.* 2013) and between arthropods and their avian predators (Reneerkens *et al.* 2016). Meanwhile, probably because the structure of open tundra vegetation is relatively simple, little attention has been given to the effects of microclimate on modulating arctic arthropod responses to warming (but see Coulson et al. 1993 and Hodkinson et al. 1996 for discussion of these effects on soil invertebrates).

In this study, we explored how global warming will affect the activity and seasonal patterns in abundance of arctic arthropods, both via the direct effects of temperature and the indirect effects of warming mediated by habitat change. We took a correlative approach, evaluating arthropod responses to seasonal development and short-term variation in temperature and weather within habitats that varied in shrub abundance. We applied this approach to total arthropod abundance and to two groups known to be both numerous and ecologically important to Alaskan arctic ecosystems (Huryn & Hobbie 2012; CAFF 2013): flies (Diptera) and wolf spiders (Araneae: Lycosidae).

To measure arthropod abundance, we monitored arthropods over five growing seasons with pitfall traps in shrub- and open-tundra habitats located at four sites in arctic Alaska. Pitfall traps rely on the movement of arthropods for capture, and thus the number of animals in a given trap (trap catch) reflects not only the number of animals per unit area (*density*) but also arthropod movement (*activity*), which determines the likelihood any given animal will fall in a trap (Southwood & Henderson 2009). Our analysis was based on the simplifying assumption that arthropod *density* should be determined mainly by seasonal changes in abundance (i.e., phenology -- emergence, death), while *activity* should be mainly determined by short-term variation in weather conditions (Taylor 1963; Southwood & Henderson 2009). Following the general approach of Høye and Forchhammer (2008), we applied a statistical technique, Generalized Additive Modeling (GAM), to disentangle and investigate the two relationships underlying pitfall trap catch.

Our hypothesis was that shrub shading would modulate the effects of warming on arthropod phenology (H1) and activity (H2). To help guide our analyses, we also made specific predictions informed by similar efforts to model arthropod trapping rates in the Arctic (Høye &

Forchhammer 2008; Tulp & Schekkerman 2008; Bolduc *et al.* 2013). First, we explored the explanatory power of common indices of seasonal development, and predicted that thawing degree-days (TDD)—an integrated measure of temperature during the snow-free period – would be a superior seasonal predictor of arthropod density relative to day of the year (DOY) or snow-free days. Second, we predicted that—after accounting for seasonal trends in density—temperature would have an approximately unimodal positive relationship with arthropod activity, solar radiation would positively affect arthropod activity, and wind speed and rain fall would negatively affect arthropod activity. From our hypotheses, we predicted that shrub shading would delay the seasonal peak in arthropod density, change the shape of arthropods' temperature-activity response curves and dampen the strength of the other weather effects on arthropod activity.

## Methods

### *Sampling design*

Our study region encompassed an area near Toolik Lake Field Station (68° 38' N, 148° 34' W), the site of the Arctic Long-term Ecological Research project (ARC LTER) in the North Slope region of arctic Alaska (Supplementary Figure 1). Within this study region, we chose four sites based on the presence of neighboring shrub-tundra and tussock-tundra habitats; access to the Dalton Highway and Toolik Lake Field Station; and the presence of passerine nesting habitat, a focus of related studies, e.g. Boelman *et al.* (2015). The sites were named for nearby landmarks: Roche Mountone (ROMO), Toolik Lake Field Station (TLFS), Imnavait Creek (IMVT) and the Sagavanirktok River Department of Transportation camp (SDOT). Each site contained two 10,000 m$^2$ plots. The first plot was placed in open tussock tundra, and the second was placed in an area of shrub tundra. The tundra plant community in these sites is described in detail in related studies (Rich *et al.* 2013; Sweet *et al.* 2015), but generally comprised a mixture of mosses, graminoids, forbs, deciduous shrubs and dwarf evergreens.

In each plot, we established two transects for arthropod sampling. We sampled arthropods with 10 pitfall traps spaced 10 m apart along each designated transect (N = 10 traps per transect, 20 traps per plot, 40 traps per site, 160 traps in total). Traps were clear plastic cups (approx. 7.5 cm in diameter and 10 cm deep) filled 2 cm deep with a clear, 1:1 water:ethanol mixture. We left traps in the field for 48 hours, at which point we transferred contents to the laboratory, sieved them of any excess plant material, and placed the remaining specimens in vials of 70% ethanol for storage. We counted arthropods and identified them to coarse taxonomic groups (usually family, see Rich et al. 2013) using published keys (Triplehorn & Johnson 2005), but did not count the soil microarthropods Collembola and Acari. We sampled at approximate weekly intervals during the 2010-2014 growing seasons for a total of 181 sampling events spread across the four sites (see Supplementary Figure 3 for start and end dates in each year). Snow cover, ice, small mammal disturbance and human error reduced the number of pitfall samples to 7072 out of a possible 7240 (40 pitfall samples per sampling event).

### *Measures of plant canopy shading*

We assessed canopy shading at each pitfall trap location once, on a clear, sunny day during peak greenness in 2014 with a SunScan SS1 (Delta-T Devices Ltd, U.K). This instrument detects incoming photosynthetically active radiation (PAR) at 64 diodes equally spaced along a narrow 1-meter long surface. Centering the wand over each pitfall trap, we measured incoming PAR twice at the ground surface in a perpendicular fashion to capture a cross-section of the habitat surrounding the trap. We then immediately measured incoming PAR once above the plant canopy. For each measure, we averaged the PAR detected by the 64 diodes, then calculated the amount of shading at each trap as:

$$[PAR_{above} - mean(PAR_{below})] / PAR_{above}$$

### *Meteorological data collection and processing*

We monitored meteorological conditions at each of the four sites with sensors placed 3 m above ground level except at the Toolik Field Station site, where sensors were placed 5 m above ground level. Environmental data for Toolik were downloaded from the Toolik Field Station Environmental Data Center (Environmental Data Center Team 2016). Data for Imnavait were downloaded from the Imnavait Arctic Observatory Network (AON) Tussock Site (Euskirchen *et al.* 2012). Air temperature was monitored with a capacitive ceramic THERMOCAP® sensor (Campbell Scientific, UT, USA) at Roche Mountonee and the Sagavanirktok River DOT, a HP45C-L temperature probe (Cambell Scientific, UT, USA) at Imnavaiat, and a HUMICAP® relative humidity and temperature probe (Vaisala, Helsinki, Finland) at Toolik. Wind speed was monitored with an RM Young potentiometer at Toolik, a 3-cup anemometer at Imnavait (Campbell Scientific, UT, USA), and a WINDCAP® sensor (Vaisala, Helsinki, Finland) at Roche Mountonee and the Sagavanirktok River DOT. Precipitation was monitored with a Pluvio N Rain Gauge (OTT) at Toolik, a TE525 rain gauge (Cambell Scientific, UT, USA) at Imnavait, and a RAINCAP® sensor (Vaisala, Helsinki, Finland) at Roche Mountonee and the Sagavanirktok River DOT.

