

Predator release from invertebrate generalists does not explain geometrid moth (Lepidoptera: Geometridae) outbreaks at high altitudes

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Abstract—Outbreaks of geometrid defoliators in subarctic birch forest in Fennoscandia often occur at high altitude in a distinct zone along the tree line. At the same time, moth larvae may not have an impact on the forest at lower altitude. Directly adjacent outbreak and nonoutbreak areas offer unique opportunities for studying the underlying mechanisms of outbreaks. Within two altitudinal gradients in coastal northern Norway, we investigated whether altitudinal outbreaks might be caused by release from pupal predation by ground-dwelling invertebrates such as harvestmen (Opiliones), spiders (Araneae), rove beetles (Coleoptera: Staphylinidae), carabid beetles (Coleoptera: Carabidae), and other beetles (Coleoptera). We predicted a consistently higher abundance of such generalist predators at low versus high altitudes. Our results did not support this prediction. There was no consistent altitudinal variation in the abundance of predators that could be related to zonal moth outbreaks in the birch forest slopes. In addition, none of the predator groups investigated showed any numerical response to a distinct outbreak of winter moth that took place during the course of the study. Consequently, localised moth outbreaks at the altitudinal tree line in northern Norway cannot be explained by the release from pupal predation by the predator groups examined here.

Résumé—Des éclosions massives de géométridés défoliateurs dans les forêts subarctiques de bouleaux de Fennoscandie se produisent souvent à haute altitude dans une zone distincte le long de la ligne des arbres. Au même moment, les larves des lépidoptères peuvent être sans impact sur la forêt à une altitude inférieure. Ces zones directement adjacentes avec et sans éclosions représentent des occasions uniques pour étudier les mécanismes sous-jacents aux éclosions. Sur deux gradients d'altitude sur la côte nord de la Norvège, nous avons vérifié si les éclosions saisonnières pouvaient être dues à la réduction de la prédation des nymphes par les invertébrés vivant au sol, tels que les opilions (Opiliones), les araignées (Araneae), les staphylins (Coleoptera: Staphylinidae), les carabes (Coleoptera: Carabidae) et les autres coléoptères (Coleoptera). Nous avons prédit des densités toujours plus élevées de ces prédateurs généralistes aux basses altitudes qu'aux altitudes plus élevées. Nos résultats n'appuient pas cette prédiction. Il n'existe pas de variation régulière de l'abondance des prédateurs en fonction de l'altitude qui pourrait être mise en relation avec les éclosions dans des zones particulières le long des pentes des forêts de bouleaux. De plus, aucun des groupes de prédateurs étudiés n'a montré de réponse numérique à une éclosion bien marquée de l'arpenreuse tardive survenue au cours de l'étude. En conséquence, il n'est pas possible d'expliquer les éclosions localisées de lépidoptères au niveau de la ligne des arbres dans le nord de la Norvège par la réduction de la prédation des nymphes par les groupes de prédateurs examinés dans notre étude.

Introduction

Population outbreaks of forest insects are conspicuous events as they often result in large-scale

defoliation of forests (Baltensweiler 1993; Jepsen *et al.* 2011; Kayes and Tinker 2012). The spatial delineation of outbreaks in alpine forests is in many cases tied to topographical features such as

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altitude (Baltensweiler 1993; Kamata 2002; Kharuk *et al.* 2007; Schott *et al.* 2010) and the transitions between affected and unaffected areas may be abrupt (Hunter *et al.* 1991; Raymond *et al.* 2002; Hagen *et al.* 2007). The adjacency of areas with contrasting dynamics offers opportunities for testing hypotheses about which mechanisms promote versus inhibit population outbreaks (Maron *et al.* 2001; Raymond *et al.* 2002).

