Elevationally biased avian predation as a contributor to the spatial distribution of geometrid moth outbreaks in sub-arctic mountain birch forest

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Abstract

1. Population dynamics and interactions that vary over a species' range are of particular importance in the context of latitudinal clines in biological diversity. Winter moth (*Operophtera brumata*) and autumnal moth (*Epirrita autumnata*) are two species of eruptive geometrids that vary widely in outbreak tendency over their range, which generally increases from south to north and with elevation.
2. The predation pressure on geometrid larvae and pupae over an elevational gradient was tested. The effects of background larval density and bird occupancy of monitoring nest boxes on predation rates were also tested. Predation on larvae was tested through exclusion treatments at 20 replicate stations over four elevations at one site, while pupae were set out to measure predation at two elevations at three sites.
3. Larval densities were reduced by bird predation at three lower elevations, but not at the highest elevation, and predation rates were 1.9x higher at the lowest elevation than at the highest elevation. The rate of predation on larvae was not related to background larval density or nest box occupancy, though there were more eggs and chicks at the lowest elevation. There were no consistent differences in predation on pupae by elevation.
4. These results suggest that elevational variation in avian predation pressure on larvae may help drive elevational differences in outbreak tendency, and that birds may play a more important role in geometrid population dynamics than the focus on invertebrate and soil predators of previous work would suggest.

Introduction

The comparison of differences in trophic interactions across latitude and elevation is a valuable area for investigation in population and community ecology, as a means to uncover how varying degrees of complexity in ecological communities affect trophic dynamics (e.g., Crête & Manseau 1996, Hanski *et al.* 2001, Hodkinson 2005, Pennings & Sillman 2005, Post 2005). Biodiversity generally decreases along latitudinal clines of climate and productivity from the equator and towards the poles (Fischer, 1960; Schemske *et al.*, 2009). Similar declines in diversity can be observed along elevational gradients, which also represent clines of climate and productivity (Rahbek, 1995). These patterns are expected to cause changes in the structure of consumer guilds which may in turn cause cascading impacts on the population dynamics of lower trophic levels (i.e., the ecosystem exploitation hypothesis: Oksanen *et al.*, 1981). In line with this prediction, some of the most well-known spatial gradients in population dynamics occur along latitudinal and elevational gradients. For many widely distributed species, populations at high latitudes – where the climate is harsh and productivity is low – show unstable dynamics, with a propensity towards cycles and outbreaks. In contrast, more southern populations – which inhabit a more productive and climatically benign environment – show comparatively stable dynamics. Examples of this includes voles in Fennoscandia, snowshoe hare in North America, several species of grouse in Europe and North America and geometrid moths in Fennoscandia (Klemola *et al.*, 2002; Ims *et al.*, 2008). In some cases, similar patterns repeat themselves along elevational gradients. For example, outbreaks of several forest insect species are most prone to occur at high elevations (Baltensweiler & Fischlin, 1988; Ruohomäki *et al.*, 1997; Hengxiao *et al.*, 1999; Kamata, 2002; Hagen *et al.*, 2007).

One of the best supported theories for latitudinal gradients in population dynamics postulates that they are linked to clines in the community structure of natural enemies (Oksanen *et al.*, 1981; Hanski *et al.*, 1991; Klemola *et al.*, 2002). According to the theory, low-productivity systems at high latitudes have a preponderance of specialized enemies, which show delayed numerical responses to changes in prey abundance, and thereby induce fluctuations in prey population dynamics. Meanwhile, more productive southern areas are postulated to have a higher diversity and abundance of generalist enemies, which are expected to have stabilizing effects on prey dynamics, owing to rapid (i.e. non-delayed) functional responses to prey abundance. If this logic is applied to elevational gradients, the importance of generalist enemies, and their stabilizing effect on population dynamics, should be expected to decline towards higher and less productive elevations, thereby explaining the tendency for prey outbreaks at higher elevations (Schott *et al.*, 2013).

The winter moth (*Operophtera brumata*) and the autumnal moth (*Epirrita autumnata*) are two species of herbivorous geometrid moths that are widely distributed in Europe, and have been observed to outbreak with greater frequency and intensity in far northern Europe than further south (Tenow, 1972; Ruohomäki *et al.*, 2000). In the north, moth outbreaks periodically cause defoliation and mortality of large areas of mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest. Spatial gradients in moth dynamics also occur locally on steep elevational gradients, where moth populations close to the treeline often display very high densities and cause severe forest damage, while populations at lower elevations remain at much lower levels. Explanations for these elevational patterns in moth dynamics have remained elusive. Previous work has examined phenological mismatch between moth larvae and their birch host plants (Mjaaseth *et al.*, 2005), predation rates, abundance and community composition of generalist pupal predators (Hansen *et al.*, 2009; Schott *et al.*, 2013) and the impact of specialist larval parasitoids (Vindstad *et al.*, 2011; Schott *et al.*, 2012). However, none of these proposed drivers have been able to explain the observed elevational differences in moth dynamics.