Incoming short-wave (solar) radiation was monitored at Toolik using a CNR-4 pyranometer (Kipp & Zonen, Delft, The Netherlands). Solar radiation at the other three sites was monitored less consistently than at Toolik (Supplementary Figure 2). Using available data, we checked that solar radiation at the temporal scale used in this study (48-hour averages) was similar across sites, and found strong correlation among sites' measures ($R^2 > 0.95$, Supplementary Figure 2). Thus, for simplicity and best coverage, we used the Toolik solar radiation values for all sites in this study.

We trimmed the meteorological dataset to span the earliest and latest pitfall trap collection dates: Julian day 135 (14-15 May) to Julian day 225 (12-13 August). Due to occasional sensor malfunction, 16% (6913 observations) of all hourly observations in the meteorological dataset were missing one or more measures. Within pitfall sampling windows, 2% (833) of hourly observations were missing. To maximize our dataset for modeling data and generating predictions, we filled these gaps with a two-step process. First, for gaps of 12 hours or less (200 missing observations), we interpolated values in a linear fashion with function *na.approx* in R (R Core Team 2017) package *zoo* (Zeileis & Grothendieck 2005). For the remaining gaps of more than 12 hours, we filled in each site's missing values with those of other sites in order of their geographic proximity.

To match our meteorological variables to arthropod data, we calculated total rainfall, average temperature and average wind speed for the 48-hour window during which the traps were active. We also calculated cumulative thawing degree days (TDD): the cumulative sum of the daily mean temperatures above zero for all dates after snow melt up to the collection date. Snow melt was defined as the first day of the year when the landscape was 50% snow free as assessed by image analysis of landscape photographs (Krause *et al.* 2016). In 2010, our cameras were not installed at Roche Mountonee or the Sagavanirktok River DOT; in these cases, we set the 50% snow free date to the mean value of the other years for that site (2011-2014). In another special case, cameras were installed at the Sagavanirktok River DOT too late to detect snowmelt in 2014. In this case, we set the snow free date to May 5, 7 days prior to camera installment date (7 days was the average number of days between 50% and 100% snow free at the Sagavanirktok River DOT in 2011-2013).

*Statistical analysis*

To evaluate the respective linear effects of weather on arthropod activity and nonlinear effects of seasonality on arthropod density, we fitted generalized additive mixed models (GAMMs) with package *mgcv* (Wood 2011; Wood *et al.* 2016) in R. Our dependent variable was the raw (untransformed) number of arthropods in each pitfall trap; these models assumed a negative binomial distribution with a log-link function, which is appropriate for low-mean count data (O'Hara & Kotze 2010). To account for the hierarchical structure of the data, models included a nested random effect term (traps nested within plots and sites). All models included a fixed effect for plot type (shrub or open). To estimate the dispersion parameter *theta* for the negative binomial distributions, we fit generalized additive models without random effects (GAMs) in *mgcv*.

First, we evaluated the relative explanatory power of different indices of seasonal development with a set of six candidate GAMMs for each arthropod group (flies and wolf spiders) and for arthropod abundance in total. The first three candidate models for each group modeled the seasonal component of pitfall trap catch as a smooth function of one of three candidate indices of seasonality: cumulative thawing degree-days (TDD), days since 50% snow-free (SNO), and day of the year (DOY). All three indices were measured at the site-level, where we expected phenological processes (arthropod emergence, death) that determine density would occur. To facilitate comparison across models, we ensured that each model was allowed the same amount of "wiggliness" (*sensu* Wood 2006) by setting the smoothing parameter for TDD and SNO models to that of the DOY model, and additionally constrained the basis dimension (*k*) to 5 (half the maximum number of weeks for arthropod sampling) for all models. For the next three GAMMs, we evaluated the effects of shrub cover on arthropod phenology (seasonal trends in density). We fit the same three candidate models as described above, this time allowing the smooth term to vary according to plot type (shrub or open). To determine which seasonal index provided the best fit, and whether the addition of plot type significantly improved model fit, we compared the AIC (Akaike Information Criterion) values for each of the six candidate GAMMs (TDD, SNO, DOY, TDD x Plot, SNO x Plot, and DOY x Plot).

Finally, to evaluate the combined effects of weather and seasonality on arthropod abundance, we fitted separate GAMMs of wolf spider, fly and total trap catch. As in the seasonality-only models (see above), all models included a nested random effect term (traps nested within plots and sites) and assumed a negative binomial error distribution. In the models, the abundances of the arthropod groups were explained with a seasonal smooth term, plot type (shrub or open), parametric effects of weather variables, and the interaction between the weather variables and canopy shading at each trap. Out of the six potential seasonal smooth terms we chose the one with best model fit (lowest AIC) separately for each of the taxonomic groups (see above). The weather variables we included were air temperature, solar radiation, rainfall and wind speed. All four weather variables as well as canopy shading were zero-mean centered and scaled prior to analysis. To approximate the expected nonlinear relationship between temperature and arthropod activity (Huey & Kingsolver 1989), we modeled temperature as a second-order polynomial. For all models, we present the proportion of null deviance explained, a goodness-of-fit measure appropriate for models with non-normal errors (Wood 2016). Because explained deviance values are not available for GAMMs fit with a negative binomial error distribution, we present the explained deviance from the identical GAMs fit without random effects.

## Results

### *Descriptive results*

We captured a grand total of 53,025 arthropods from the four sites over the course of the five years of pitfall trap sampling. An average of 7 individuals were in each sample. One-third (33%; 17,415 individuals) of the individuals caught were flies, while 29% (15,131 individuals) were wolf spiders. Other common groups included ground beetles (Coleoptera: Carabidae), parasitoid wasps (Hymenoptera: Parasitica), and rove beetles (Coleoptera: Staphylinidae) (data not shown, but see Rich et al. 2013 for a general description of the community). Weather conditions and pitfall trap catch varied across sites and years (Supplementary Figures 3, 4). Peak temperature occurred between 11 June and 10 July, depending on the site and year (DOY 162-191; mean DOY 178±2 days). Peak solar radiation occurred between 20 May and 14 June, depending on the year (DOY 140-165; mean DOY 159±6 days). Within 48-hour sampling events, mean temperatures were between -1 and 22°C (mean: 10±0.3°C), and 48-hour solar radiation means were between 106 – 361 W·m$^{-2}$ (mean: 222 ±11 W·m$^{-2}$), indicating that we sampled during a wide range of weather conditions. In addition, we sampled across a wide range of canopy shading (Supplementary Figure 1). Open plots were less shaded than shrub plots (means 19% and 48%; ranges 0-57% and 3-98%; respectively; Supplementary Figure 1).

### *Seasonal trends in arthropod in shrub and open habitats*

The best (most parsimonious) predictor of seasonal trends of pitfall trap catch differed according to taxa (Table 1). For arthropods in total, days after snowmelt was the best predictor, with the lowest AIC. The GAMM of total arthropod trap catch with plot as a factor and days after snowmelt as the seasonal smooth term predicted two peaks in trap catch, the first around 25 days after snowmelt, and the second late in the season (Figure 1A). For wolf spiders, day of the year was the most parsimonious predictor (Table 1); the GAMM of wolf spider trap catch with plot as a factor and day of the year as the seasonal smooth term predicted a single peak in wolf spider abundance at day 163, or June 11-12 (Figure 1C). Modeling the seasonal trend in total arthropod and wolf spider trap catch separately for each plot type did not improve the AIC in either case (Table 1). Meanwhile, the most parsimonious model for trap catch of flies was the one that incorporated not only plot as a factor, but also separate smooth terms for day of the year for each plot type, indicating that habitat type (shrub or open) affected the seasonal trend in trap catch of flies. The GAMM of fly abundance that incorporated a smooth term for each plot type predicted that trap catch would be greater in open plots compared to shrub plots early in the season, but that shrub plots would harbor more flies late in the season after day 169, or June 17-18 (Figure 1B).