In northern Fennoscandia, population outbreaks of the two geometrid defoliators autumnal moth (*Epirrita autumnata* (Borkhausen); Lepidoptera: Geometridae) and winter moth (*Operophtera brumata* (Linnaeus); Lepidoptera: Geometridae) show a distinct altitudinal distribution (Tenow 1972; Hågvar 1976; Ruohomäki *et al.* 1997; Hagen *et al.* 2007). In sloping terrain, the highest larval abundances of both species tend to be found at intermediate to high altitudes, causing defoliation in distinct zones that follow the altitudinal tree line. This phenomenon is especially conspicuous in the mountainous coastal region of northern Norway (Hagen *et al.* 2007). Consequently, tree defoliation and the subsequent outbreak effects (such as fertilisation) on the forest ecosystem can be severe close to the tree line, while the forest at lower altitudes (typically just a few hundred metres away from the outbreak zone) may remain largely unaffected. Similar altitudinal outbreak patterns have been found for other herbivorous insects and in other geographic regions and forest ecosystems, such as larch bud moth (*Zeiraphera diniana* (Guenée); Lepidoptera: Tortricidae) in the European Alps (Baltensweiler 2008; Johnson *et al.* 2010), winter moth in Scotland, United Kingdom (Raymond *et al.* 2002) and pine sawfly (*Neodiprion xiangyunicus* (Xiao and Huang); Hymenoptera: Diprionidae) in China (Hengxiao *et al.* 1999).

In topographically varied terrain in the coastal districts of northwestern Fennoscandia, outbreaks can be extremely local (Hagen *et al.* 2007). In contrast, they may expand over hundreds of square kilometres (Jepsen *et al.* 2009) in topographically more homogenous terrain, such as the interior and coastal eastern parts of northern Fennoscandia. The mechanism shaping this distinct topographical pattern, in which geometrid outbreak amplitudes appear to be dampened at lower altitudes, is not known. Mortality of eggs during temperature inversion episodes in winter

has been offered as an explanation for the same pattern observed at continental localities (Tenow and Nilssen 1990; Virtanen *et al.* 1998; Virtanen and Neuvonen 1999), but this fails to explain the occurrence of altitudinal abundance gradients in mild coastal regions, where temperatures never drop to levels critical for geometrid egg survival (Hagen *et al.* 2007). Interestingly, on a regional scale (*e.g.*, from south to north in Fennoscandia) there is a similar pattern in moth outbreak amplitude as found in altitudinal gradients of northern Fennoscandia. Outbreak amplitudes of *E. autumnata* and *O. brumata* are high in northern Fennoscandia and gradually dampened towards the south (Tanhuanpää *et al.* 1999; Klemola *et al.* 2002). It has been hypothesised that this large-scale geographical gradient in moth outbreak dynamics, along with similar dynamics in other herbivores such as voles (Mammalia: Cricetidae) (Hansson and Henttonen 1988; Turchin and Hanski 1997), may be caused by the diverging effects of generalist versus specialist predators (Tanhuanpää *et al.* 1999; Klemola *et al.* 2002). Accordingly, generalist predators (which are expected to dampen prey abundance fluctuations) dominate the food web in high-productivity regions (the south) while specialist predators (which are expected to amplify prey abundance fluctuations) dominate food webs in low-productivity regions (the north) under harsher environmental conditions (Klemola *et al.* 2002). Following this logic, small-scale altitudinal gradients in moth outbreaks might be explained by a release from generalist predators at high altitudes, characterised by relatively low temperatures, low productivity, and consequently low generalist predator abundance. Conversely, a dampening of moth outbreaks due to regulation by high abundance of generalist predators could take place at low altitudes.

In the three-year study reported here, we evaluated this hypothesis in two altitudinal gradients in northern Norway. The study was carried out in the mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti; Betulaceae) forest and we assessed the spatial and temporal variation in the abundance of five groups of ground-dwelling generalist invertebrate predators. If generalist invertebrate predators regulated low-altitude moth populations, we would expect to find consistently higher predator abundances at low altitudes.

Materials and methods

Study system and design

The study was carried out during the years 2008–2010 at the two localities Skogsfjord and Storelva in the coastal district of Troms County in northern Norway (Fig. 1). Both sites were characterised by continuous mature mountain birch forest. At each locality the study design consisted of four transects at increasing altitude from close to sea level to the tree line (*i.e.*, at 50, 100, 170, and 240 m). Each transect was sampled at 10–12 replicated sampling stations with 200 m intervals (Fig. 1). The abundance of geometrid larvae at each sampling station was estimated annually in late June to early July by haphazard sampling of 10 equal-sized mountain birch branches (length about 60–80 cm), cut ~1–2 m above the ground from 10 different trees (one branch per tree) in a

radius of ~30 m around the sampling stations. The branches were carefully shaken in a large plastic box until all larvae had detached and the number of larvae were subsequently counted and determined to species (Hagen *et al.* 2003; Ims *et al.* 2004; Mjaaseth *et al.* 2005).