In the present study, we focus on a group of generalist predators that have received little attention in the study of moth population dynamics, namely insectivorous birds. The impact of birds on the population dynamics of forest insects has often been overlooked in favor of invertebrate predators and parasitoids, particularly in recent work, presumably because birds are assumed to be unable to respond numerically to caterpillar density. However, many studies have found that avian predation can have a significant impact on forest insect densities or leaf damage (e.g., Buckner & Turnock 1965, Holmes *et al.* 1979, Crawford & Jennings 1989, Marquis & Whelan 1994, Tanhuanpää *et al.* 2001, Mäntylä *et al.* 2008, Singer *et al.* 2012, Bereczki *et al.* 2014), suggesting that bird predation should receive more attention in studies of insect dynamics. Following the theoretical framework outlined above, we hypothesized that elevational trends in moth outbreak dynamics may be explained by a lower abundance and impact of generalist avian predators at high elevations. To test this hypothesis, we applied a bird exclusion treatment to estimate avian predation rates on moth larva along an elevational gradient that has a history of moth outbreaks at the treeline. In addition, we estimated the presence of avian predators along the gradient with the help of nest boxes.

While birds have received little attention in studies of moth dynamics, generalist pupal predators, especially invertebrates, have long been considered to be important drivers of the population dynamics of the winter moth (Varley & Gradwell, 1968; East, 1974; Raymond *et al.*, 2002) and the autumnal moth (Tanhuanpää *et al.*, 1999, 2001). As outlined above, previous work in coastal northern Norway failed to find elevational trends in pupal predation rates (Hansen *et al.*, 2009). However, the work by Hansen et al. reported unexplained removal of about 80 % of the experimental pupae, raising some concerns about the accuracy of the method used for recovering pupae in this study. Hence, in the present study, we re-examine the hypothesis that elevational trends in moth dynamics are caused by lower predation rates by generalist pupal predators at high elevations, using a more reliable method to recover the experimental pupae. Moreover, we replicate the study in three separate elevational gradients, including the gradient originally used by Hansen *et al.* (2009).

Materials and Methods

Study system

The study was conducted at three sites [Skogsfjord (69°55´N, 19°18´E), Storelva (69°38´N, 18°57´E) and Reinøya (70°00´N, 19°49´E)] in the coastal region of Troms County, northern Norway, during the summer of 2016 (Fig. 1). The region is characterized by an oceanic, sub-arctic climate, meaning that summers are cool with significant precipitation (average temperature in July: 12 to 13 °C), and winters are relatively mild (average temperature in January: -2 to -5 °C). The forest in the region is strongly dominated by mountain birch, with some scattered occurrences of rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and planted stands of spruce (*Picea abies*). The landscape is dominated by fjords and steep mountains, and forests of mountain birch typically occur as narrow belts between the sea and the alpine tree line, at about 250-300 meters above sea level.

Three species of spring-feeding geometrids (winter moth, autumnal moth and scarce umber moth (*Agriopis aurantiaria*)) are the most important insect folivores at the study sites (Schott *et al.*, 2013). These three moths are all univoltine, polyphagous species that feed primarily on mountain birch in northern Fennoscandia during their larval stage. The larval stage lasts from around birch budburst, usually occurring in mid-May, to late June or early July. Larvae then drop off of host trees to pupate in soil or ground cover, and remain as pupae until September and October, when adults emerge. Females of scarce umber moth and winter moth are flightless, while autumnal moth females are capable of flight. Adults mate on trees, and eggs are subsequently laid on bark and twigs, where they overwinter until the following spring.

Larval predation experiment

To assess elevational variation in bird predation pressure on moth larvae, we established a manipulative field experiment in the Skogsfjord study area (Fig. 1). The experiment was established on a slope covered with mature mountain birch forest, and had five sampling stations on each of the altitudes 50, 100, 170 and 240 meters above sea level. Within elevation, stations were arranged in a horizontal transect, with a spacing of roughly 400 meters between stations. The distance between transects at neighboring elevations was between 400 and 750 m.

Two exclusion treatments and a control treatment were applied haphazardly to branches on 10 trees at each station. On each tree, one branch was covered with a 45 cm x 80 cm bag of 0.47 x 0.77 mm mesh (Howi insect netting type L; Howitec, Bolsward NL) designed to prevent dispersal and all predation, while another was covered by roughly 4 cm bird netting over looped wire attached to branches designed to prevent only avian predation. A third branch was marked and left unmanipulated as a control. With this design, a difference between the mesh bag and bird netting treatments could be interpreted as invertebrate predation or dispersal, and a difference between bird netting and controls as avian predation. Each section of branch contained roughly 35-45 leaf clusters, and was checked before placing treatments to make sure there was at least one naturally occurring geometrid larva present (almost entirely winter moth, but inclusive of some autumnal and scarce umber moth larvae). Larval phenology in elevational gradients in the study region is generally delayed by roughly one week at 240 m relative to 30 m (Mjaaseth *et al.*, 2005). Therefore, to match the phenological window within which we measured predation, manipulations at the 170 m and 240 m stations were set up 5 days later than those at the 50 m and 100 m stations (16-17 June and 22 June respectively). Fourteen days after setup of the experiment (30 June-1 July and 6 July), the branches were cut down and shaken into a large plastic box until all geometrid larvae had detached. Subsequently, all larvae in the box were sorted to species and counted. Larvae were mostly 2-3rd instar at the beginning of the experiment, and 4-5th at the end. Experience with error generated by undercounting in field counts of early instar larvae in previous work led us to choose not to conduct initial counts.