### *Weather effects on arthropod activity across levels of shrub shading*

In the GAMMs that incorporated a seasonal trend smooth term and all linear effects, Temperature$^2$ was always a significant predictor of arthropod trap catch, either alone or via an interaction with canopy shading (Table 2, Figure 1D-F). In all three models, estimates for temperature$^2$ were negative and estimates for temperature$^1$ were positive (Table 2), indicating concave-downward shapes of the temperature-trap catch response curves (Figure 1D-F). In the case of total arthropod trap catch, the model estimated positive effects of temperature on abundance along the range of temperatures we observed (-1.4°C to 20.9°C, Figure 1D), and predicted negative effects of temperature on total trap catch only past 28°C, beyond the temperatures measured here (Table 2, Figure 1D). For fly abundance, the predicted optimum temperature was 12.7°C; beyond this temperature, flies responded negatively to increased temperatures (Figure 1E).

In addition, models of wolf spider catch had a significant, positive interaction between canopy shading and temperature$^2$ (Table 2), indicating that shape (concavity) of the temperature-abundance relationship differed across levels of shrub shading (Figure 1F). In less shaded canopies (77% shaded or less, Table 2), the temperature-wolf spider trap catch response was concave-down (i.e., estimates of temperature$^2$ were negative), with a predicted optimum of 20°C in completely unshaded canopies. In moderately shaded canopies, the predicted thermal optimum exceeded observed temperatures (Figure 1F), and the temperature-trap catch response relationship switched to concave-up (Figure 1F).

Solar radiation had a positive effect on the trap catch of wolf spiders and flies (Table 2, Figure 1H and 1I), and interacted with canopy shading to affect total trap catch. Solar radiation had a positive effect on total trap catch in open and moderately shaded canopies (less than 75% shaded), but a negative effect on total trap catch in densely shaded canopies (Table 2, Figure 1G). Wind speed had no effect on wolf spider catch, but interacted with canopy shading to affect total trap catch and fly catch (Table 2, Figure 1J-K). Wind speed had a slightly negative effect on fly catch and total trap catch in open canopies (less than 60% and 34% shaded, respectively), but a positive effect on trap catch in more densely shaded canopies (Figure 1J-K).

Rainfall decreased total trap catch (Table 2, Figure 1L), but had no effect on trap catch of flies or wolf spiders.

The addition of weather variables improved the ability to model within-season variability in trap catch (Figure 2), improving AIC values over the seasonality-only models in all three cases (∆AIC = 1046, 554, and 82 for total, wolf spider and fly catch, respectively). In addition, incorporating weather variables improved model fit, increasing explained deviance over seasonality-only models in all three cases (4.7% vs. 22.4% for total trap catch; 18.1 vs. 33.8% for wolf spider catch; 14.3 vs. 21.2% for fly catch; Table 1, Table 2).

## Discussion

### *Seasonality of flies, but not arthropods in total, differs across shrub and open habitats*

We found partial support for our hypothesis that shrub cover would alter the seasonality of arthropod abundance: our models predicted that fly abundances were lower in shrub habitats compared to open habitats early in the season. This result is consistent with research showing that canopy-dwelling insect biomass at our study sites (the majority of which is comprised of flies) is strongly related to within-season changes in plant greenness (NDVI), and that open plots tend to be greener than shrub plots early in the growing season (Sweet *et al.* 2014). However, we found no such effects on wolf spiders or on arthropods in total, indicating that the effects of shrub cover on arthropod seasonality differ among arthropod taxa, perhaps owing to differences in the seasonality of their resources (plants, nectar and fungi for flies; or soil invertebrates for spiders).

As part of our exploration of arthropod seasonality, we predicted that cumulative TDD would be a superior predictor of arthropod abundance relative to the number of snow-free days or the day of the year. Instead, we found that days after snowmelt was a more parsimonious explanatory variable for the seasonal trend in total trap catch, and that day of the year was a more parsimonious explanatory variable for the seasonal trend of wolf spider and fly catch. This was somewhat surprising, given that it is generally expected that in warmer conditions, arthropods develop faster, emerge earlier and complete their life cycle sooner. These results suggest that, at least under the conditions we observed in our five-year study, arctic arthropods may be somewhat constrained by the short duration of the arctic growing season. These highly mobile taxa may employ strategies like behavioral thermoregulation to compensate for colder growing season temperatures in order to complete their development between spring snowmelt and the end of the season.

### *Shrub shading and weather interact to affect arthropod activity*

Consistent with our predictions, warmer temperatures and more intense solar radiation generally increased arthropod trap catch, while wind and rainfall often had a negative effect. Additionally, we found some evidence to support our second hypothesis, that shrub cover would modulate the effects of weather on arthropod activity. Our findings from models of total trap catch indicate that solar radiation has a stronger, more positive effect on trap catch under open canopies than under closed canopies. This is consistent with the fact that the densest canopies in our study intercepted up to 98% of incoming PAR. Similarly, at high wind speeds, trap catch of flies and arthropods in total was greater in shade than in open plots. This makes sense given that greater shrub structure should dampen wind velocities.

The effects of shrub shading on temperature- trap catch relationship for wolf spiders were complicated by the quadratic form of temperature effects. For example, our model predicted greater wolf spider catch in open habitats relative to shaded habitats only at low to moderate air temperatures; at high temperatures, the opposite was true. This interaction between shading and temperature likely results from the effects of shading and shrub structure on the microenvironment. In arctic tundra, shrubs lessen the compounding effects of solar radiation on near-surface temperatures. This cooling effect could restrict wolf spider activity at low temperatures, and release wolf spiders from the risks of desiccation and heat stress at high temperatures.

In addition to per capita arthropod activity rates, microhabitat selection may underlie some of the patterns we observed. Specifically, arthropods may move into sheltered (shrub) environments during unfavorable weather (and vice versa). For example, in the case of flies, the strongly positive response of flies to greater wind speed in shrub environments may have resulted from movement of arthropods from open canopies to shrub canopies on windy days. In contrast, the slightly negative effect of solar radiation on total trap abundance in shrub canopies could have resulted from the movement of arthropods from dense canopies to open canopies to engage in basking. Regardless of whether movement among habitats or movement within habitats was the underlying mechanism, our results illustrate that daily weather interacts with microhabitat to determine environmental suitability for arthropods.