The two study sites differed in their history of moth dynamics. The geometrid moth communities at both localities were dominated by *E. autumnata*, *O. brumata*, and *Agriopis aurantiaria* (Hübner) (scarce umber moth). All three species are polyphagous with similar, univoltine life cycles and nonoverlapping generations. Larvae of all species feed on birch foliage and drop to the forest floor for pupation in the soil approximately during late June/early July, depending on altitude. The pupal stage lasts for approximately three months and adult moths eclose during September/October. The geometrid *A. aurantiaria* is a relatively new species in our study system, which invaded part

Fig. 1. A map of the study region in Troms County, northern Norway, with the two localities Skogsfjord (SK) and Storelva (ST). The four transects within each location were located at 50, 100, 170, and 240 m. Each transect had 10–12 sampling stations separated by 200 m (small black dots in inserted detail).

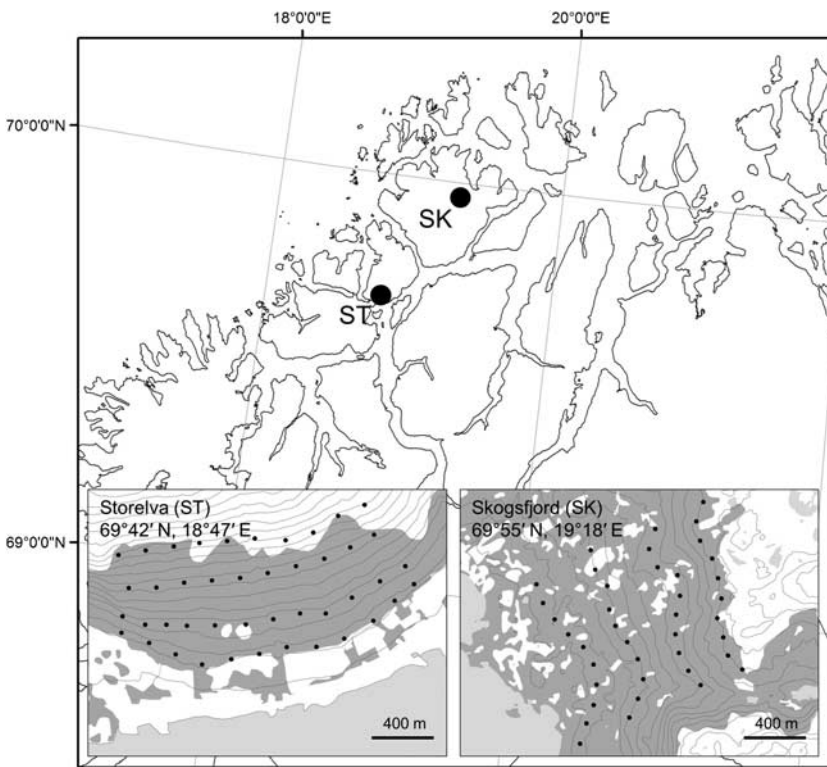
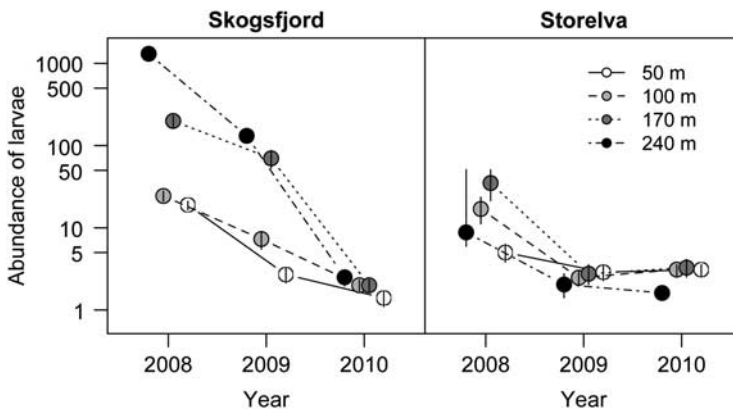