Background larval densities (i.e., not on experimental branches) were also measured at each sampling station using standard methods used for long-term monitoring at this and other sites in the region (Hagen *et al.*, 2003), on 21 June for 50 & 100 m, and 1 July for 170 & 240 m. Density measurements were conducted by haphazard sampling of 10 equally sized mountain birch branches (length about 60– 80 cm), cut 1–2 m above the ground from different trees in a radius of 30 m around the sample stations. The branches were shaken in a large plastic box until all larvae had detached and the number of larvae was counted. Density measurements have been conducted every year since 2008 at Skogsfjord, in order to monitor the long-term dynamics of moth populations.

To assess the presence of avian predators at the sampling stations, two wooden nest boxes (32 mm entrance hole) were installed at each station. The boxes were located 60-90 m apart, on opposite sides of the sampling station. The boxes are part of a long-term study of bird population responses to larval densities, and have been examined annually at the time of larval density sampling since 2008. At each visit, the presence or absence of nesting birds was recorded and the species, the number of eggs and the number of chicks counted. Boxes were visited in 2016 at the same dates as larval density monitoring was conducted. Two species of cavity-nesting birds commonly use nest boxes in the study area; the great tit (*Parus major*) and the pied flycatcher (*Ficedula hypoleuca*). Both species prey heavily on insect larvae during the breeding season, but also utilize a variety of other insect prey items (Haftorn, 1971).

Pupal predation experiment

Pupal predation rates were assessed by experimentally exposing winter moth pupae to predators in the field. To obtain pupae, winter moth larvae were collected in June from natural populations in the study region. The larvae were reared to maturity on birch foliage in large plastic containers (32l & 50l), with mesh ventilation and sand on the bottom for cocoon formation. In July, pupae were sifted from the sand, and glued to double layer 4x4 cm jute burlap squares using melted beeswax, which were then strung in groups of three on 1 m sections of twine (Smith, 1985; Cook *et al.*, 1994; Elkinton *et al.*, 2004). Twenty sets of three pupae were deployed at each of two elevations at three sites: Skogsfjord (50 m & 240 m), Reinøya (30 m & 240 m), and Storelva (50 m & 240 m), all of which are previously established sampling locations for long term monitoring of larvae (Fig. 1). Each set of three pupae was treated as a sampling unit, resulting a total sample size of N=120. Pupae were set on a 4x5 grid, with each string spaced roughly 10 m apart. The squares of burlap were set just under the soil or groundcover surface, with pupae facing up, and marked with flagging attached to a wire to facilitate relocation. Pupae were deployed on July 27-29 and recovered after 21 days on August 17-19, when they were transported to the laboratory. Missing pupae were considered to be predated, though strings or sections of string that were disturbed (i.e., pulled out of the soil) previous to recovery were excluded from analyses (N= 4 strings, 6 pupae). After collection of pupae, pupae were dissected to assess parasitism status.

Statistical analyses

The effect of our predator exclusion treatments during the larval stage was analyzed using a log link Poisson generalized mixed model. Larval count at the end of the experimental period was taken as the response variable, while elevation (treated as a factor variable), treatment and their interaction were taken as predictors. Sampling station was included as a random effect.

We also assessed how bird predation rates were influenced by elevation, bird density, and background larval density. For this we calculated an average effect size of bird netting for each station. This effect was taken as average larval count in bird netting minus average larval count on control branches. The effect size was subsequently taken as the response variable in a linear model with elevation as the predictor. To determine the relationship between bird density and predation rates, a linear model was fitted to the predation effect as the response variable and nest box occupancy (1 or 2 boxes occupied at each station) and total egg and nestling count for both nest boxes at each station as predictors. In addition, to assess whether predator saturation was occurring, the predation treatment effect was regressed against background larval density in a linear model, with density as a simple linear effect, a second order polynomial effect, and as an effect of log density (each as a separate model to avoid collinearity). In the event of predator saturation, the treatment effect would be expected to decline with increasing larval density. The netting treatment effect was tested for normality using normal quantile-quantile plots and a Shapiro normality test.

Proportional survival of pupae (out of 3 on each string) was analyzed using a logit link proportional logistic GLM, with high and low elevation (30 and 50 m vs 240 m), site and their interaction as predictors.

Models were implemented in R (Version 3.3.1, R Core Team, 2016), using lme4 for mixed models (Bates *et al.*, 2014) and ggplot2 for graphics (Wickham, 2009). Wald Z-tests built into lme4 were used to generate p-values for mixed models, which were confirmed using 95% profile likelihood confidence intervals. Original untransformed parameter estimates and profile confidence intervals are reported in the text, while inverse transformed least squares means and asymptotic confidence intervals generated by the lsmeans package were used in plotting to improve interpretability of results (Lenth, 2016).