### *Thermal optima of arthropod activity exceed typical temperatures in Arctic tundra*

Ectotherm performance (activity, efficiency, metabolism) has an approximately unimodal relationship with temperature (Huey & Kingsolver 1989). Our analysis found significant effects of the polynomial term temperature$^2$ on arthropod trapping rates, confirming that such temperature-activity relationships underlie arthropod movement in natural environments. Using our model, we estimated “optimal” temperatures at which arthropod trapping rates reached their predicted maxima. In the case of wolf spiders and arthropods in total, the thermal optima were near or greater than the maximum air temperature observed in this study, suggesting that these arthropods may be able to tolerate a substantial amount of warming. Flies, on the other hand, had a temperature optimum at 13°C, suggesting that the effects of warming are more likely to be negative for this group. Flies are the most important insect pollinators in the Arctic (Høye *et al.* 2013; Tiusanen *et al.* 2016). Empirical evidence already points to the disruptive effects of warming for the phenological matches between pollinating flies and plants; our results suggest that these effects on seasonality could be compounded by short-term effects of heat stress on activity.

*Conclusion*

In sum, our findings show that warming will affect both arthropod activity—movement within and among habitats—and seasonality, but that the exact nature of these effects will depend on traits of the various arthropod groups and species. Previous studies have documented differences in arctic arthropod community structure across gradients of shrub abundance, suggesting that climate change-induced shrub expansion will alter arthropod communities (Rich *et al.* 2013; Hansen *et al.* 2016). This study builds upon such findings by showing that changes to arthropod community structure will likely be accompanied by altered arthropod activity rates, because shrub cover buffers the stressful effects of high temperatures and negates the dampening effects of wind speed on arthropod activity. Because the rates of ecological processes are ultimately controlled by activity at the organismal level, these effects could have long-term ecosystem-level consequences on processes like herbivory, decomposition, predation and pollination.

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## Short Legends for Supporting Information Files

Supplementary Figure 1. Locations of the four field sites used in this study.

Supplementary Figure 2. Correlation plots for sites' two-day average solar radiation values.

Supplementary Figure 3. Average daily weather conditions in each site and year.

Supplementary Figure 4. Observed pitfall abundances by group, site, plot, and year.

Supplementary Figure 5. Boxplot of canopy shading values by site and plot.

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**Figure Captions**

Figure 1. GAMM-predicted responses of arthropod trap catch for each significant model term. Where statistical interactions between canopy shading and weather were significant, predictions for temperature and wind speed were made over a range of values of canopy shading shown by different line colors; otherwise, predictions were made with all other covariates set to their means. Shaded areas are ±SE of predictions.

Figure 2. Observed and GAMM-predicted arthropod abundance. Points represent observed abundances averaged across traps, sites, and years; the size of each point corresponds to the number of pitfall samples collected on the indicated date (flies and spiders). GAMM-predicted values and standard errors of arthropod trap catch are shown as lines and shaded areas, respectively. Predictions were made for the average weather and shading conditions across years and sites. For flies and wolf spiders, observed and predicted values are separated by plot type (open and shrub) owing to a significant difference in seasonal trends across plot types (flies) and a significant main effect of plot type on abundance (flies and wolf spiders).

Table 1. AIC values of GAMMs of arthropod abundance fit with random effects, a fixed effect for plot type (shrub or open), and a smooth term for one of three indices of seasonal development: cumulative thawing degree-days (TDD), number of snow-free days (SNO), or day of the year (DOY), with and without separate smooths for each plot type (shrub or open). Lowest AIC values for each group are indicated with bold type. Explained deviance values, a measure of model fit, are from identical GAMs fit without random effects.

| Group | Predictor | AIC | Explained Deviance (%) |
|---|---|---|---|
| Total | DOY | 18956 | 6.2 |
| | **SNO** | **18849** | **4.7** |
| | TDD | 18859 | 8.7 |
| | DOYxPlot | 19091 | 6.9 |
| | SNOxPlot | 18994 | 5.9 |
| | TDDxPlot | 19016 | 9.6 |
| Wolf Spiders | **DOY** | **23710** | **18.1** |
| | SNO | 23807 | 4.5 |
| | TDD | 23740 | 21.2 |
| | DOYxPlot | 23736 | 18.2 |
| | SNOxPlot | 23773 | 4.9 |
| | TDDxPlot | 23755 | 21.3 |
| Flies | DOY | 24389 | 11.4 |
| | SNO | 24794 | 10.3 |
| | TDD | 25206 | 13.3 |
| | **DOYxPlot** | **23797** | **14.3** |
| | SNOxPlot | 24389 | 12.5 |
| | TDDxPlot | 24240 | 17.0 |

Table 2. Summaries of GAMMs of arthropod abundance fit with a smooth term for seasonality (SNO: days after snowmelt; TDD: cumulative thawing degree-days; DOY: day of the year) and all linear effects for weather, shrub shading and their interactions. Significant terms ($P<0.05$) are indicated with bold type. Explained deviance values are from identical GAMs fit without random effects.

| Total | | | | | Wolf Spiders | | | | | Flies | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Linear terms* | Est | SE | t | P | *Linear terms* | Est | SE | t | P | *Linear terms* | Est | SE | t | P |
| **Intercept** | 0.89 | 0.08 | 22.5 | <0.001 | **Intercept** | 0.61 | 0.12 | 5.2 | <0.001 | **Intercept** | 0.69 | 0.12 | 5.7 | <0.001 |
| **Temp** | 0.36 | 0.01 | 30.8 | <0.001 | **Temp** | 0.39 | 0.02 | 21.3 | <0.001 | **Temp** | 0.13 | 0.02 | 6.5 | <0.001 |
| **Temp$^2$** | -0.04 | 0.01 | -5.1 | <0.001 | **Temp$^2$** | -0.05 | 0.01 | -4.9 | <0.001 | **Temp$^2$** | -0.11 | 0.01 | -8.4 | <0.001 |
| Shade | 0.03 | 0.03 | 1.1 | 0.261 | **Shade** | -0.08 | 0.04 | -2.0 | 0.044 | **Shade** | 0.13 | 0.03 | 3.7 | <0.001 |
| **Solar** | 0.09 | 0.01 | 6.8 | <0.001 | **Solar** | 0.30 | 0.02 | 14.1 | <0.001 | **Solar** | 0.07 | 0.02 | 3.0 | 0.002 |
| Wind | -0.01 | 0.01 | -0.8 | 0.452 | Wind | 0.01 | 0.02 | 0.5 | 0.636 | Wind | 0.00 | 0.02 | -0.1 | 0.945 |
| **Rain** | -0.03 | 0.01 | -2.5 | 0.013 | Rain | 0.02 | 0.02 | 0.8 | 0.399 | Rain | -0.03 | 0.02 | -1.7 | 0.085 |
| Plot (Shrub) | 0.07 | 0.08 | 0.9 | 0.366 | **Plot (Shrub)** | -0.33 | 0.09 | -3.7 | <0.001 | **Plot (Shrub)** | 0.33 | 0.11 | 2.9 | 0.004 |
| Temp*Shade | 0.01 | 0.01 | 0.8 | 0.415 | Temp*Shade | -0.02 | 0.02 | -1.1 | 0.275 | Temp*Shade | 0.02 | 0.02 | 1.1 | 0.283 |
| Temp$^2$*Shade | 0 | 0.01 | 0.3 | 0.743 | **Temp$^2$*Shade** | 0.03 | 0.01 | 2.4 | 0.017 | Temp$^2$*Shade | 0.00 | 0.01 | 0.0 | 0.998 |
| **Solar*Shade** | -0.06 | 0.01 | -5 | <0.001 | Solar*Shade | -0.01 | 0.02 | -0.5 | 0.589 | Solar*Shade | -0.01 | 0.02 | -0.5 | 0.616 |
| **Wind*Shade** | 0.04 | 0.01 | 3.9 | <0.001 | Wind*Shade | -0.01 | 0.02 | -0.7 | 0.498 | **Wind*Shade** | 0.08 | 0.02 | 4.8 | <0.001 |
| Rain*Shade | -0.02 | 0.01 | -1.6 | 0.111 | Rain*Shade | -0.02 | 0.02 | -0.9 | 0.361 | Rain*Shade | -0.04 | 0.02 | -1.8 | 0.066 |
| *Smooth Terms* | EDF | RefDF | F | P | *Smooth Terms* | EDF | RefDF | F | P | *Smooth Terms* | EDF | RefDF | F | P |
| **s(SNO)** | 3.9 | 3.9 | 15.0 | **<0.001** | **s(DOY)** | **4.0** | **4.0** | **265.7** | **<0.001** | **s(DOY, open)** | **4.0** | **4.0** | **50.6** | **<0.001** |
| | | | | | | | | | | **s(DOY, shrub)** | **3.9** | **3.9** | **144.3** | **<0.001** |
| | | | *AIC* | 17803 | | | | *AIC* | 23156 | | | | *AIC* | 23715 |
| | | | *Explained Deviance (%)* | 22.4 | | | | *Explained Deviance (%)* | 33.8 | | | | *Explained Deviance (%)* | 21.2 |

