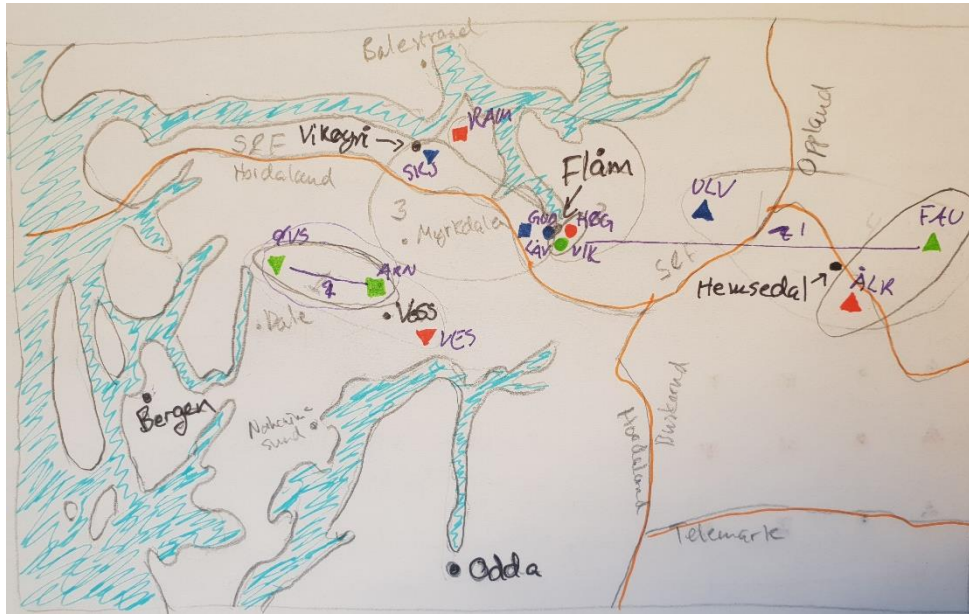# A climate for seed predation: Precipitation affects seed removal by the major groups of granivores differently across boreal, sub-alpine and alpine grasslands

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Acknowledgements

Abstract

Granivory, the seed predation by animals, plays an important role for plant and animal populations, and impact species composition and functioning of ecosystems. The intensity in granivory depends on various biotic and abiotic factors, including animal groups, seed type, vegetation structure and environmental conditions. We expect a warmer and more wet climate in the future, affecting both vegetation structure and productivity, but also animal abundance and activity. These changes are likely to affect animal-plant interactions, such as seed predation. Mountain calcareous grassland habitats are hotspots for alpine biodiversity, but also especially vulnerable to climate change. Therefore, understanding these underlying factors affecting plant species composition and selection pressure in alpine areas is critically important.

To better understand underlying processes driving seed predation, a multi-species assessment was conducted to investigate how granivory rates by different animal groups (insects, rodents and birds) responded to both direct and indirect effects of temperature and precipitation. An exclusion method was used to quantify predation rates for the three granivorous animal groups separately, across three bioclimatic zones (boreal, sub-alpine and alpine) and along a precipitation gradient (spanning from 600-2700mm annual precipitation).

In this system, we found that insects are the most active predators on boreal and sub-alpine zones (36% and 21% of available seeds predated, respectively), but their impact varies across sites and decrease with increasing precipitation. Birds are the dominant seed predator in the alpine zone with 49% of available seeds predated, which increased with precipitation. This trend is reversed in boreal and sub-alpine sites, reflecting an interaction between temperature zones and precipitation levels in governing bird seed predation. These interactions imply that responses to temperature must be put in context of precipitation, and vice versa, and that looking at one climate driver alone may give misleading conclusions.

My study shows that the two climate variables, precipitation and temperature, are both affecting seed predation, but in interacting ways that also differs between animal types. The dominance in predation by some of the animal groups in some sites also show that animal groups prefer different physical conditions and vegetation structures. Further research on seed preference, responses in predation to vegetation structures and climate parameters could potentially give an indication on how animal-plant interactions in alpine environment will look like in the future.

Table of content

Introduction

Granivory, the feeding on seeds by animals, plays an important role for plant and animal populations and for the composition and functioning of ecosystems. Seeds are a nutrient rich and reliable food source for a wide range of animals with both specialist and generalist feeding habits (Menalled & Liebman, 2008), and they are preyed upon either directly from the plant (pre-dispersed), or off the ground or in the soil (post-dispersed). Seed predation, defined as seeds being eaten and destroyed by animals, thus preventing germination (Janzen, 1971), can be intense enough to limit plant recruitment (Sanguinetti & Kitzberger, 2010; Muñoz & Cavieres, 2006; Hulme & Benkman, 2002), thus decreasing incorporation of new individuals into a population (Harper, 1977; Hulme & Kollmann, 1998). In this way, granivory can function as a biological control in plant communities (Holmes & Froud-Williams, 2005). As van der Wall (2005) points out, however, the fate of seeds taken by granivorous animals is far from certain, as it is not given whether seed removal will ultimately result in predation or in dispersion. Many granivores are hoarders, caching seeds for later consumption, but as they are not able to retrieve all seeds, they may function as efficient secondary seed dispersers, taking seeds to new areas where they can germinate and establish (Hulme & Kollmann, 1998; Vander Wall, 2005). These processes have been extensively studied across a wide range of environments ranging from Mediterranean-type-climate scrublands (e.g. Parker & Kelly, 1989), tropical forests (e.g. Schupp, 1988), temperate forests (e.g. Diaz et al., 1999) and semi-arid and desert lands (e.g. Brown et al., 1986). For instance, Castro et al. (1999) pointed out that seed predation was an important limiting factor for regeneration of Scots pine after investigating both pre- and post-dispersal seed predation by rodents and birds.

The relationship between biotic factors and seed removal has been studied since the 70's, with the Janzen-Connell hypothesis (Janzen, 1971) explaining maintenance of tree species biodiversity in tropical forests. The conclusion was that predation rates were higher close to the mother plant. Since then, a wide range of research methods have been applied to further investigate predation rates by manipulation of vegetation (for instance mowing sites) on both local-scale and large-scale (e.g. Mittelbach & Gross, 1984; Castro et al., 1999), seed preference studies among different guilds of granivores (e.g. Muñoz & Cavieres, 2006;

Holmes & Froud-Williams, 2005) and climatic influences (e.g. Hargreaves et al., 2018; Orrock et. al, 2015).

An example of how seed predation by rodents respond to vegetation structure is Mittelbach & Gross' (1984) study on seed removal in old-fields, -formerly cultivated or grazed lands that have now been abandoned. They investigated how seed removal was affected by vegetation disturbance on a local-scale, which animal group (rodents or ants) predated on the seeds, and finally, if seed size affected the predation rate by using two different sized seed species. The results showed significantly higher seed removal rates in densely vegetated areas than in plowed fields. This supports the hypothesis that heavier vegetation leads to more seed removal by rodents, as rodents' activity increases with vegetation density, thus functioning as shelter lowering risk while scavenging for seeds (Hulme & Kollmann, 1998). Birds, on the other hand, are hypothesized to be more active and predate more on high elevations (Muñoz & Arroyo, 2002). Birds, mainly using their sight when foraging for seeds, could also be obstructed from seeing the seeds at densely vegetated sites.

For seeds, size does matter, but this is not the only characteristic that constitutes the attractiveness of seeds. Nutrient content, availability and defense mechanisms also play a role on predation rates (Hulme & Kollmann, 1998). Some plants have even evolved to attract granivores to facilitate secondary dispersal, developing seeds with elaiosomes (fleshy structures, rich in protein and lipids to attract granivores) (Vander Wall, 2005). Others have developed cryptic strategies like "hard shells" (water-impermeable seed coat) avoiding leakage of olfactorial cues which might function as "invisibility cloaks" hiding them from granivores (Paulsen et al., 2013). Variation in seed predation is also related to differences in seed preferences among the main groups of granivores, including ants, rodents and birds (Figueroa et al., 2002; Muñoz & Cavieres, 2006). For example, Mittelbach & Gross (1984) found that rodents predated more on big seeds, while ants were more actively preying on smaller sized seeds. Muñoz & Cavieres (2006) found that seed predation rates varied as a response to both size and nutrient content of the different seeds.

We have so far reviewed examples of studies looking at seed predation rates as a response to the biotic factors seed species, animal groups and vegetation structure. But how will these preferences be in light of climatic changes? Climatic projections for the oceanic regions in the north-western Europe indicate a warming rate greater than the global average coupled

with marked increases in precipitation and in the snow-to-rain ratio (Hanssen-Bauer et al., 2009). We know that abiotic environmental conditions such as higher temperature and precipitation directly affect species richness and species composition in plant communities (Orrock et al., 2015; Kaspari et al., 2000b; Wu et al., 2011) and the abundance of animals and their herbivory activity (Orrock et al., 2015; Kaspari et al., 2000a; Brown & Ernest, 2002; Roslin et al., 2017), leading to stronger trophic interactions and stronger selection among plant species (Benkman, 2013). By looking at Mittelbach & Gross' (1984) study, we learnt that vegetation structure directly affects rodents' predation activity. So what role does these direct and indirect effects of increased temperature and precipitation have on seed removal?

Temperature is a dominant abiotic factor affecting the abundance and activity of granivores, as higher insect diversity and herbivory intensity increases towards higher temperatures (Bale et al., 2002; Hodkinson, 2005) activity and abundance of both ants (Porter & Tschinkel, 1987) as well as rodents (Schmidt-Nielsen, 1990). Seed predation responses to other climatic variables, such as precipitation, is less studied (Bale et al., 2002). However, it is surmised that heavy rainfall events are a mortality factor for ants (Bale et al., 2002). Arid systems can also alter granivory, as consumption of storable seeds may be advantageous in arid systems where resources are more unpredictable, hence lead to more seed predation by insects and rodents on dry sites (Orrock et al., 2015). Increased precipitation may have a more indirect effect on birds and rodents, as it alters productivity, and hence result in a higher and denser vegetation. More vegetation is beneficial for rodents, giving shelter, reducing their predation risk while scavenging for seeds. For birds, in contrast, increased productivity could limit seed predation, as seeds will be less visible for avian granivores. The direct effect of precipitation and temperature on abundance and activity on birds is more uncertain. On alpine sites, birds have shown higher predation rates than insects (Muñoz & Cavieres, 2006). However, this was a study conducted on one site, with an annual precipitation of around 445mm, giving no information of how bird predation rates are affected by precipitation. However, one can assume that birds might be unaffected by precipitation, as they are mobile predators, covering vast areas, making them able to avoid rainfall if necessary and forage for seeds when dry.