Fig. 2. Altitudinal variation in the abundance of moth larvae at the two localities Skogsfjord and Storelva, Norway. Both outbreak intensity and the tendency for larval abundances to increase with altitude were more pronounced at Skogsfjord. Error bars correspond to standard errors (SE).



of the study area during the years 2004–2005. It is now established at Storelva but not so at Skogsfjord. Recently (~2006–2009, Jepsen *et al.* 2009), the forest at Skogsfjord has experienced a massive population outbreak of *O. brumata* with a steep altitudinal gradient in moth abundance. Mean abundance at the tree line in 2008 was around 1300 larvae per 10 branches, as opposed to <20 larvae per 10 branches at the lowest altitude (Fig. 2). Moth densities at the tree line had decreased by a factor of 10 in 2009 (130 larvae) and were hardly detectable in 2010 (1.5 larvae; Fig. 2). At Storelva, by contrast, larval abundances were comparably low and less variable between altitudes and years (Fig. 2). The moderate peak in moth abundance at Storelva in 2008 was mainly caused by *A. aurantiaria* (Jepsen *et al.* 2011), which constituted on average >90% of the total number of larvae. *Epirrita autumnata* was the least abundant of all three moth species at both localities (on average 2% of the total number of larvae at Skogsfjord and 4% at Storelva).

Abundance indices of invertebrate predators

To assess the relative abundances of invertebrate predators throughout the altitudinal gradients, each sampling station (40 at Skogsfjord and 44 at Storelva) was equipped with eight pitfall traps, arranged on two perpendicular lines centred on the sampling station. The traps were dug into the ground ~2 and 4 m from the centre of the sampling station. Pitfall traps were supplied with a diluted solution of glycol

and rinsing agent and activated in mid-August. Trapping continued for three weeks until shortly before adult moths eclosed in September. Samples were transported to the laboratory for sorting. Several groups of invertebrate predators are known to prey on moth larvae/prepupae and pupae. Accordingly, we identified and counted the number of specimens of five different functional groups of invertebrate predators: (1) harvestmen (order: Opiliones) (Ashby 1974); (2) spiders, mainly (but not exclusively) wolf spiders (Araneae: Lycosidae) (Nyffeler 1999); (3) ground beetles (Coleoptera: Carabidae) (Frank 1967); (4) rove beetles (Coleoptera: Staphylinidae) (Horgan 2005); and (5) other predatory beetles (Coleoptera, *i.e.*, carnivorous beetles not belonging to Carabidae and Staphylinidae).

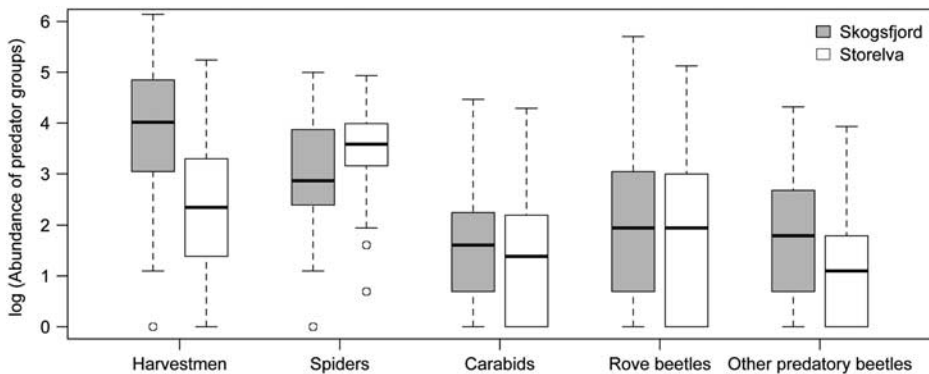
Data analysis

We analysed the spatio-temporal variation in the abundance of all five predator groups at the level of sampling stations (*i.e.*, pooling the samples for the eight pitfalls per station) separately for each locality with linear models. We assessed whether a release from invertebrate predators at high altitudes was a likely explanation for the altitudinal variation in moth outbreak amplitude. In this, we tested our data for consistent negative relationships between predator abundance and altitude. That is, we tested for decreasing predator abundances with increasing altitude. Doing so, we expected altitude to be the main explanatory variable for predator abundance.

Table 1. R^2 for the spatial, temporal, and spatio-temporal linear models of all invertebrate predators at the two localities Skogsfjord and Storelva.