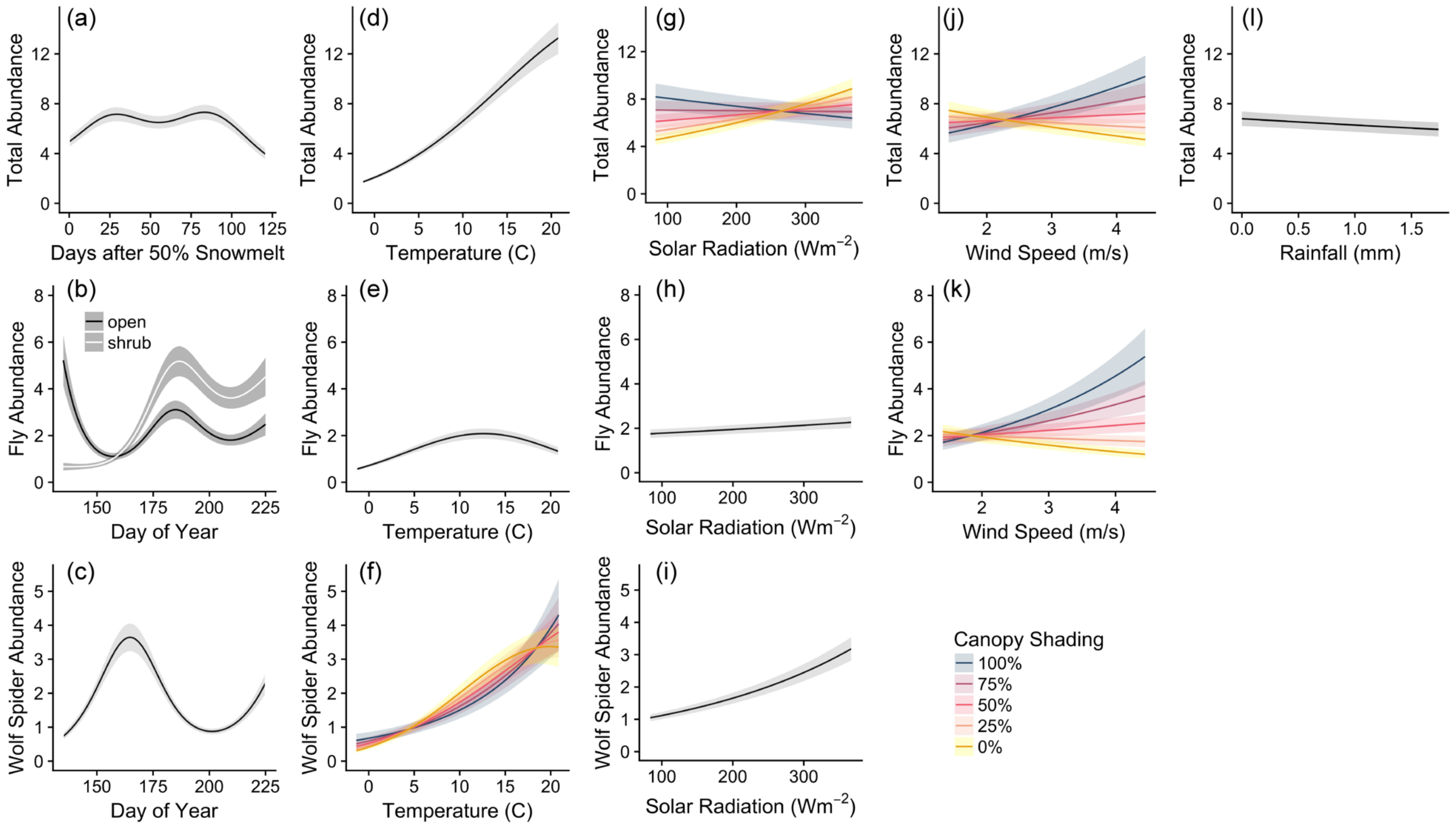

(a)
Total Abundance
Days after 50% Snowmelt
0
25
50
75
100
125
(b)
open
shrub
Fly Abundance
Day of Year
(c)
Wolf Spider Abundance
Day of Year
150
175
200
225
(d)
(e)
(f)
Temperature (C)
0
5
10
15
20
(g)
(h)
(i)
Solar Radiation ($Wm^{-2}$)
100
200
300
(j)
(k)
Wind Speed (m/s)
2
3
4
(l)
Rainfall (mm)
0.0
0.5
1.0
1.5
Canopy Shading
100%
75%
50%
25%
0%