To study responses to temperature, widely used methods are *in situ* warming experiments (Elmendorf et al., 2012) and large-scale space-for-time studies (e.g. Orrock et al., 2015). As decreasing temperature is closely correlated with higher elevation, a well-acknowledged approach for studying responses to temperature is to use elevation and latitudinal gradients as analogous traits to temperature variation (Hargreaves et al., 2018). By using these methods, results from large-scale studies suggest higher predation rates at lower latitudes and elevation (Orrock et al., 2015). Where warming experiments are well fitted for testing responses to temperature, space-for-time approaches allows including of more climatic variables, such as annual precipitation.

Although there has been a substantial amount of research on seed predation in low-elevation habitats, seed-predation in alpine habitats has not received the same attention (Muñoz & Cavieres, 2006). Activity of seed predators varies spatially (Hulme & Kollmann, 1998), and the characterization of alpine systems as low ambient temperature and low productivity compared to boreal habitats, could result in differences in seed predation intensity among different animal groups. Understanding seed predation dynamics in the alpine habitats compared to low-land habitats is important, because alpine environments are widely recognized as biodiversity hotspots, with taxonomically and functionally distinct and species-rich ecosystems (Diaz et al., 2003). Unfortunately, they are also especially vulnerable to the projected climate change, as alpine plant species are highly temperature limited (Diaz et al., 2003). We are already experiencing a wetter and warmer climate (Kovats et al., 2014; Walther et al., 2002) and it is predicted that temperature will increase by 2.3 - 4.6 ℃ in Northern Europe by year 2100, and precipitation will increase by 5 - 30% (Hanssen-Bauer et al., 2009). Alpine plant species specialized to withstand harsh conditions (low mean and extreme temperatures, wind, drought stress, frost stress, unstable soil and short seasons) will suffer under warmer and wetter climate (Körner, 1999). Higher temperature will increase productivity (Wu et al., 2011), due to generalist plant species being able to grow at higher elevations and cause heavier interspecific interactions. Many of the typical granivorous species, like ants, carabid beetles, rodents and birds are all commonly found in the Nordic alpine environment, indicating that seed removal also will play an essential role in alpine environments. Climate change will alter generalist species to be able to grow higher up in the mountains, but what indirect effects could it have on seed predation? As animal

abundance and plant productivity rises, how will this affect seed predation rates? Will generalist species benefit from the intensified selection pressure, or will apomictic plants (plants that reproduce asexually) have an advantage? To be able to predict the importance of these interactions and how they will change under future climates, investigation of the mechanisms behind seed removal as a response to climate and change deserves more of our attention.

Previous studies have examined granivory responses to vegetation structure (e.g. Mittelbach & Gross, 1984), latitudinal and elevational gradients (e.g. Hargreaves et al., 2018; Muñoz & Arroyo, 2002) and responses to seed species and organism groups (e.g. Mittelbach & Gross, 1984; Holmes & Froud-Williams, 2005). However, a link to how seed predation is affected by plant species composition in grasslands as a response to changes in climate, both temperature and precipitation, is highly unclear. Therefore, a study combining temperature zones and precipitation gradients will help address these issues.

In this study, I will conduct a seed removal experiment to investigate predation rates of three different animal groups (insects, rodents and birds) as a response to three bioclimatic zones over a precipitation gradient. The three different bioclimatic zones differ in temperature (ranging from 6.5 ℃ to 10.5 ℃) and vegetation structure as the boreal sites will be surrounded by typical pine or birch forests, taller vegetation and higher productivity compared to sub-alpine (around the tree line) sites and alpine sites (above the tree line). The precipitation gradient spans over an annual rainfall of 600-2700 mm. I used predator exclusion cages to assess predation rates between the three animal groups. My main research question is whether there are differences in how seed predation by insects, rodents and birds respond to changes in temperature, vegetation structure and annual precipitation. I hypothesize that (1) Insect activity is altered by higher temperature, therefore, I expect to see increased seed predation by insects in dry, boreal sites (lowlands). (2) I expect rodent activity to be mostly affected by vegetation density. Therefore, I expect to see increased seed predation by rodents with higher temperature. I will also expect seed predation by rodents to increase with precipitation, driven by the indirect effect on productivity. But to a certain extent, too much precipitation can also cause nutrient stress, and the productivity might not increase. (3) I expect more predation by birds on alpine sites, where the seeds may be more visible due to lower and less dense vegetation. Their mobility and covering of

large areas would also make them less affected directly by precipitation. (4) Finally, plots where all organisms can predate could give us an indication of what organism group that dominates the predation at each site. Here, competition between the different organism groups must be accounted for.

Methods

Site description

The fieldwork for this study was conducted during the summer season 2018, between July 23rd and August 10th corresponding with the peak flowering/seed dispersal season. To investigate how seed predation rates respond to temperature and annual precipitation, this study was conducted using twelve sites on the SeedClim climate grid, in the boreal, sub-alpine and alpine grasslands, south west in Norway (figure 1)
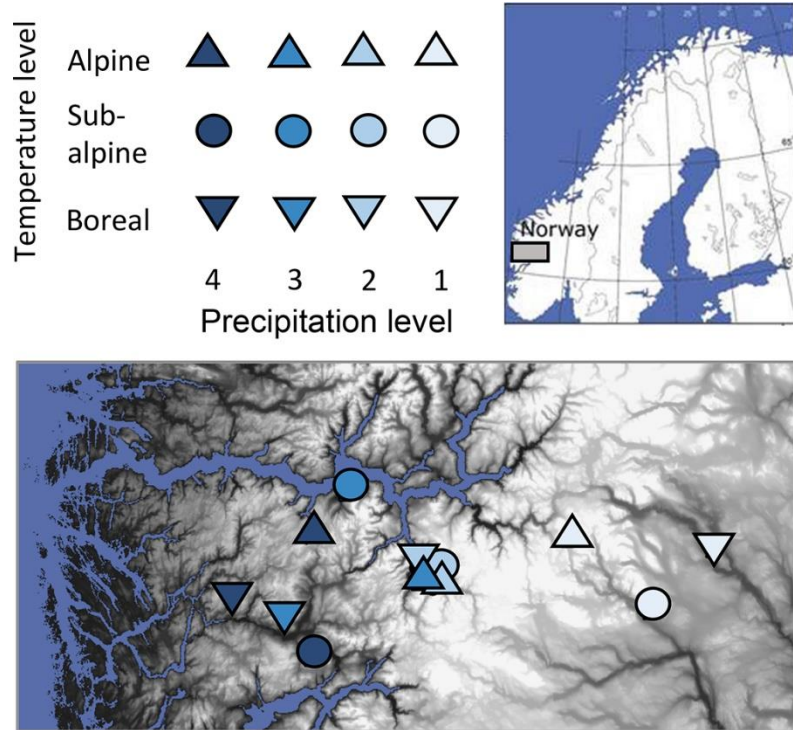
Figure 2.1: The SeedClim climate grid, 12 locations spanning over the south western parts of Norway. Figure from Klanderud et. al, 2015.

(Klanderud et al., 2017). This abiotic stress-gradient has been used for several studies with the aim of better understanding the complexity of interactions between the projected change in climate, and the consequences it may have on alpine environments. The twelve sites are divided into four levels of annual precipitation (With annual precipitation at around 600, 1200, 2000 and 2700 mm) and three bioclimatic zones; boreal, sub-alpine and alpine (that differ in mean summer temperature (over the four warmest months) of around 6.5, 8.5 and 10.5℃ respectively) (met.no, figure 1). Apart from precipitation and temperature, all other conditions are held as constant as possible. All sites are slopes facing south westwards, have similar calcareous bedrock, and similar grazing and land-use history (Vandvik et al., 2016). Although biotic conditions are held as constant as possible, there will be a difference in vegetation structure between bioclimatic zones, as the tree line separates boreal sites from alpine sites. All sites are fenced in the summer season, to avoid trampling and grazing, excluding larger mammals, but allowing smaller mammals (e.g. rodents), invertebrates and birds to enter. The sites are categorized as semi-natural grassland with a tendency towards

alpine grasslands of snow bed and leeside type in the alpine (Klanderud et al., 2016) with common species in this system being the graminoids *Agrostis capillaris, Anthoxanthum odoratum, Deschampsia cespitosa* and *Nardus stricta*, and the forbs *Achillea millefolium, Bistorta vivipara*, and *Potentilla erecta* (Gya, 2017, p.5). The wetter, colder sites experience a later start of growing and flowering season, because a large amount of precipitation falls as snow in the winter. Therefore, the dry, warm sites were visited earlier during the sampling period, and the wet, cold areas towards the end to correspond to the time that seeds are ripe.

Table 2.1: Showing elevation (m.a.s.l), annual precipitation (mm), coordinates in longitude and latitude and mean temperature (℃) during the four warmest months at each site.