Results

Spatiotemporal dynamics of birds and moths

The autumnal moth displayed a single population peak (2014) during the study period (Fig. 2a), while two peaks were observed in the winter moth (2008 and 2015) (Fig. 2b). During all of these population peaks, moth densities were consistently higher at 170 and 240 m than at the two lowest elevations in the gradient. This pattern was especially pronounced in 2008, when the winter moth reached extremely high densities and caused complete defoliation at 240 m, while densities remained low and defoliation was nearly undetectable at 50 and 100 m.

The proportion of nest boxes occupied by pied flycatchers (Fig. 2c) and great tits (Fig. 2d) fluctuated considerably throughout the study period. However, both species showed a relatively clear tendency to prefer nesting at 50 and 100 m in most years.

Larval predation experiment

The fine mesh and bird netting treatments had significantly higher larval counts than the control treatment (β fine mesh=0.89 [CI: 0.61, 1.21], z=5.7, P<0.001, β bird netting=1.14 [CI: 0.85, 1.44], z=7.5, P<0.001), though were not significantly different from each other (overlapping 95% confidence intervals). This suggests a significant effect of bird exclusion on larval densities, but no added effect of also excluding invertebrate predators or preventing dispersal. There was a significant interaction between the experimental treatment and altitude owing to smaller effect of the fine mesh and bird netting treatments at 240 m of elevation than 50 m (β fine mesh=-0.47 [CI: -0.86, -0.07], z= -2.3, P<0.001, β bird netting=-0.69 [CI: -1.08, -0.32], z=-3.6, P<0.001). There was a significant effect of bird exclusion at all elevations except at 240 m (Fig. 3). The predation rate on larvae, measured as a percentage of the average larval count of controls relative to bird netting, was 68% at 50 m, 66% at 100 m, 52% at 170 m, and 36% at 240 m.

There was no significant relationship between background larval density and treatment effect in the linear models (β density=-0.023±0.016, df=18, t=-1.5, P=0.15; β density^2=-0.0005±0.0007, df=18, t=-1.8 P=0.51, β log density=-0.69±0.38, df=18, t=0.6, P=0.09), indicating that the elevational patterns in the predation rate were not caused by predator saturation effects. Elevation was a better predictor of treatment effect than background larval density (multiple R^2= 0.40 vs. 0.15). Neither nest box occupancy or egg and nestling count were predictive of treatment effect (β bird presence =-0.107±0.468, df=18, t=-0.23, P=0.82, β bird count= 0.001±0.058, df=18, t=-0.023, P=0.98). Egg and nestling counts were significantly higher at 50 m than higher elevations (negative effects with P<0.001 for all elevations compared to the reference elevation of 50 m [100m: β =-0.76, z=-4.6, 170m: β =-0.53, z=-3.5, 240m: β =-0.57, z=-3.8], Fig 4a), but nest box occupancy showed no elevational trend ($P>0.05$ and negligible effects of all elevations compared to the reference elevations of 50 m, Fig 4b). Egg and nestling counts were 43% higher at the lowest elevations than the highest elevations.

Pupal predation experiment

In general, pupal survival was high at most sites and elevations (overall survival: 75.3%), except at the 240 m plot at Reinøya (survival: 37.5%). In the model for pupal survival, this resulted in a significantly lower predation rate at Reinøya than the other sites ($\beta=-2.38$, df=112, $z=-5.08$, $P<0.001$) and a significant interaction between the site of Reinøya and the 240 m elevation (β 240 m = 3.39 [CI: -1.80, -0.15], df=112, $z=4.57$, $P<0.001$) but no other significant effects (fig. 5). Parasitism rates of pupae were quite low (18.8%), with 17% overall at high elevation and 20% at low elevation. The only identifiable parasitoids were larval-pupal parasitoids, *Agrypon flaveolatum.* As a larval-pupal parasitoid *A. flaveolatum* attacks larvae before pupation, and thus attack rates could not have been affected by the pupal predation experiment.

Discussion

The tendency for moth outbreaks to be most intense at high elevations has been a long-standing enigma in the study of moth population dynamics in Fennoscandia. The present study sheds some new light on this matter, by demonstrating that elevational trends in the impact of avian predators may contribute to these elevational outbreak patterns. Bird netting had a strong effect on larval survival at the lower elevations, while there was only a marginal effect of the netting treatment at the treeline. Thus, the estimated avian predation rate was almost twice as high at the lowest elevation compared to the highest. In accordance with this, the long-term occupancy rates of cavity-nesting passerines were consistently lower at high elevations. These findings suggest that birds may have a substantial suppressive effect on moth densities at low elevations, while moth populations at higher elevations experience a release from this suppression. This is in accordance with previous work by Tanhuanpää et al. (2001), who documented high avian predation rates in an *E. autumnata* population in southern Finland, and suggested that birds (along with invertebrate predators) contribute to the suppression of outbreaks in southern populations. It conforms with predictions that generalist predators should be more important at lower elevations and latitudes (e.g.,Klemola *et al.*, 2002) though there is no evidence that specialist natural enemies play a correspondingly lesser role at lower elevations in coastal northern Norway (Vindstad *et al.*, 2011; Schott *et al.*, 2012). Our results also align with a large body of research showing that predation by birds can suppress the densities of herbivorous insects in natural and agricultural systems (Holmes, 1990; Kirk *et al.*, 1996). Although it is unlikely that predation by birds alone is sufficient to prevent outbreaks (although some birds do respond numerically to geometrids; see Lindström, 1987; Enemar *et al.*, 2004; Hogstad, 2005), it seems plausible that avian predation in combination with other factors could dampen the peaks of geometrids at lower elevations.