Figure 1

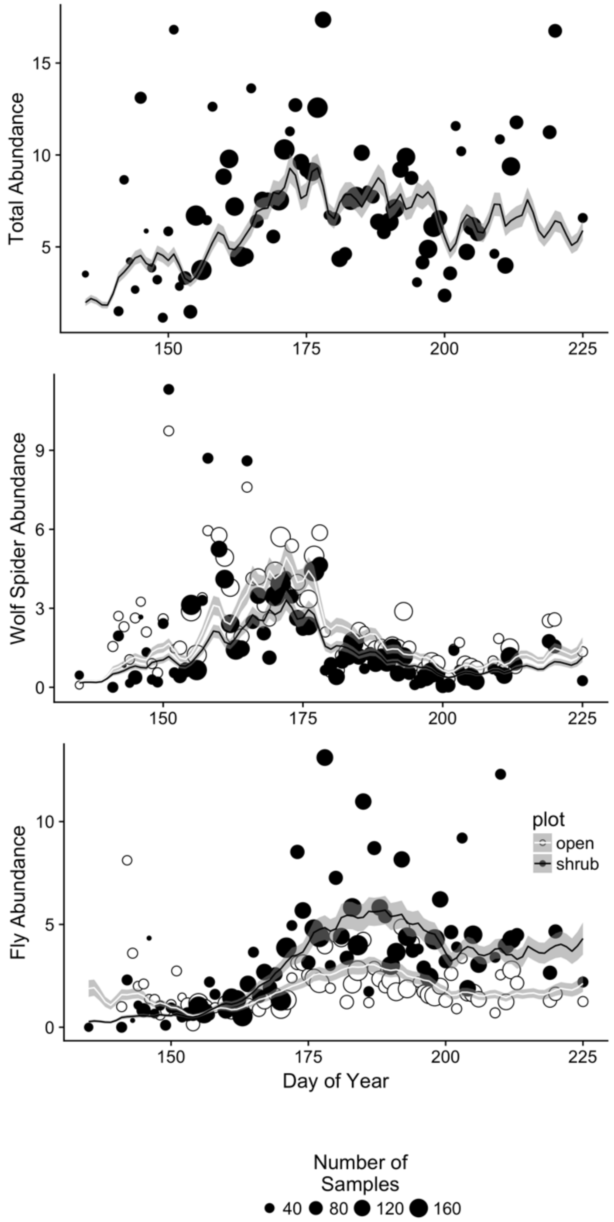
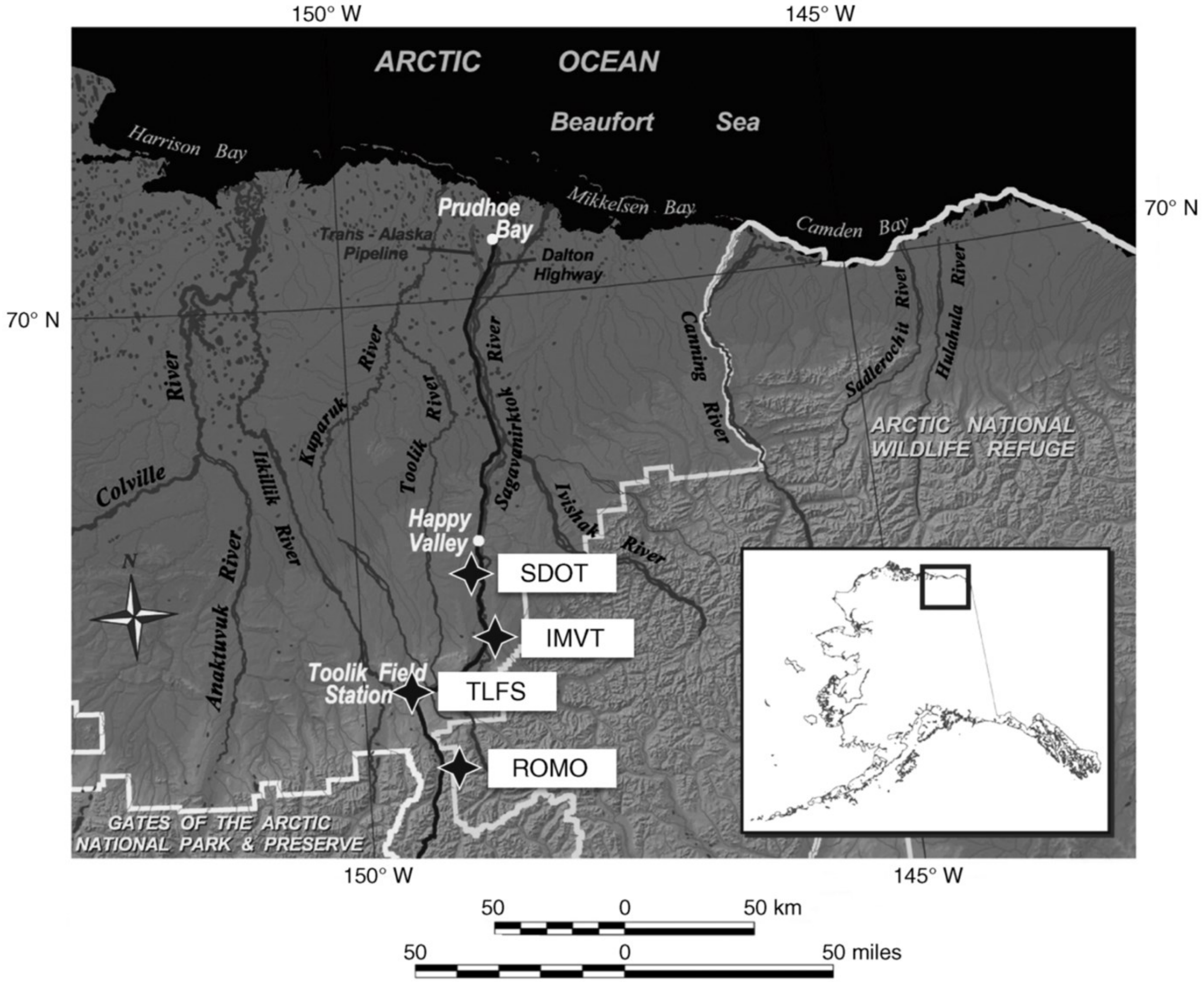
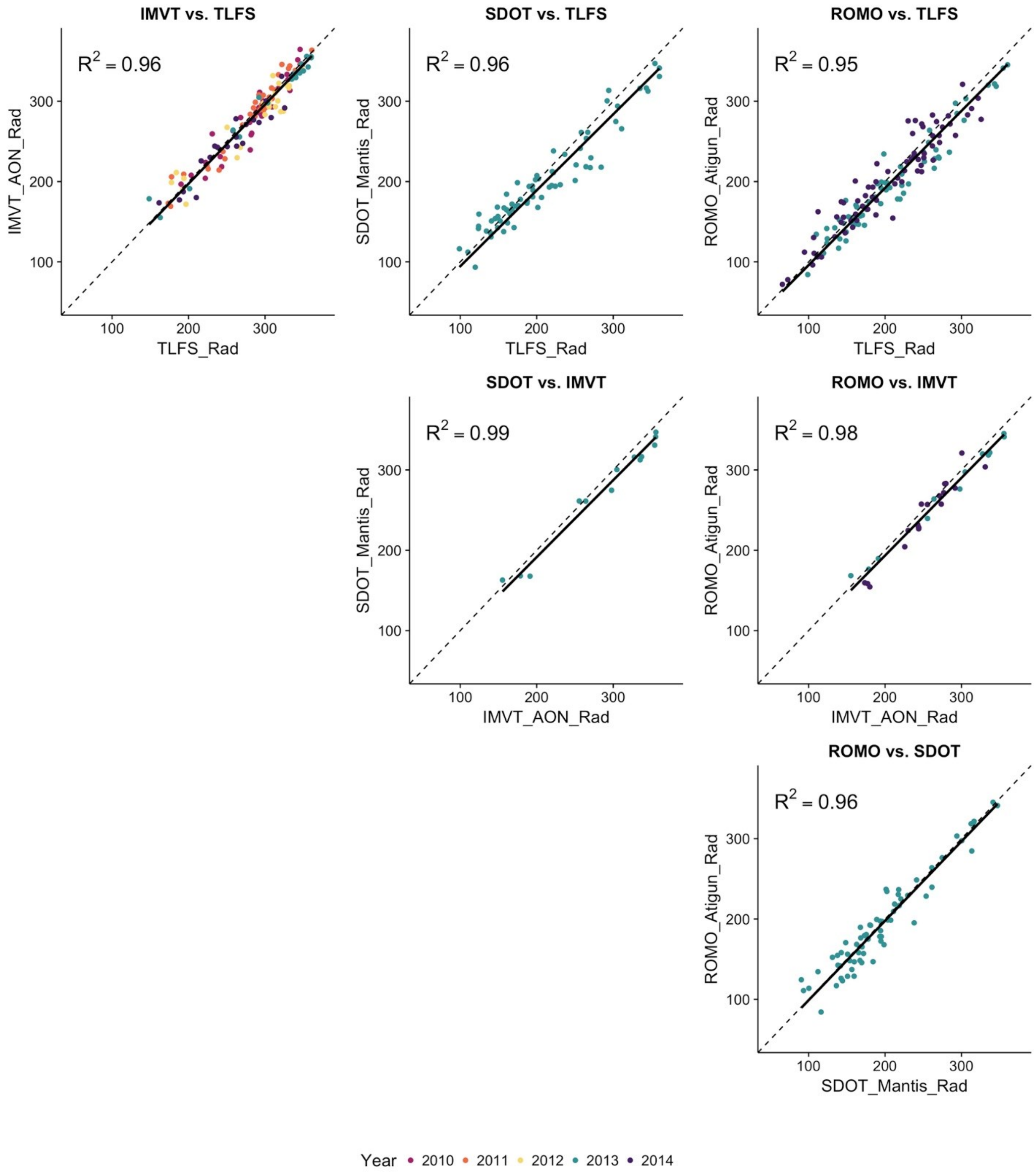