Bioclimatic zones	Site name	Longitude	Latitude	Altitude (m.a.s.l)	Precipitation (mm)	Temperature (°C)
Alpine	Ulvhaugen	61.0243	8.12343	1208	596	6.17
Alpine	Låvisdalen	60.8231	7.27596	1097	1321	6.45
Alpine	Gudmesdalen	60.8328	7.17561	1213	1925	5.87
Alpine	Skjellinga-haugen	60.9335	6.41504	1088	2725	6.58
Sub-alpine	Ålrust	60.8203	8.70466	815	789	9.14
Sub-alpine	Høgsete	60.8760	7.17666	700	1356	9.17
Sub-alpine	Rambæra	61.0866	6.63028	769	1848	8.77
Sub-alpine	Veskre	60.5445	6.51468	797	3029	8.67
Boreal	Fauske	61.0355	9.07876	589	600	10.30
Boreal	Vikesland	60.8803	7.16982	474	1161	10.55
Boreal	Arhelleren	60.6652	6.33738	431	2044	10.60
Boreal	Øvstedal	60.6901	5.96487	346	2923	10.78

Seed species

The seeds for this study were chosen based on the types of seeds that would normally be found at these sites, both in regard to size and nutrition content. Seeds from the *Viola* genus stood out as an obvious choice as study species, based on a range of violet species (e.g. *V. biflora, V. riviniana, V. palustris*) being common on most sites. Viola seeds are relatively big for the study system, ensuring that they contain enough nutrients to potentially attract a wide range of granivores, while having additional advantage of making them possible to handle (counting was done manually, requiring seeds that are large enough to distinguish from one another by eye). To avoid learnt relations between granivores and seed species, it is ideal to choose a species that doesn't occur naturally at any sites (Hargreaves et al., 2018). Based on these criteria, *Viola arvensis* was therefore chosen as study species. *V. arvensis* is an annual species of the Violaceae family, it is native in Europe and found mainly in fields and along roadsides. (https://gobotany.newenglandwild.org/species/viola/arvensis/). The typical seed mass for this species is around 250 seeds per gram (=0.004 grams per seed). All seeds were bulk purchased from the garden supply service LOG AS, Oslo, Norway, importing the seeds from Hem Zaden BV, Hem, The Netherlands in July 2018. *V. arvensis* does not occur naturally in our study sites, and we therefore sterilized the seeds using a heat treatment (heated up to 150 ℃) to make them non-viable prior to deployment (Orrock et al., 2015)

Experimental design

At each site we selected a sampling area (maximum 50 m in diameter), where we set up five blocks (replicates). Each block contained five plots (seed depots, 90 mm petri-dish, see below), each with a different exclusion mechanisms (cages) to control what group of animals were preying on the seeds: Excluding rodents, excluding birds, excluding insects, excluding none, and excluding all animals (this we refer to as the control). This design totals 300 plots across the 12 sites. Each plot contained a petri-dish (90 mm diameter) filled with 50 seeds of the species *Viola arvensis*. The dishes were perforated, and filter paper was placed at the bottom allowing water to sieve through, without washing out the seeds. In the event that seeds got stuck between the petri-dish and the filter paper, these were categorized as "not available for predation", reducing the start number of seeds in the model (see below). This

happened at some of the plots not covered by a roof (i.e. treatments where birds were not excluded, see below), but normally did not exceed ten seeds. Some sampling days also experienced heavy winds, compromising some of the cages. These data were excluded from the dataset. This happened at eleven occasions. The seeds were deployed between 10am and 1pm and collected again 24 hours later and stored in small plastic bags. These were taken back to the lab for seed counting.

The animals that could potentially remove seeds from the plots were categorized into three different groups: Insects, rodents and birds. To control what type of organism preyed on the seeds, exclusion cages were constructed, allowing none, one or all animal groups (depending on the treatment) to enter and hence predate on the seeds. Constructing cages as exclusion methods for differentiating seed removal between animal groups is a widely used method (Holmes & Froud-Williams, 2005; Muñoz & Cavieres, 2006). Only minor

Figure 2.2: A block containing five seed depots; one with each treatment. (a) allows only birds, (b) allows all organisms, (c) allow only rodents, (d) allows only insects and (e) allows none of the organism types (control). Photo: Joris Schwitters. Photo taken at Arnhelleren, boreal, semi-wet site.

modifications are done to fit the species studied in this experiment. Insects were excluded by elevating the petri-dish from the ground by using metal pegs lubricated with the fluorpolymer Insect-a-slip® (BioQuip products, Inc.), and overlaying taller grasses was removed to prevent any crawling insects from entering (fig. 2.2b). This would exclude all crawling insects, but not flying ones. The fluorpolymer was mixed with water by a 1:3 ratio and was applied to the metal pegs by using a paint brush. The fluorpolymer functions as an insect barrier; making the metal pegs so slippery that crawling insects are unable to crawl up. Rodents were excluded by a steel wire cages (30x30x20 cm, mesh size 12,7mm). Tarp was used to construct a roof over the plots, screening out birds. Plots where all animals could predate were deployed in a petri-dish uncaged, excluding none of the animal groups.

For control plots, a combination of all exclusion methods was used to screen out potential predation from all animal groups.

Data curation and statistical analysis

Before conducting any statistical analysis, some adjustments had to be made to the dataset. All plots started out with 50 seeds each, but it did happen that some seeds partly got washed out and stuck between the petri-dish and filter-paper, which rendered them unreachable for predators. Therefore, these unreachable seeds were subtracted from the numbers of seeds prior to analysis. Instead of number of seeds predated at each plot, proportion of seeds predated was used, and calculated by the following equation:

$$\% \ of \ seeds \ removed = \frac{number \ of \ seeds \ at \ start - number \ of \ seeds \ at \ end}{number \ of \ seeds \ at \ start} \times 100$$

At eleven occasions, heavy winds knocked down the cages and compromised the exclusion methods. Therefore, these data were excluded from the dataset, leaving us with 289 seed sampling units for the analysis.

All statistical analyses were conducted using R version 3.4.4 (R Foundation for Statistical Computing, Vienna, Austria) with the packages ggplot2 (Wickham, 2016) and dplyr (Wickham et al., 2018). Proportion seeds predated was used as the response variable, the three different bioclimatic zones were categorical predictor variables, and the annual precipitation given in meters was a continuous predictor variable. To analyze the responses in predation to these predictors, an analysis of covariance (ANCOVA) was conducted with a 95% confidence interval. A normal distribution of residuals and a homogenous variance was expected, and I therefore used a normal error distribution. Expecting linear responses to precipitation for insects, birds, uncaged plots and control plots, a linear model was used for analyzation. For rodents, we expected precipitation to be limiting both on dry sites and the wettest sites, therefore a polynomial model was used for analyzing predations plots.

Results

Main findings

My results showed predation by all animal groups on all sites. Highest seed predation rates were found on the uncaged 'all predator' treatment plots, with a mean predation rate of 31% of available seeds predated across all sites, followed by birds (24%), insects (23%) and rodents (8%). On non-predator control plots, 9% of available seeds were predated. Insects were the most dominant predators on boreal sites, with 36% of available seeds predated. On sub-alpine sites, insects and birds predated the same proportion of seeds, with 21% of available seeds. On alpine sites, birds dominated, as 49% of available seeds were predated on these plots. In contrast, insects and rodents removed 13% and 3% of available seeds on alpine sites respectively. On boreal and sub-alpine sites, all animal groups show patterns of decreasing predation with increased precipitation, while on alpine sites, birds and the uncaged plots show an increase in predation as a response to increased precipitation. On all sites, the sum of predation by insects, rodents and birds was higher than the uncaged plots, where all animal groups could predate.

Insects, birds and uncaged plots all show responses to precipitation on alpine sites that differed from the direction of the response found in boreal and sub-alpine sites. The response to precipitation is thus bioclimatic zone dependent, and we see a significant interaction between the two predictors. This is however not the case for rodents and the control plots.
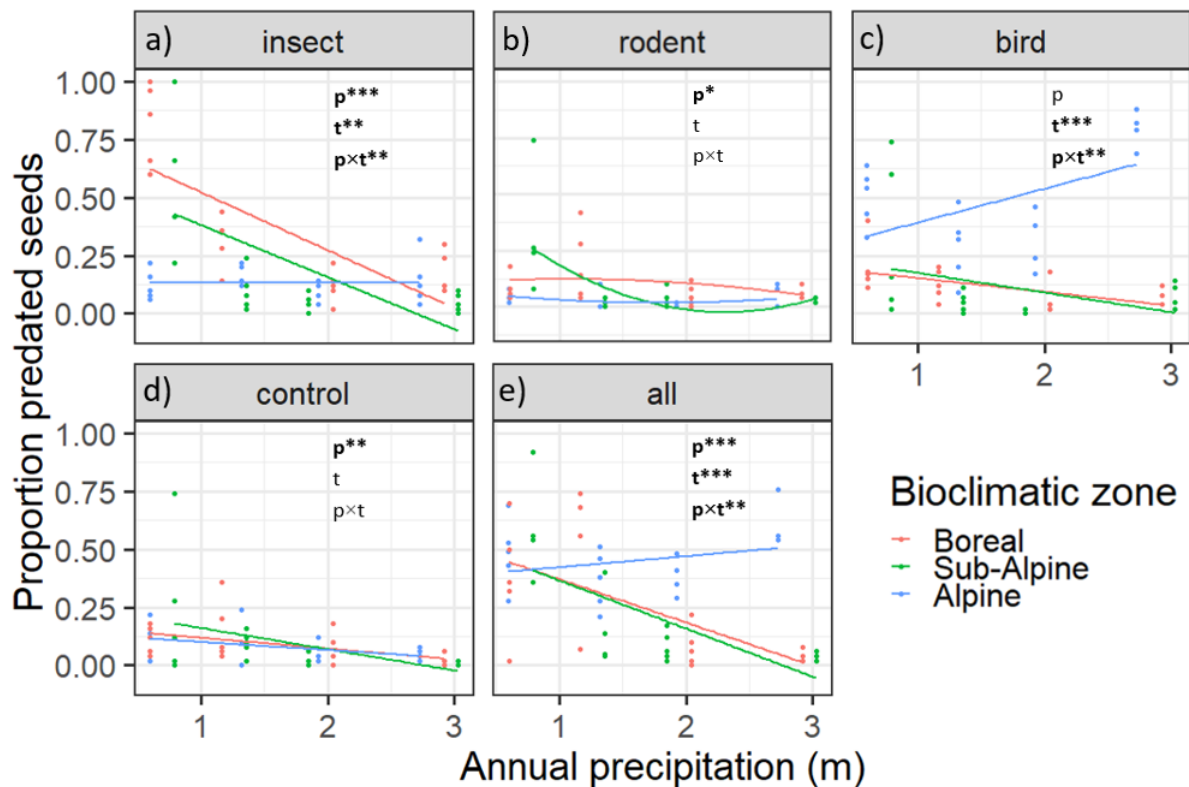
Figure 3.1 Proportion predated seeds along precipitation gradients in different bioclimatic zones for (a) insects, (b) rodents, (c) birds, (d) control, and (e) all predators. Predated seeds are given in proportion, where 1 (100%) indicates that all available seeds predated. Annual precipitation is given in meters (ranging from 0.9-2.7 m/year), and bioclimatic zones reflect three levels of mean temperature during the four warmest months; Boreal (red, ≈ 6.5 °C), Sub-Alpine (green, ≈ 8.5 °C) and Alpine (blue, ≈ 10.5 °C). Significant effects of precipitation (p), bioclimtatic zone (t) and the interaction between them (p×t) are indicated with bold font, and the level of significance with stars (* = p < 0.05, ** = p < 0.01, *** = p < 0.001).