It is important to emphasize that the pied flycatchers and great tits inhabiting our nestboxes represent only a small subset of the bird community in the study system. At least 20 other passerine species occur in Scandinavian mountain birch forest (Vindstad *et al.*, 2015). Some of these, like the brambling (*Fringilla montifringilla*), the willow warbler (*Phylloscopus trochilus*) and the common redpoll (*Carduelis flammea*), are very common and prey heavily on moth larvae (Hogstad, 2005). Thus, incomplete representation of the bird community may explain why there was no relationship between measured bird densities in nestboxes and the bird exclusion treatment effects.

Past work on the effect of predators on moth population dynamics have tended to emphasize the regulating effects of generalist pupal predators, especially for the winter moth (Varley & Gradwell, 1968; East, 1974; Tanhuanpää *et al.*, 1999, 2001; Raymond *et al.*, 2002). However, substantial evidence now suggests that pupal predation cannot account for the distinct elevational structuring that is often observed in moth dynamics in Fennoscandia. Both the present study and former work by Hansen *et al.* (2009) failed to find elevational trends in pupal predation rates that could account for the elevational patterns in moth dynamics. Schott *et al.* (2013) obtained a corresponding negative result in their study of elevational patterns in the community structure of invertebrate generalist predators. Hence, it seems safe to conclude that release from pupal predation alone probably does not explain the tendency for moth populations to outbreak at high elevations (Klemola *et al.*, 2014). This conclusion is somewhat at odds with that of Tanhuanpää *et al.* (1999), who documented lower impacts of pupal predation in northern (outbreaking) than southern (non-outbreaking) populations of *E. autumnata*, and suggested that release from pupal predation contributes to outbreak formation in the north. Thus, currently available evidence suggests that the mechanisms underlying the development of moth outbreaks at high latitudes and elevations are not fully known, and possibly quite different.

The relatively low pupal predation rates shown in the present study suggest that there may indeed have been problems with the methods used for recovering pupae by Hansen *et al.* (2009), who reported predation rates of ca. 90%, in contrast to overall predation rates of just under 25% in the present study. However, our present results align with those of Hansen *et al.* (2009) in the sense that no consistent elevational pattern in predation could be detected across the gradients included in the study. Though it could be argued that the methods used in the present study might have deterred predators due to excessive manipulation of pupae and thus generated low predation rates, the relatively high predation rate of 62.5% at 240 m on Reinøya suggests otherwise. This method has also been successfully used in multiple other predation studies on pupae (Smith, 1985; Cook *et al.*, 1994; Elkinton *et al.*, 2004).

Studies of predation rates in outbreaking moth populations can be difficult to interpret because predator saturation may occur when moth densities are high. Hence, it may be impossible to determine whether low predation rates in a high-density moth population are a cause or a consequence of the high densities. This problem has been encountered in previous work that compared parasitism rates between elevations with contrasting moth densities (Vindstad *et al.*, 2011). In the present study, we circumvented this problem by conducting our experiments in a non-outbreak situation, when predator saturation was not likely to occur at any elevation. The fact that the estimated avian predation rates (i.e., station-level effect sizes between controls and coarse mesh treatments in the predator exclusion experiment) were not statistically related to background larval density confirms that predator saturation is unlikely to have affected our results. It therefore seems reasonable to attribute the lower predation rates at high elevations to lower densities of birds and/or lower bird foraging activity.

Our results in the present study highlight a number of valuable directions for further research. First, our results emphasize the importance of avian predation and generally predation on the larval stage over the pupal stage for elevational differences in geometrid dynamics. This suggests that the traditional focus on pupal predation in studies of moth dynamics should be reconsidered, and that greater attention to avian predation is warranted. Second, the interpretation of our results would be greatly aided by a complete census of the insectivorous bird community at different elevations. Automated sound stations are increasingly used for such purposes (e.g., Holmes *et al.* 2014, Stevenson *et al.* 2015) and could be useful also in our system. Finally, our results are based on a single year of data, and more long-term studies of avian predation along altitudinal gradients are clearly necessary to fully substantiate our conclusions.

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Conflicts of Interest

The authors declare no conflicts of interest.