Total Abundance
15
10
5
150
175
200
225
Wolf Spider Abundance
9
6
3
0
150
175
200
225
Fly Abundance
10
5
0
150
175
200
225
Day of Year
plot
open
shrub
Number of Samples
40
80
120
160

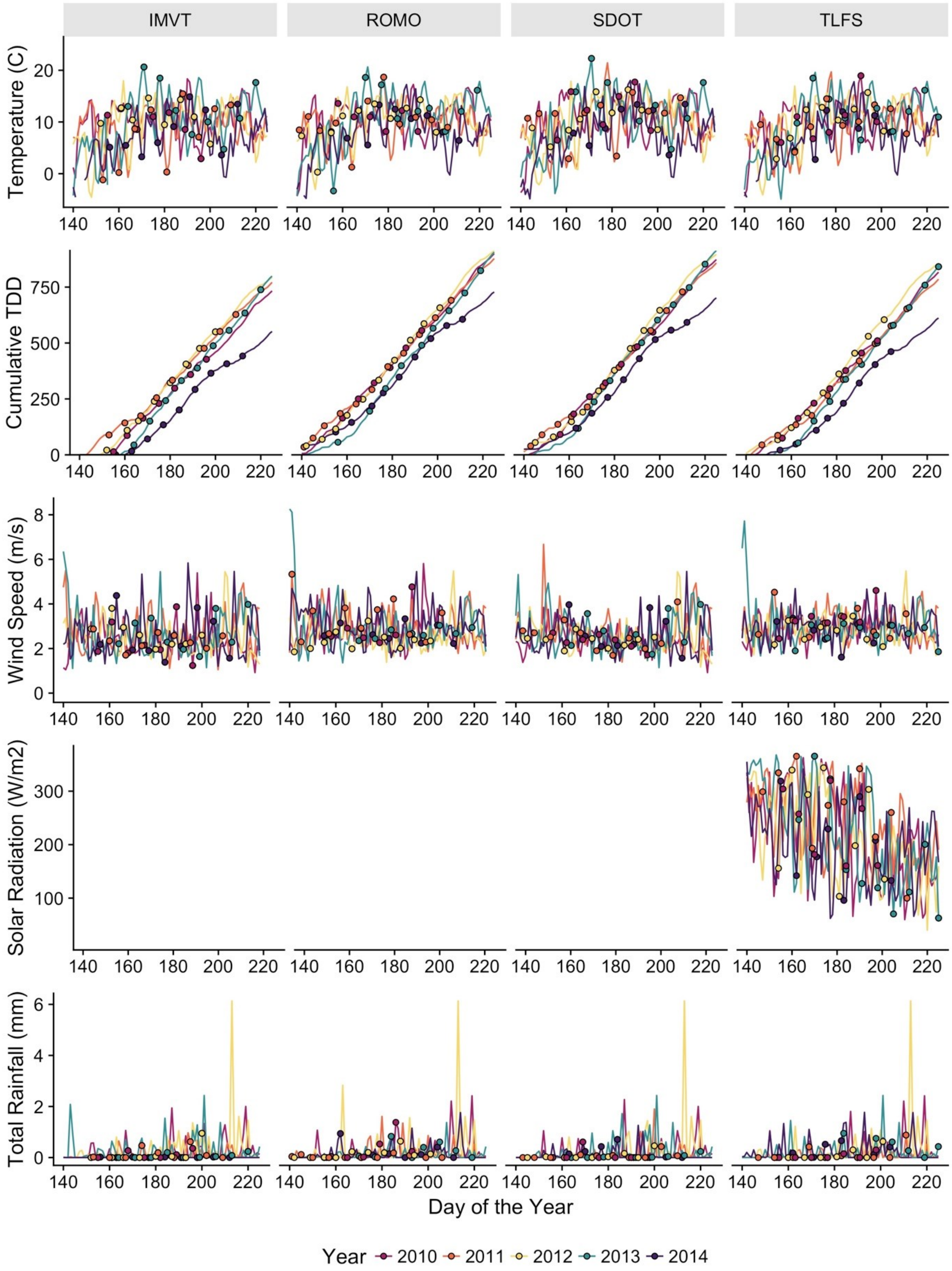
Figure 2



Supplementary Figure 1. Locations of the four field sites used in this study: ROMO (Roche Mountonee), TLFS (Toolik Lake Field Station), IMVT (Imnavait Creek) and SDOT (Sagavanirktok River–Department of Transportation camp).