Findings by animal group

Insects

Overall, there is significant response of seed predation by insects to precipitation (p < 0.001) and bioclimatic zone (p < 0.01), as well as interactions between them (p < 0.01). The overall trend of decrease in seed predation with increased precipitation is not significant within each bioclimatic zone. On boreal and sub-alpine sites, seed predation decreased significantly with increased precipitation (t-value 3.216, p < 0.01 and t-value = -2.885, p < 0.01 respectively, figure 3.1a, Appendix II). On alpine sites however, the response to precipitation slightly positive, but insignificant (t-value = 0.023, p > 0.05).

Rodents

For all bioclimatic zones, we can see on figure 3.1b that there is a slight negative response in seed predation by rodents with increasing precipitation ($p < 0.05$). This overall trend is however not statistically significant within each of the bioclimatic zones. Further, there is no significant response to bioclimatic zone or the interaction between bioclimatic zone and precipitation.

Birds

Overall, seed predation by birds depends both on the bioclimatic zone and precipitation (significant interaction, $p < 0.01$). Predation significantly increases towards the colder bioclimatic zones ($p < 0.001$). There is also a significant response to precipitation, but this is bioclimatic zone dependent. Figure 3.1d shows us that predation in the alpine zone increases with increased precipitation ((t-value = -2.783, $p < 0.01$), while in boreal and sub-alpine zones, we see the contrary with predation decreasing with increased precipitation (t-value = -3.145, $p < 0.01$ and t-value = -3.429, $p < 0.01$ respectively) (Appendix II).

Control

The control plots in this study was designed to not allow any predators to reach the seed depots. Ideally, this would result in no seed predation at all, regardless of bioclimatic zone or precipitation level. However, Figure 3.1d shows that there was some predation at all sites, and an overall significant decrease in predation with increased precipitation ($p < 0.01$). This response is not bioclimatic zone dependent and there is no significant response in predation to temperature alone either.

Uncaged

On uncaged plots, allowing all organism types to predated on the seeds, there is a significant effect from both precipitation and bioclimatic zone (both $p < 0.001$), and a clear interaction between them ($p < 0.01$). Figure 3.1e shows that the response to precipitation is bioclimatic zone dependent. On alpine sites, there is a trend for an increase in predation with higher precipitation, however, insignificantly (t-value = 0.858, $p > 0.5$). On boreal and sub-alpine sites, we see a significant decrease in predation with increased precipitation (t-value = -3.236, $p < 0.01$ and t-value = -3.435, $p < 0.01$) (Appendix II).

Discussion

Different animals, different trends

There was seed predation by all organisms on all sites, but to different extents and with different trends along the gradients. The uncaged plots where all animal groups could predate, experienced on average the highest predation rates across all sites with 31% of available seeds predated, but less than the predation at insects, rodents and birds combined. Birds predated a mean of 24%, insects 23% and rodents 8% of available seeds across all sites. The control plots experienced a mean seed predation of 9% of available seeds. My results revealed large differences in seed predation rates both between bioclimatic zones (birds on alpine sites 49% predation and boreal sites 11% predation), and precipitation (insects on dry sites 53% predation and wet sites 12% predation). Many of the responses to predation being bioclimatic zone dependent, also underlines the importance of including both predictors when studying responses to changes in climate.

Trends by each animal group individually

Insects

Insect predation increased towards warmer temperatures, and to a lesser extent towards drier climates. On boreal sites, 36% of available seeds were predated, with a peak on the dry site, with 82% of all available seeds being predated in the insects only treatment. These patterns are as expected, given that insects as ectotherm organisms are limited by low temperatures (Hargreaves et al., 2018; Porter & Tschinkel, 1987). The negative response to precipitation supports the surmise that rainfall generally can be an enhanced mortality factor for insects (Bale et al., 2002). On the alpine, dry site, there was a 12% seed predation of available seed by insects. For comparison, Muñoz & Cavieres (2006) found 25% (including removal by wind) in the Chilean Andes. Comparing these studies should however be done with caution, as both exposure time and study system differ. 12% seed predation after 24h exposure time is a lot compared to 25% seed predation over a 20-day exposure time, and an annual precipitation of 445mm makes it an arid system, even compared to my driest sites.

Rodents

Although we expected higher predation rates by rodents as a response to denser vegetated areas (Hulme & Kollmann, 1998; Mittelbach & Gross, 1984) and hence towards warmer and

wetter climates. However, my results reflect no such trends. As seed predation rates in all bioclimatic zones was low (8% predation of available seeds), in fact, comparable to the seed loss in the no-predator control plots (9%), we cannot really be sure if there has been any rodent predation at all.

Rodents use their smell as well as sight and touch when scavenging for seeds (Paulsen et. al, 2013). The heat treatment used to sterilize the seeds may have compromised the olfacotrial cues these seeds may release, making them less attractive for rodents. However, these limitations are not likely to screen out all predation by rodents, as the seeds were deployed on top of the soil surface, being fully visible for any potential rodent predators. However, one should not ignore that the plastic petri-dish will appear quite unnatural and could potentially be deterrent to rodents. A third possible factor which might affected predation by rodents is temporal variations in rodent abundance between years. A common sight in Norwegian mountains are lemmings, a rodent adapted to alpine environments. Their population cycles are characterized with dramatic population peaks every 3-5 years (Kausrud et al., 2008). This year, there was relatively low rodent activity compared to previous years (personal observations), making long term studies over several years necessary to cope with these annual variations.

Birds

Birds showed a higher predation rate on alpine sites (50% of available seeds) than boreal and sub-alpine sites (20% and 32% respectively). These results reflect my expectations, as I expected birds to predated more on low productivity sites (alpine sites) as they are vision dependent. An interesting observation looking at the response to precipitation on alpine sites, is a decrease in predation from boreal to semi-dry and semi-wet areas, before peaking at the wet site. This could reflect that precipitation, at a certain point, will be a limiting factor, and that birds reach a bottom in predation on semi-dry and semi-wet sites as a response to a peak in vegetation for alpine zones on these sites. Local biomass measurements done on this study (Bruvoll, 2013) area support this assumption, as biomass is reported to be heaviest at the semi-wet site in the alpine zone.

Birds predating more than insects on alpine sites is also supported by Muñoz & Cavieres (2006). On a study on seed predation on alpine sites in the Chilean Andes, they found 34% seed predation of available seeds by birds. On boreal sites and sub-alpine sites, my

assumption of less predation with increased precipitation as a response to denser vegetation matches my results.

Uncaged and control

One would expect that seed predation rates for the uncaged plots would be the sum of predation rates at the three animal groups combined, which the results show is not true for any of the twelve sites. We didn't expect any predation on the control plots either, but with an overall of 9% of available removed, there are indications of some seed loss caused by something else than predation by animals which may apply for all plots. Flying insects, which are not being excluded by any of the treatments, could be a factor that causes some seed loss at all sites. Another explanation could be seed loss caused by wind and weather, as Norwegian alpine regions, even in the summer, could experience heavy winds and rain sideways. On boreal and sub-alpine sites, we see the same trend of decreasing predation with increased precipitation as all animal groups. On alpine sites, the positive response in predation increased precipitation follows the same trend as predation by birds, implying predation by birds also in these plots.

The importance of including precipitation

Temperature is a climate parameter which is extensively studied, for example by conducting *in-situ* warming experiments (Elmendorf et al., 2012), or using different elevations or latitudes as a temperature gradient (e.g. Orrock et al., 2015). The direct impacts of precipitation, unfortunately, has been neglected in current research on climate change (Bale et. al, 2002). There have been approaches on quantifying seed predation on different elevations, but without including precipitation as a factor (Muñoz & Arroyo, 2002; Orrock et al., 2015). Precipitation is extensively correlated with plant productivity, and these indirect effects via plant productivity can be important for seed predation. However, the effect of precipitation on plant productivity is context dependent. In arid systems, increased precipitation is usually beneficial for the plants, and precipitation can be resource limiting. Contrary, in a more humid systems (like western Norway), precipitation is not a limiting factor, but more a disturbance/stress. For example, increased precipitation can wash out important nutrients in the soil. Biomass measurements on the SeedClim study system shows

an increase in biomass with precipitation in the alpine zone up to the semi-wet site, before it dips down again towards the wettest site (Bruvoll, 2013). On boreal sites, biomass decreases with increased precipitation. The importance of including precipitation as a factor is highlighted by my results, which show that the response in predation with precipitation is bioclimatic zone dependent. Further, it is important to reflect about the role precipitation might have on the study system, as both too much, and too little precipitation can be limiting.