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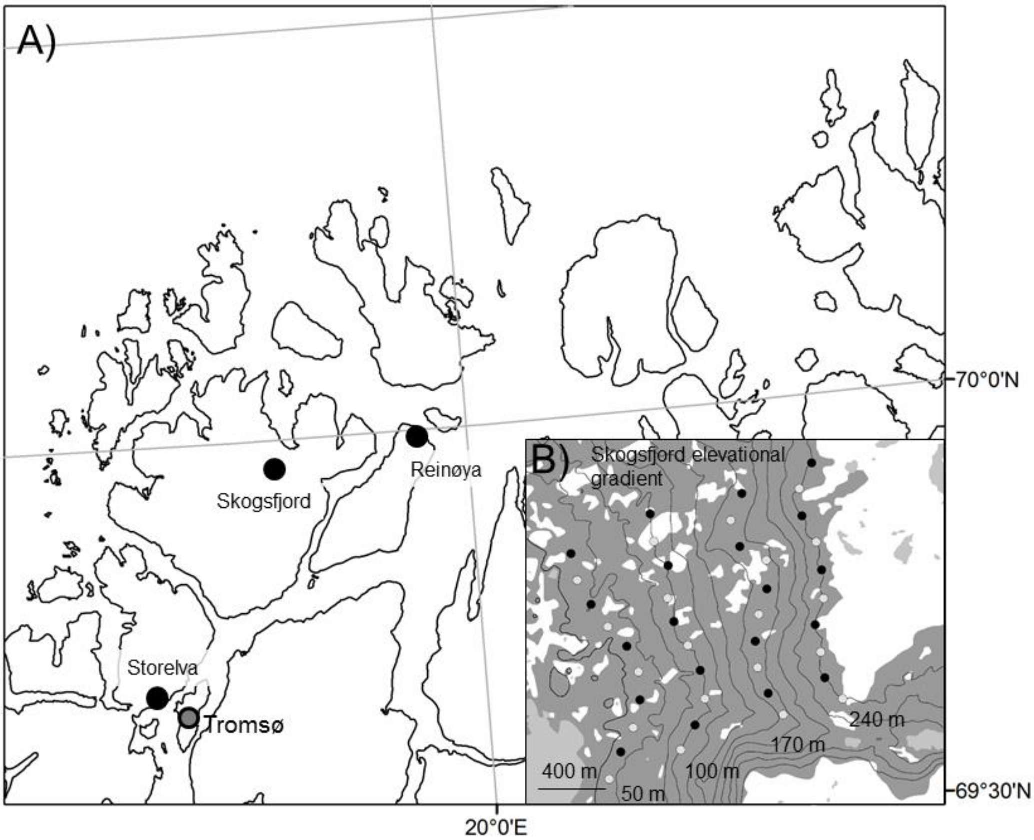

Figure 1. (a) Map of the three elevational gradients, Skogsfjord, Reinøya and Storelva in Troms County, northern Norway. (b) A detailed map of the Skogsfjord elevational gradient with the 20 samplings locations used for the larval predation experiment as unfilled circles. The long term monitoring of larval and bird populations takes place at all 40 sampling locations (filled and unfilled circles). Background shading on (b) shows the distribution of birch forest.