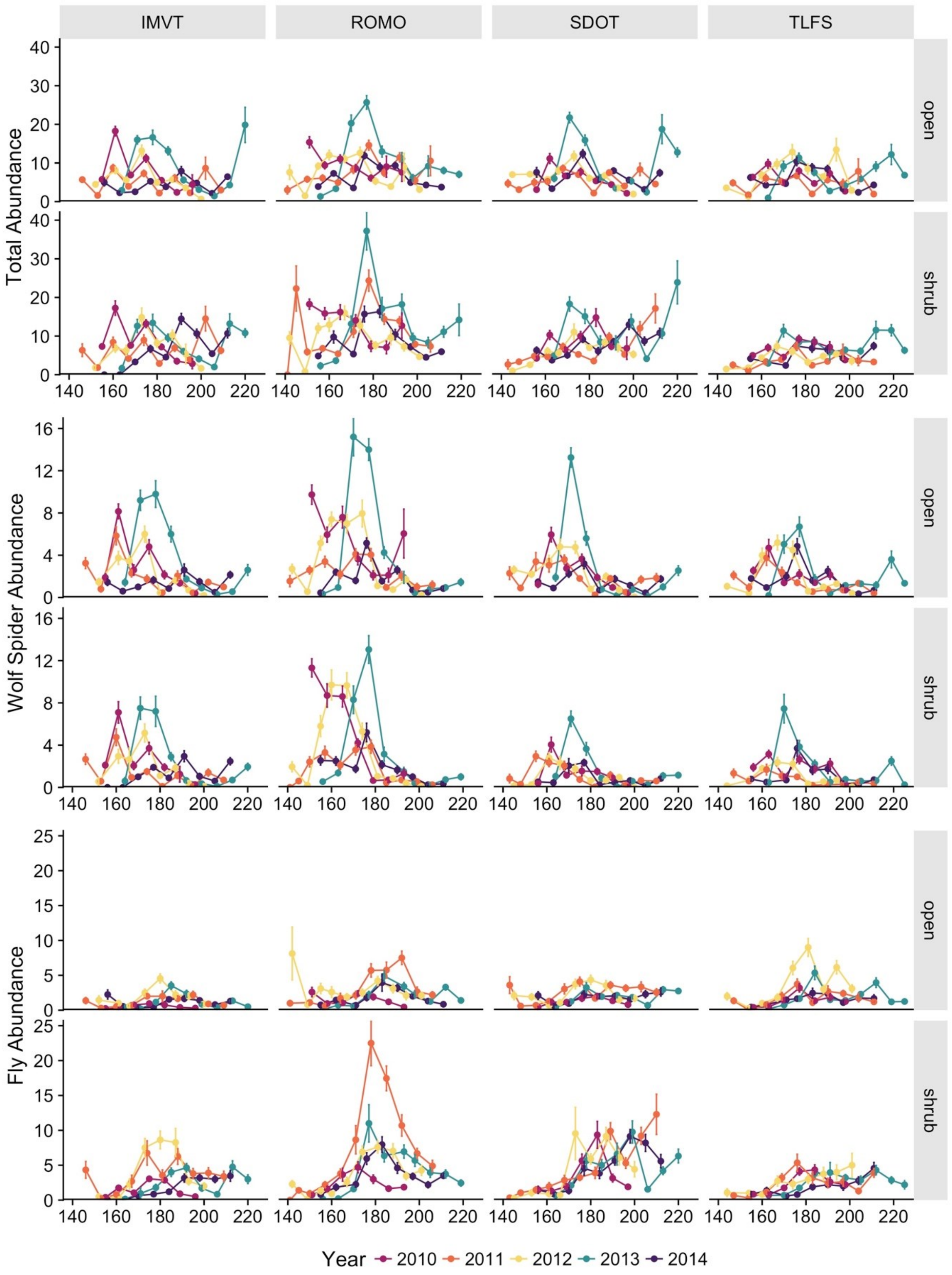


Supplementary Figure 2. Correlation plots for sites' two-day average solar radiation values. These data were trimmed to dates encompassing the range of arthropod sampling (Julian dates 135 – 225). $R^2$ values are Pearson's correlation coefficients. Dotted lines represent 1:1 relationships. Solid lines represent the linear fits of the data, made with a 0-intercept. Data for ROMO were made available by C. Williams (unpubl. data).

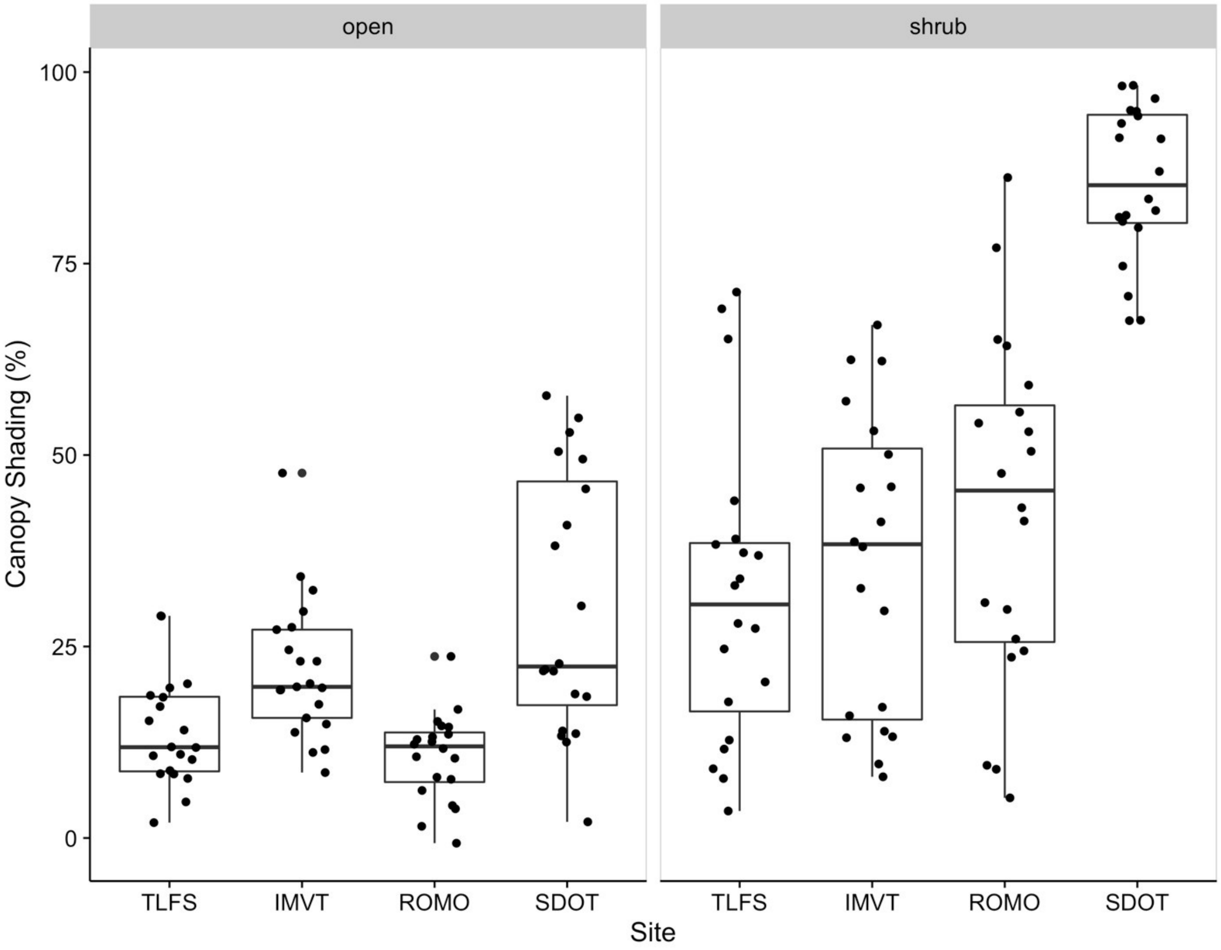


645

646 Supplementary Figure 3. Average daily weather conditions in each site and year. Points are
647 pitfall collection dates. Snowmelt dates occur where TDD first becomes >0.



Supplementary Figure 4. Observed pitfall abundances by group, site, plot, and year. Error bars are ±SE of 20 traps.



Supplementary Figure 5. Boxplot of canopy shading values by site and plot. Observed raw values are represented as points.