Projected animal-plant interactions

Mountains are hotspots for biodiversity and are priority regions for conservation (Körner, 2004). To be able to predict how species composition in alpine regions will be in the future, we need to understand how climatic changes as higher temperature and more annual precipitation both directly and indirectly will affect species composition. Steep environmental gradients make mountain ecosystems very vulnerable to slight changes of temperatures and extreme precipitation events (Diaz et al., 2003). As shown in this study, we have seen that by differences in vegetation structure (Orrock et al., 2015; Kaspari et al., 2000b), and animal abundance and activity (Orrock et al., 2015; Kaspari et al., 2000a; Brown & Ernest, 2002) resulted in different spatial predation intensities. Birds dominate in the alpine regions, while insects dominate in lowlands.

With projected higher temperatures and heavier precipitation in alpine regions in the future, we can expect increased productivity in these areas and may reach conditions more similar to what we find in sub-alpine and boreal sites today. Hence it will be reasonable to assume that predation intensities by the different animals will follow these changes. My results show that birds are the most dominant predator in alpine regions compared to rodents and insects. Should predation responses follow climate projections, we may see more predation by insects in mountains in the future as a consequence of a warmer and wetter climate, and hence taller and denser vegetation. Rodents predation and activity would theoretically also respond positively to higher temperature and denser vegetation, but this is not reflected by my results.

Muñoz & Arroyo (2002) did a similar experiment, looking at insect and bird seed predation responses to elevations in the Chilean Andes, concluding that non-mutually, exclusive factors may play a role, showing that general assumptions not always have to be the truth on local scale. They expected more predations by insects on lower elevations but found the opposite. Temperature limitation on local ants, may have provided results that contradicted their expectations. This again stressed the importance of spatial and temporal variations, and exclusive effects in study systems. Here, my study has to take lemming cycles and too much precipitation as a limiting factor into account.

Seed removal as dispersal

In this study, all seed removal is counted as predation. However, the fate of the seeds is not certain, as seeds fate also can result in secondary dispersal, thus germination and establishment on new populations (Vander Wall, 2005). Many granivores are hoarders, caching seeds for later consumption, but as they are not able to retrieve all seeds, they may function as efficient secondary seed dispersers, taking seeds to new areas where they can germinate and establish (Hulme & Kollmann, 1998; Vander Wall, 2005). This is a convenient dispersal strategy, and some seed species have even developed elaiosomes, especially associated with attracting ants, taking them to microsites which favor seedling establishment (vander Wall, 2005). Also, larder hoarding and scatter hoarding by rodents and birds are well known strategies for secondary dispersal (Hulme & Kollmann, 1998). For this study, the risk of introducing new species to the system was low, as the seeds were heat treated prior to deployment. But the chance that some of these seeds could have been dispersed without being consumed, cannot be neglected. Even though it is just a small percentage that would be dispersed instead of predated, these are often the ones that drive population plant recruitment. (Vander Wall, 2005).

Conclusions and further research

This multi-species assessment study has used an exclusion method to quantify seed predation rates as a response to direct and indirect influence by both temperature and precipitation. I found that predation by different animal groups responded different to precipitation and bioclimatic zones, and that the response with precipitation is very dependent on bioclimatic zones, and vice versa. The results show that birds are the dominant predator in the alpine zone and that insects show a clear increase in predation towards warmer sites. The different response in predation to temperature and precipitation by each animal group underlines the importance of including the direct and indirect effects of both temperature and precipitation as response to one of the predictors is dependent on the other, and vice versa.

This study brings up some questions to explore for further research. Using different seed species with different traits (size, nutrition content, elaiosomes) could be useful to investigate what seed traits attracted which animal group. The driest sites in this study (600mm annual precipitation) is still wetter than other studies conducted on this topic (Muñoz & Cavieres, 2006). Expanding this gradient to more arid sites would help to understand precipitation as a limiting versus abiotic stress factor. Also, conducting this experiment over a longer period of time, giving the seed samples longer exposure time, would give us an indication of when and how predation takes place, and would to a greater extent eliminate the effect of local weather. This could give and understanding about what seed traits will be beneficial in alpine habitats as climate changes and may give an indication of how the species composition will look like.

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Appendix I

Table A.1: Data from all plots, at all sites. Proportion predated seeds is calculated by $1 - \frac{Seeds\ left}{Seeds\ start}$. Site name abbreviations: Ulv = Ulvehaugen, Lav = Låvisdalen, Gud = Gudmedalen, Skj = Skjellingahugen, Alr = Ålrust, Hog = Høgsete, Ram = Rambæra, Ves = Veskre, Fau = Fauske, Vik = Vikesland, Arn = Arnhelleren, Ovs = Øvstetun.

site	Bioclimatic zone	precipitation	treat	seeds start	seeds left	proportion Predated
Ulv	alpine	dry	all	42	24	0,43
Ulv	alpine	dry	all	48	15	0,69
Ulv	alpine	dry	all	43	22	0,49
Ulv	alpine	dry	all	50	36	0,28
Ulv	alpine	dry	all	36	17	0,53
Ulv	alpine	dry	control	50	44	0,12
Ulv	alpine	dry	control	50	47	0,06
Ulv	alpine	dry	control	50	49	0,02
Ulv	alpine	dry	control	50	39	0,22
Ulv	alpine	dry	control	50	43	0,14
Ulv	alpine	dry	bird	40	17	0,58
Ulv	alpine	dry	bird	46	21	0,54
Ulv	alpine	dry	bird	49	28	0,43
Ulv	alpine	dry	bird	44	16	0,64
Ulv	alpine	dry	bird	42	28	0,33
Ulv	alpine	dry	rodent	50	48	0,04
Ulv	alpine	dry	rodent	50	48	0,04
Ulv	alpine	dry	rodent	50	49	0,02
Ulv	alpine	dry	rodent	50	48	0,04
Ulv	alpine	dry	rodent	50	46	0,08
Ulv	alpine	dry	insect	50	45	0,10
Ulv	alpine	dry	insect	50	39	0,22
Ulv	alpine	dry	insect	50	46	0,08
Ulv	alpine	dry	insect	50	42	0,16
Ulv	alpine	dry	insect	50	47	0,06
Lav	alpine	semi.dry	all	43	21	0,51
Lav	alpine	semi.dry	all	33	26	0,21
Lav	alpine	semi.dry	all	48	26	0,46
Lav	alpine	semi.dry	all	46	33	0,28
Lav	alpine	semi.dry	all	48	30	0,38
Lav	alpine	semi.dry	control	50	45	0,10
Lav	alpine	semi.dry	control	50	50	0,00
Lav	alpine	semi.dry	control	50	NA	NA
Lav	alpine	semi.dry	control	50	38	0,24
Lav	alpine	semi.dry	control	50	NA	NA
Lav	alpine	semi.dry	bird	40	26	0,35
Lav	alpine	semi.dry	bird	43	39	0,09
Lav	alpine	semi.dry	bird	42	22	0,48
Lav	alpine	semi.dry	bird	47	32	0,32

Lav	alpine	semi.dry	bird	44	35	0,20	
Lav	alpine	semi.dry	rodent	50	50	0,00	
Lav	alpine	semi.dry	rodent	50	50	0,00	
Lav	alpine	semi.dry	rodent	50	NA	NA	
Lav	alpine	semi.dry	rodent	50	45	0,10	
Lav	alpine	semi.dry	rodent	50	NA	NA	
Lav	alpine	semi.dry	insect	50	43	0,14	
Lav	alpine	semi.dry	insect	50	NA	NA	
Lav	alpine	semi.dry	insect	50	44	0,12	
Lav	alpine	semi.dry	insect	50	40	0,20	
Lav	alpine	semi.dry	insect	50	39	0,22	
Gud	alpine	semi.wet	all	46	27	0,41	
Gud	alpine	semi.wet	all	44	23	0,48	
Gud	alpine	semi.wet	all	46	30	0,35	
Gud	alpine	semi.wet	all	48	31	0,35	
Gud	alpine	semi.wet	all	49	35	0,29	
Gud	alpine	semi.wet	control	50	44	0,12	
Gud	alpine	semi.wet	control	50	49	0,02	
Gud	alpine	semi.wet	control	50	49	0,02	
Gud	alpine	semi.wet	control	50	48	0,04	
Gud	alpine	semi.wet	control	50	48	0,04	
Gud	alpine	semi.wet	bird	46	38	0,17	
Gud	alpine	semi.wet	bird	46	25	0,46	
Gud	alpine	semi.wet	bird	42	32	0,24	
Gud	alpine	semi.wet	bird	50	27	0,46	
Gud	alpine	semi.wet	bird	39	24	0,38	
Gud	alpine	semi.wet	rodent	50	NA	NA	
Gud	alpine	semi.wet	rodent	50	50	0,00	
Gud	alpine	semi.wet	rodent	50	NA	NA	
Gud	alpine	semi.wet	rodent	50	49	0,02	
Gud	alpine	semi.wet	rodent	50	48	0,00	
Gud	alpine	semi.wet	insect	50	NA	NA	
Gud	alpine	semi.wet	insect	50	44	0,12	
Gud	alpine	semi.wet	insect	50	43	0,14	
Gud	alpine	semi.wet	insect	50	46	0,08	
Gud	alpine	semi.wet	insect	50	48	0,04	
Skj	alpine	wet	all	32	14	0,56	
Skj	alpine	wet	all	50	22	0,56	
Skj	alpine	wet	all	46	11	0,76	
Skj	alpine	wet	all	50	23	0,54	
Skj	alpine	wet	all	50	NA	NA	
Skj	alpine	wet	control	50	47	0,06	
Skj	alpine	wet	control	50	49	0,02	
Skj	alpine	wet	control	50	48	0,04	
Skj	alpine	wet	control	50	46	0,08	
Skj	alpine	wet	control	50	48	0,04	
Skj	alpine	wet	bird	34	4	0,88	
Skj	alpine	wet	bird	42	9	0,79	