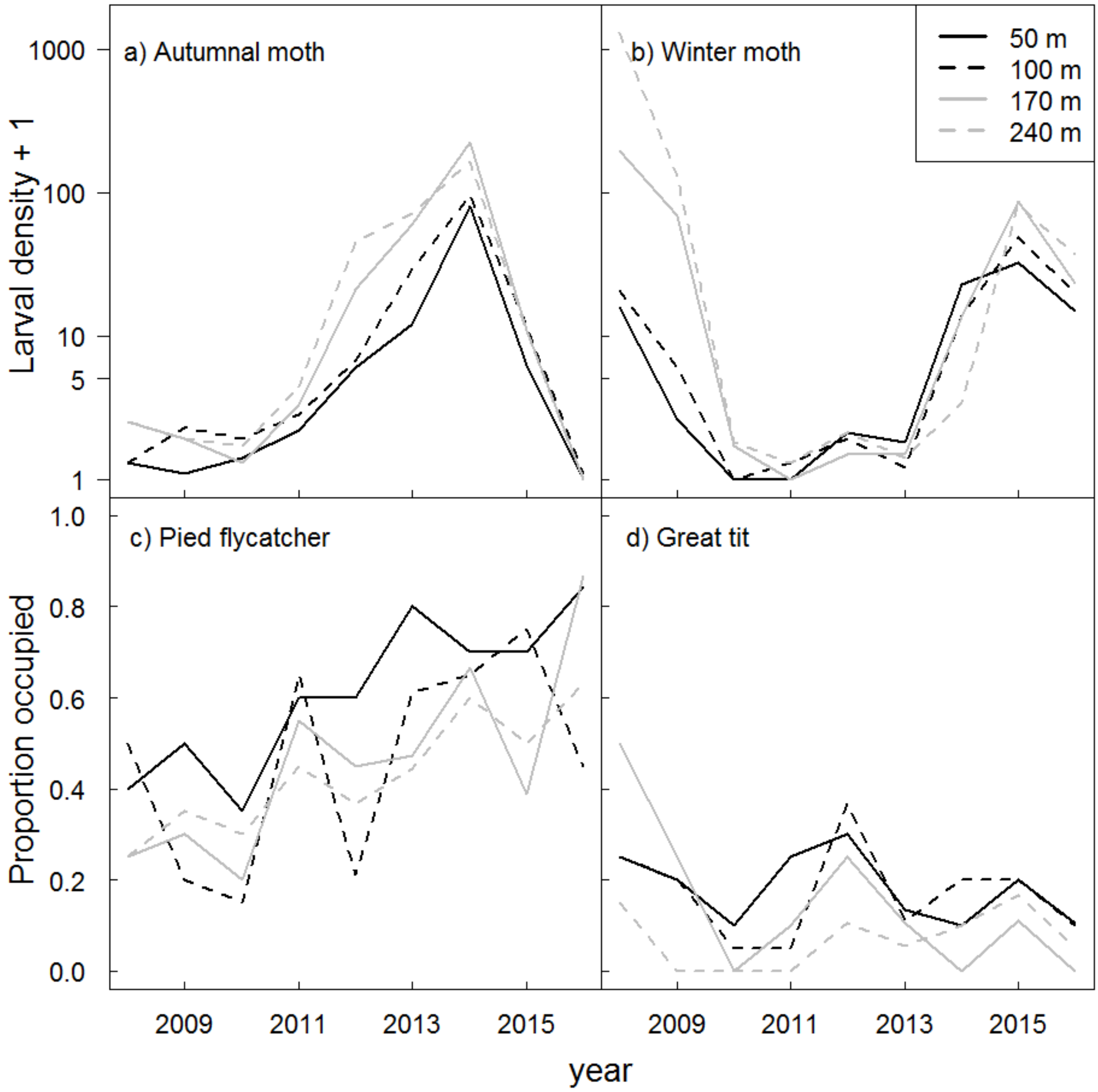

Figure 2. Population density indices of autumnal moth (a) and winter moth (b), and nest box occupancy of pied flycatchers (c) and great tits (d) at four different elevations at Skogsfjord for the years 2008 – 2016. Larval density index refers to the number of larvae per 10 birch branches (mean across the 10 sampling stations within each altitude). Nest box occupancy refers to the proportion of nestboxes occupied out of a total of 20 boxes per elevation.

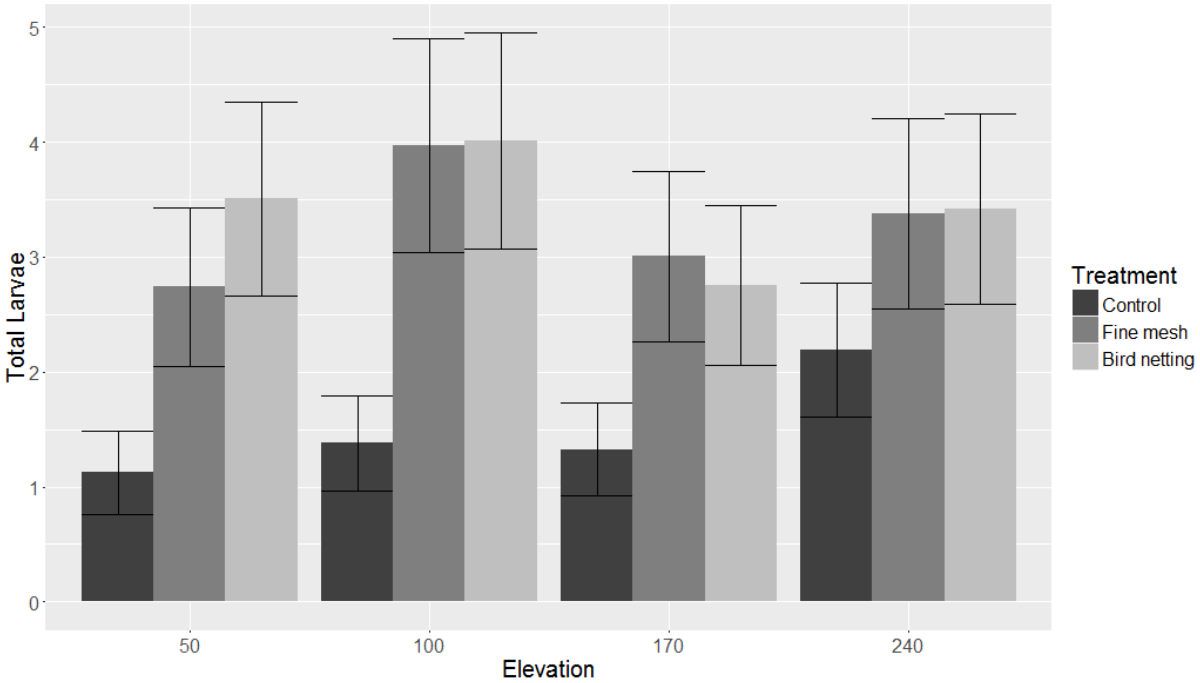

Figure 3. Model-derived mean estimates of larval count by exclusion treatment and elevation, with asymptotic 95% confidence intervals.