Skj	alpine	wet	bird	25	3	0,88
Skj	alpine	wet	bird	50	9	0,82
Skj	alpine	wet	bird	48	15	0,69
Skj	alpine	wet	rodent	50	50	0,00
Skj	alpine	wet	rodent	50	46	0,08
Skj	alpine	wet	rodent	50	50	0,00
Skj	alpine	wet	rodent	50	45	0,10
Skj	alpine	wet	rodent	50	50	0,00
Skj	alpine	wet	insect	50	42	0,16
Skj	alpine	wet	insect	50	48	0,04
Skj	alpine	wet	insect	50	44	0,12
Skj	alpine	wet	insect	50	34	0,32
Skj	alpine	wet	insect	50	46	0,08
Alr	sub.alpine	dry	all	50	23	0,54
Alr	sub.alpine	dry	all	50	32	0,36
Alr	sub.alpine	dry	all	50	22	0,56
Alr	sub.alpine	dry	all	50	4	0,92
Alr	sub.alpine	dry	all	50	23	0,54
Alr	sub.alpine	dry	control	50	36	0,28
Alr	sub.alpine	dry	control	50	44	0,12
Alr	sub.alpine	dry	control	50	13	0,74
Alr	sub.alpine	dry	control	50	49	0,02
Alr	sub.alpine	dry	control	50	50	0,00
Alr	sub.alpine	dry	bird	50	42	0,16
Alr	sub.alpine	dry	bird	50	47	0,06
Alr	sub.alpine	dry	bird	50	13	0,74
Alr	sub.alpine	dry	bird	50	20	0,60
Alr	sub.alpine	dry	bird	50	49	0,02
Alr	sub.alpine	dry	rodent	50	13	0,74
Alr	sub.alpine	dry	rodent	50	46	0,08
Alr	sub.alpine	dry	rodent	50	38	0,24
Alr	sub.alpine	dry	rodent	50	37	0,26
Alr	sub.alpine	dry	rodent	50	46	0,08
Alr	sub.alpine	dry	insect	50	17	0,66
Alr	sub.alpine	dry	insect	50	39	0,22
Alr	sub.alpine	dry	insect	50	0	1,00
Alr	sub.alpine	dry	insect	50	0	1,00
Alr	sub.alpine	dry	insect	50	29	0,42
Hog	sub.alpine	semi.dry	all	50	30	0,40
Hog	sub.alpine	semi.dry	all	50	48	0,04
Hog	sub.alpine	semi.dry	all	39	37	0,05
Hog	sub.alpine	semi.dry	all	43	41	0,05
Hog	sub.alpine	semi.dry	all	49	42	0,14
Hog	sub.alpine	semi.dry	control	50	44	0,12
Hog	sub.alpine	semi.dry	control	50	49	0,02
Hog	sub.alpine	semi.dry	control	50	46	0,08
Hog	sub.alpine	semi.dry	control	50	42	0,16
Hog	sub.alpine	semi.dry	control	50	45	0,10

Hog	sub.alpine	semi.dry	bird	48	47	0,02
Hog	sub.alpine	semi.dry	bird	44	39	0,11
Hog	sub.alpine	semi.dry	bird	46	43	0,07
Hog	sub.alpine	semi.dry	bird	40	38	0,05
Hog	sub.alpine	semi.dry	bird	43	43	0,00
Hog	sub.alpine	semi.dry	rodent	50	50	0,00
Hog	sub.alpine	semi.dry	rodent	50	48	0,04
Hog	sub.alpine	semi.dry	rodent	50	49	0,02
Hog	sub.alpine	semi.dry	rodent	50	48	0,04
Hog	sub.alpine	semi.dry	rodent	50	50	0,00
Hog	sub.alpine	semi.dry	insect	50	38	0,24
Hog	sub.alpine	semi.dry	insect	50	49	0,02
Hog	sub.alpine	semi.dry	insect	50	46	0,08
Hog	sub.alpine	semi.dry	insect	50	44	0,12
Hog	sub.alpine	semi.dry	insect	50	48	0,04
Ram	sub.alpine	semi.wet	all	45	44	0,02
Ram	sub.alpine	semi.wet	all	50	48	0,04
Ram	sub.alpine	semi.wet	all	50	44	0,12
Ram	sub.alpine	semi.wet	all	49	46	0,06
Ram	sub.alpine	semi.wet	all	46	38	0,17
Ram	sub.alpine	semi.wet	control	50	50	0,00
Ram	sub.alpine	semi.wet	control	50	49	0,02
Ram	sub.alpine	semi.wet	control	50	47	0,06
Ram	sub.alpine	semi.wet	control	50	47	0,06
Ram	sub.alpine	semi.wet	control	50	49	0,02
Ram	sub.alpine	semi.wet	bird	48	48	0,00
Ram	sub.alpine	semi.wet	bird	44	44	0,00
Ram	sub.alpine	semi.wet	bird	50	50	0,00
Ram	sub.alpine	semi.wet	bird	47	46	0,02
Ram	sub.alpine	semi.wet	bird	45	45	0,00
Ram	sub.alpine	semi.wet	rodent	50	50	0,00
Ram	sub.alpine	semi.wet	rodent	50	45	0,10
Ram	sub.alpine	semi.wet	rodent	50	45	0,10
Ram	sub.alpine	semi.wet	rodent	50	48	0,04
Ram	sub.alpine	semi.wet	rodent	50	49	0,02
Ram	sub.alpine	semi.wet	insect	50	50	0,00
Ram	sub.alpine	semi.wet	insect	50	48	0,04
Ram	sub.alpine	semi.wet	insect	50	50	0,00
Ram	sub.alpine	semi.wet	insect	50	45	0,10
Ram	sub.alpine	semi.wet	insect	50	47	0,06
Ves	sub.alpine	wet	all	47	44	0,06
Ves	sub.alpine	wet	all	48	47	0,02
Ves	sub.alpine	wet	all	47	45	0,04
Ves	sub.alpine	wet	all	47	46	0,02
Ves	sub.alpine	wet	all	49	47	0,04
Ves	sub.alpine	wet	control	50	50	0,00
Ves	sub.alpine	wet	control	50	50	0,00
Ves	sub.alpine	wet	control	50	49	0,02

Ves	sub.alpine	wet	control	50	50	0,00
Ves	sub.alpine	wet	control	50	49	0,02
Ves	sub.alpine	wet	bird	46	41	0,11
Ves	sub.alpine	wet	bird	43	37	0,14
Ves	sub.alpine	wet	bird	41	39	0,05
Ves	sub.alpine	wet	bird	44	43	0,02
Ves	sub.alpine	wet	bird	43	41	0,05
Ves	sub.alpine	wet	rodent	50	48	0,04
Ves	sub.alpine	wet	rodent	50	49	0,02
Ves	sub.alpine	wet	rodent	50	49	0,02
Ves	sub.alpine	wet	rodent	50	48	0,04
Ves	sub.alpine	wet	rodent	50	NA	NA
Ves	sub.alpine	wet	insect	50	49	0,02
Ves	sub.alpine	wet	insect	50	50	0,00
Ves	sub.alpine	wet	insect	50	46	0,08
Ves	sub.alpine	wet	insect	50	45	0,10
Ves	sub.alpine	wet	insect	50	48	0,04
Fau	boreal	dry	all	41	40	0,02
Fau	boreal	dry	all	42	21	0,50
Fau	boreal	dry	all	44	28	0,36
Fau	boreal	dry	all	46	14	0,70
Fau	boreal	dry	all	41	28	0,32
Fau	boreal	dry	control	50	44	0,12
Fau	boreal	dry	control	50	41	0,18
Fau	boreal	dry	control	50	42	0,16
Fau	boreal	dry	control	50	47	0,06
Fau	boreal	dry	control	50	48	0,04
Fau	boreal	dry	bird	46	39	0,15
Fau	boreal	dry	bird	48	40	0,17
Fau	boreal	dry	bird	44	39	0,11
Fau	boreal	dry	bird	40	33	0,18
Fau	boreal	dry	bird	45	27	0,40
Fau	boreal	dry	rodent	50	48	0,04
Fau	boreal	dry	rodent	50	46	0,08
Fau	boreal	dry	rodent	50	46	0,08
Fau	boreal	dry	rodent	50	47	0,06
Fau	boreal	dry	rodent	50	41	0,18
Fau	boreal	dry	insect	50	2	0,96
Fau	boreal	dry	insect	50	20	0,60
Fau	boreal	dry	insect	50	7	0,86
Fau	boreal	dry	insect	50	0	1,00
Fau	boreal	dry	insect	50	17	0,66
Vik	boreal	semi.dry	all	43	11	0,74
Vik	boreal	semi.dry	all	45	20	0,56
Vik	boreal	semi.dry	all	45	42	0,07
Vik	boreal	semi.dry	all	40	13	0,68
Vik	boreal	semi.dry	all	50	NA	NA
Vik	boreal	semi.dry	control	50	40	0,20