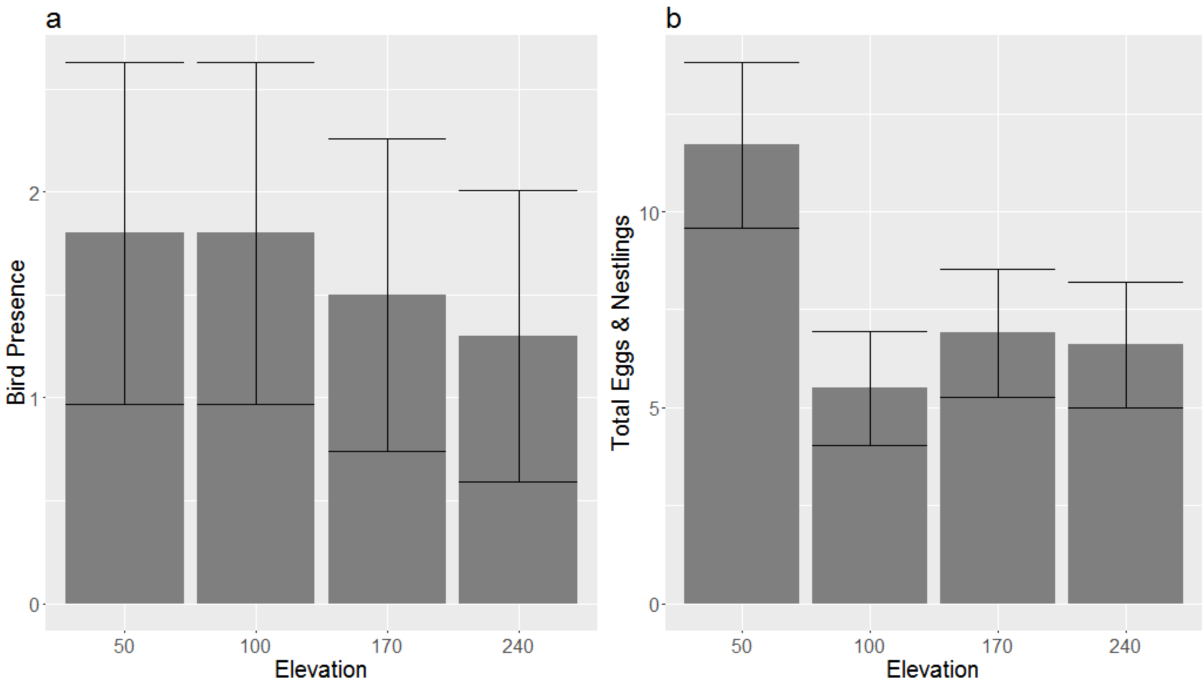

Figure 4. (a) Estimated bird occupancy out of two nestboxes at stations by elevation error and (b) estimated total eggs and nestlings per station by elevation, from model-derived mean estimates, both with asymptotic 95% confidence intervals.

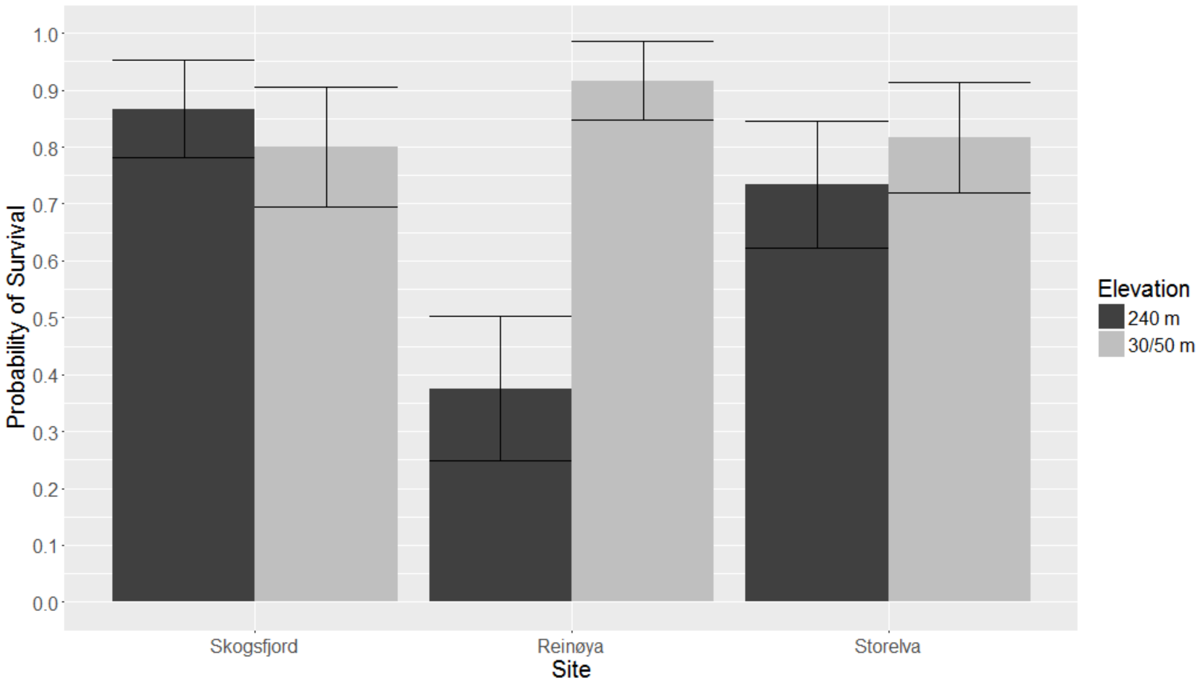

Figure 5. Model-derived mean estimates of pupal survival by elevation and site, with asymptotic 95% confidence intervals.