Vik	boreal	semi.dry	control	49	45	0,08
Vik	boreal	semi.dry	control	50	48	0,04
Vik	boreal	semi.dry	control	50	32	0,36
Vik	boreal	semi.dry	control	50	47	0,06
Vik	boreal	semi.dry	bird	44	40	0,09
Vik	boreal	semi.dry	bird	45	36	0,20
Vik	boreal	semi.dry	bird	43	38	0,12
Vik	boreal	semi.dry	bird	47	45	0,04
Vik	boreal	semi.dry	bird	45	37	0,18
Vik	boreal	semi.dry	rodent	50	47	0,06
Vik	boreal	semi.dry	rodent	50	48	0,04
Vik	boreal	semi.dry	rodent	50	43	0,14
Vik	boreal	semi.dry	rodent	50	36	0,28
Vik	boreal	semi.dry	rodent	50	29	0,42
Vik	boreal	semi.dry	insect	50	36	0,28
Vik	boreal	semi.dry	insect	50	43	0,14
Vik	boreal	semi.dry	insect	50	32	0,36
Vik	boreal	semi.dry	insect	50	28	0,44
Vik	boreal	semi.dry	insect	50	36	0,28
Arn	boreal	semi.wet	all	50	39	0,22
Arn	boreal	semi.wet	all	50	49	0,02
Arn	boreal	semi.wet	all	50	47	0,06
Arn	boreal	semi.wet	all	50	50	0,00
Arn	boreal	semi.wet	all	50	45	0,10
Arn	boreal	semi.wet	control	50	48	0,04
Arn	boreal	semi.wet	control	50	45	0,10
Arn	boreal	semi.wet	control	50	50	0,00
Arn	boreal	semi.wet	control	50	41	0,18
Arn	boreal	semi.wet	control	50	50	0,00
Arn	boreal	semi.wet	bird	50	49	0,02
Arn	boreal	semi.wet	bird	50	49	0,02
Arn	boreal	semi.wet	bird	50	49	0,02
Arn	boreal	semi.wet	bird	50	48	0,04
Arn	boreal	semi.wet	bird	50	41	0,18
Arn	boreal	semi.wet	rodent	50	46	0,08
Arn	boreal	semi.wet	rodent	50	50	0,00
Arn	boreal	semi.wet	rodent	50	44	0,12
Arn	boreal	semi.wet	rodent	50	49	0,02
Arn	boreal	semi.wet	rodent	50	48	0,04
Arn	boreal	semi.wet	insect	50	49	0,02
Arn	boreal	semi.wet	insect	50	43	0,14
Arn	boreal	semi.wet	insect	50	44	0,12
Arn	boreal	semi.wet	insect	50	45	0,10
Arn	boreal	semi.wet	insect	50	39	0,22
Ovs	boreal	wet	all	50	46	0,08
Ovs	boreal	wet	all	50	49	0,02
Ovs	boreal	wet	all	50	48	0,04
Ovs	boreal	wet	all	50	49	0,02

Ovs	boreal	wet	all	50	48	0,04
Ovs	boreal	wet	control	50	49	0,02
Ovs	boreal	wet	control	50	49	0,02
Ovs	boreal	wet	control	50	50	0,00
Ovs	boreal	wet	control	50	49	0,02
Ovs	boreal	wet	control	50	47	0,06
Ovs	boreal	wet	bird	50	48	0,04
Ovs	boreal	wet	bird	50	48	0,04
Ovs	boreal	wet	bird	50	48	0,04
Ovs	boreal	wet	bird	50	46	0,08
Ovs	boreal	wet	bird	50	44	0,12
Ovs	boreal	wet	rodent	50	47	0,06
Ovs	boreal	wet	rodent	50	48	0,04
Ovs	boreal	wet	rodent	50	48	0,04
Ovs	boreal	wet	rodent	50	45	0,10
Ovs	boreal	wet	rodent	50	45	0,10
Ovs	boreal	wet	insect	50	44	0,12
Ovs	boreal	wet	insect	50	44	0,12
Ovs	boreal	wet	insect	50	45	0,10
Ovs	boreal	wet	insect	50	38	0,24
Ovs	boreal	wet	insect	50	35	0,30

Appendix II

Testing model for insects:

mod.insect<-lm(predated~precipitation*temp, data=insect.df)

```
>anova(mod.bird):

Analysis of Variance Table

Response: predated
                  Df  Sum Sq Mean Sq F value    Pr(>F)
precipitation      1 1.15132 1.15132 29.2401 1.631e-06 ***
temp               2 0.49006 0.24503  6.2231  0.003775 **
precipitation:temp 2 0.49390 0.24695  6.2717  0.003630 **
Residuals         52 2.04749 0.03937
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1


>summary(mod.bird):

Call:
lm(formula = predated ~ precipitation * temp, data = insect.df)

Residuals:
     Min      1Q  Median      3Q     Max
-0.34309 -0.12916 -0.01897  0.08454  0.57050

Coefficients:
                             Estimate Std. Error t value Pr(>|t|)
(Intercept)                  0.131144   0.104953   1.250  0.21706
precipitation                0.001331   0.057146   0.023  0.98150
tempboreal                   0.641834   0.141915   4.523 3.57e-05 ***
tempsub.alpine               0.475904   0.147962   3.216  0.00223 **
precipitation:tempboreal    -0.251021   0.076126  -3.297  0.00176 **
precipitation:tempsub.alpine -0.226366   0.078464  -2.885  0.00569 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1984 on 52 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared:  0.5105,   Adjusted R-squared:  0.4634
F-statistic: 10.85 on 5 and 52 DF,  p-value: 3.531e-07
```
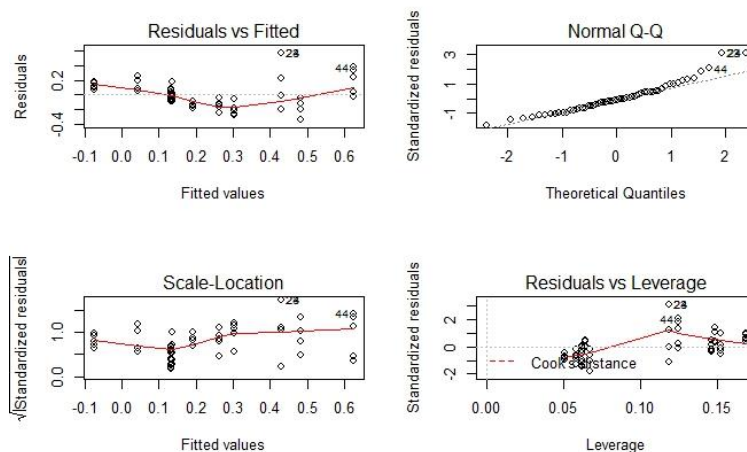
Diagnostics plot:

Figure A.1: Diagnostics plots for model of predation by insects

moda.rodent<-lm(predated~precipitation*temp, data=rodent.df)

```
> anova(moda.rodent)
Analysis of Variance Table

Response: predated
                  Df  Sum Sq  Mean Sq F value  Pr(>F)
precipitation      1 0.06299 0.062995  4.9693 0.03042 *
temp               2 0.05250 0.026250  2.0707 0.13699
precipitation:temp 2 0.04774 0.023869  1.8829 0.16299
Residuals         49 0.62116 0.012677
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> summary(moda.rodent)

Call:
lm(formula = predated ~ precipitation * temp, data = rodent.df)

Residuals:
     Min       1Q   Median       3Q      Max
-0.12937 -0.05920 -0.02314  0.03935  0.55874

Coefficients:
                             Estimate Std. Error t value Pr(>|t|)
(Intercept)                  0.041358   0.060725   0.681   0.4990
precipitation               -0.005379   0.032675  -0.165   0.8699
tempboreal                   0.106240   0.081396   1.305   0.1979
tempsub.alpine               0.212100   0.085956   2.468   0.0171 *
precipitation:tempboreal    -0.023514   0.043382  -0.542   0.5903
precipitation:tempsub.alpine -0.086130   0.046171  -1.865   0.0681 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1126 on 49 degrees of freedom
  (5 observations deleted due to missingness)
Multiple R-squared:  0.2081,   Adjusted R-squared:  0.1273
F-statistic: 2.575 on 5 and 49 DF,  p-value: 0.03805
```
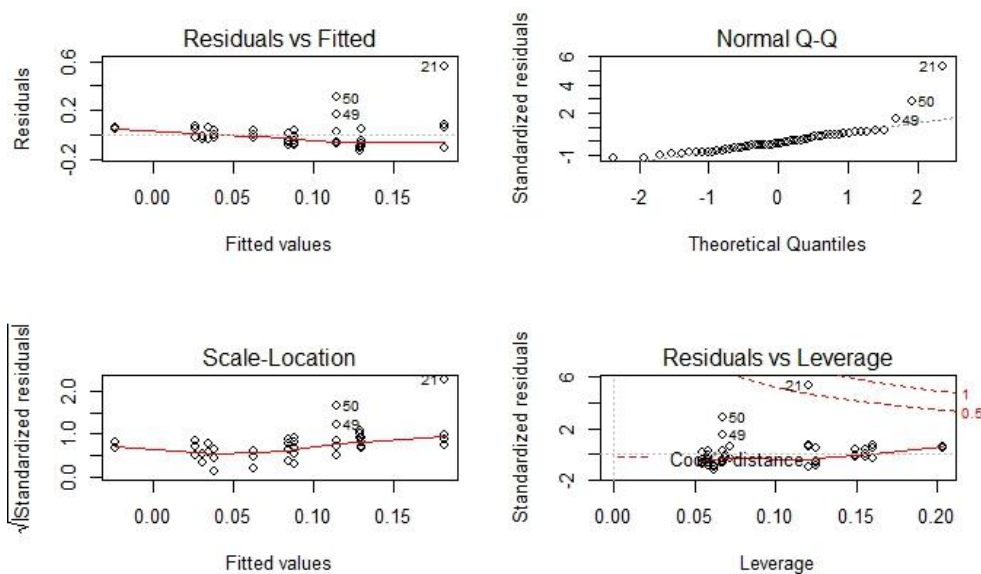
Diagnostics plot:

Figure A.2: Diagnostics plots for model of predation by rodents

Testing model for birds

mod.bird<-lm(predated~precipitation*temp, data=bird.df)

```
> anova(mod.bird)
Analysis of Variance Table

Response: predated
                 Df  Sum Sq  Mean Sq F value   Pr(>F)
precipitation     1 0.01099 0.01099  0.3768 0.541897
temp              2 1.86607 0.93304 32.0033 6.81e-10 ***
precipitation:temp 2 0.41077 0.20539  7.0448 0.001912 **
Residuals        54 1.57433 0.02915
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> summary(mod.bird)

Call:
lm(formula = predated ~ precipitation * temp, data = bird.df)

Residuals:
     Min       1Q   Median       3Q      Max
-0.35778 -0.09685 -0.02450  0.06323  0.54712

Coefficients:
                            Estimate Std. Error t value Pr(>|t|)
(Intercept)                  0.24701    0.08877   2.783  0.00741 **
precipitation                0.14585    0.04880   2.989  0.00421 **
tempboreal                  -0.03532    0.12098  -0.292  0.77142
tempsub.alpine               0.01271    0.12623   0.101  0.92015
precipitation:tempboreal    -0.20512    0.06523  -3.145  0.00270 **
precipitation:tempsub.alpine -0.23057   0.06725  -3.429  0.00117 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1707 on 54 degrees of freedom
Multiple R-squared:  0.5924,   Adjusted R-squared:  0.5546
F-statistic: 15.69 on 5 and 54 DF,  p-value: 1.603e-09
```
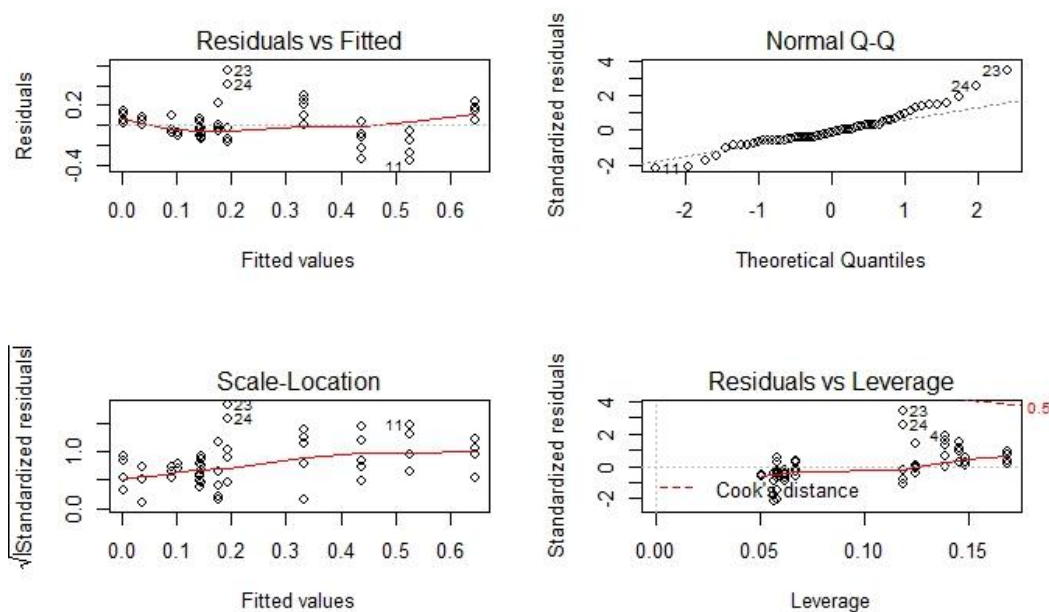
Diagnostics plot:

Figure A.3: Diagnostics plots for model of predation by birds

```
> anova(mod.all)
Analysis of Variance Table

Response: predated
                 Df  Sum Sq Mean Sq F value    Pr(>F)
precipitation     1 0.78072 0.78072 23.2876 1.263e-05 ***
temp              2 0.55048 0.27524  8.2099 0.0007968 ***
precipitation:temp 2 0.47751 0.23876  7.1216 0.0018467 **
Residuals        52 1.74331 0.03353
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> summary(mod.all)

Call:
lm(formula = predated ~ precipitation * temp, data = all.df)

Residuals:
     Min      1Q  Median      3Q     Max
-0.42680 -0.12603  0.01767  0.09266  0.50992

Coefficients:
                           Estimate Std. Error t value Pr(>|t|)
(Intercept)                 0.37545    0.09704   3.869 0.000306 ***
precipitation               0.04736    0.05519   0.858 0.394732
tempboreal                  0.18347    0.13264   1.383 0.172495
tempsub.alpine              0.19837    0.13667   1.451 0.152661
precipitation:tempboreal   -0.23424    0.07239  -3.236 0.002112 **
precipitation:tempsub.alpine -0.25490  0.07421  -3.435 0.001173 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1831 on 52 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared:  0.5092,   Adjusted R-squared:  0.462
F-statistic: 10.79 on 5 and 52 DF,  p-value: 3.768e-07
```
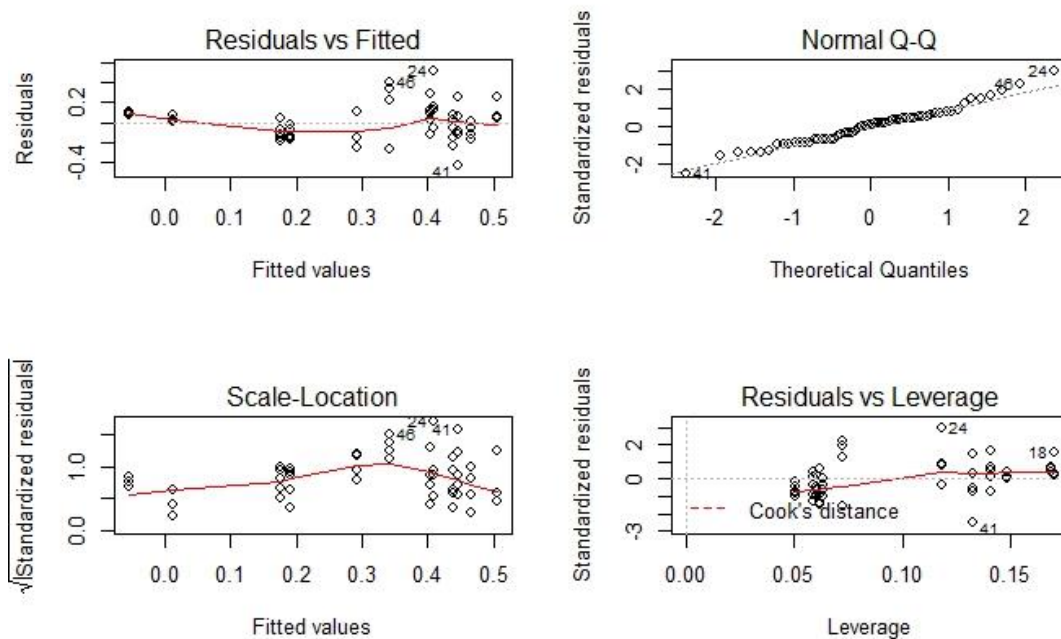
Diagnostics plot:

Figure A.4: Diagnostics plots for model of predation by all

moda.control<-lm(predated~precipitation*temp, data=control.df)

```
> anova(moda.control)
Analysis of Variance Table

Response: predated
                  Df  Sum Sq  Mean Sq F value   Pr(>F)
precipitation      1 0.13717 0.137168 11.6733 0.001238 **
temp               2 0.00373 0.001864  0.1586 0.853754
precipitation:temp 2 0.02391 0.011955  1.0174 0.368624
Residuals         52 0.61103 0.011751
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
> summary(moda.control)

Call:
lm(formula = predated ~ precipitation * temp, data = control.df)

Residuals:
     Min      1Q  Median      3Q     Max
-0.18050 -0.05338 -0.01329 0.02891 0.55950

Coefficients:
                           Estimate Std. Error t value Pr(>|t|)
(Intercept)                 0.13473    0.05836   2.309    0.025 *
precipitation              -0.03461    0.03128  -1.107    0.274
tempboreal                  0.03079    0.07829   0.393    0.696
tempsub.alpine              0.11801    0.08156   1.447    0.154
precipitation:tempboreal   -0.01207    0.04163  -0.290    0.773
precipitation:tempsub.alpine -0.05695  0.04291  -1.327    0.190
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1084 on 52 degrees of freedom
  (2 observations deleted due to missingness)
Multiple R-squared:  0.2124,   Adjusted R-squared:  0.1367
F-statistic: 2.805 on 5 and 52 DF,  p-value: 0.02569
```
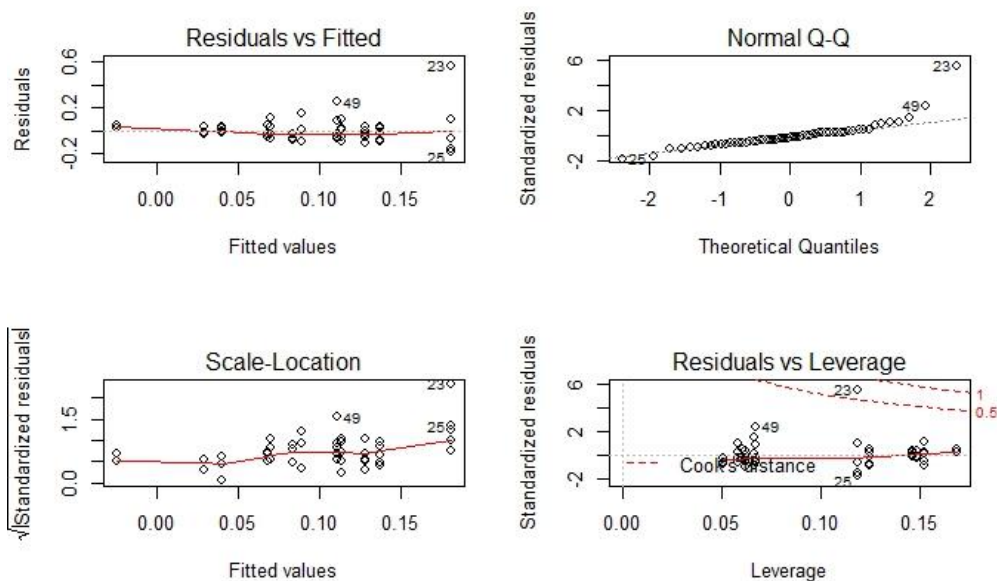
Diagnostics plot:

Figure A.5: Diagnostics plots for model of control