Locality	Skogsfjord			Storelva		
Model	Spatial	Temporal	Spatio-temporal	Spatial	Temporal	Spatio-temporal
Predictor	Altitude	Year	Altitude \times year	Altitude	Year	Altitude \times year
Response						
Harvestmen	0.20	0.43	0.69	0.16	0.08	0.28
Spiders	0.01	0.65	0.71	0.11	0.06	0.21
Carabid beetles	0.01	0.16	0.23	0.09	0.09	0.21
Rove beetles	0.21	0.24	0.50	0.02	0.02	0.08
Other predatory beetles	0.15	0.27	0.49	0.02	0.11	0.18

Note: Values in bold denote terms with statistically significant effect sizes $P < 0.01$.

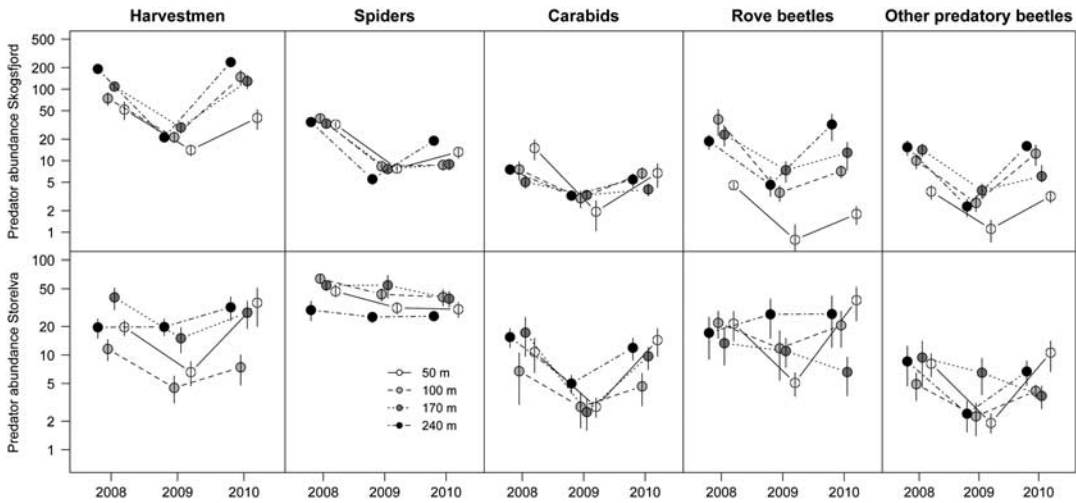
Fig. 3. Comparison of overall variation in the abundance of the five invertebrate predator groups (log scale) between the two localities Skogsfjord and Storelva, Norway.

In all models, the natural logarithm of predator abundance was applied as the response variable. We tested how much of the variation in invertebrate abundance was explained by three different models: a spatial model (altitude as predictor), a temporal model (year as predictor), and a spatio-temporal model (altitude, year and the altitude \times year interaction as predictors). We then compared R^2 derived from the three different models to assess which model (predictor) explained predator abundance distributions best (Table 1). The predictor's altitude and year were applied as categorical variables. Altitude was modelled as a categorical variable as the responses could be nonlinear (*i.e.*, owing to threshold). Altitude estimates were checked for trends that would conform with expectations of decrease in abundance with altitude. All analyses were carried out with the statistical software R version 2.11.0 (R Development Core Team 2010).

Results

In general, the levels of variation in invertebrate predator abundances across altitudes and years were comparable between the two localities (Fig. 3). However, harvestmen were distinctly more abundant at Skogsfjord than at Storelva. A similar tendency was found for other predatory beetles while spiders tended to be more abundant at Storelva than at Skogsfjord (Fig. 3). The linear models showed that a substantial amount of the variation in predator abundance could generally be attributed to the spatial and/or temporal predictors at Skogsfjord, but not at Storelva (compare R^2 values in Table 1). However, the variation in predator abundance that was accounted for by altitude was small. Moreover, the estimates from the linear model showed no tendency for increasing predator abundance with decreasing altitude (compare Fig. 4 for altitude-specific mean abundances).

Fig. 4. Altitude and year-specific variation in the abundance of the five invertebrate predator groups at the two localities Skogsfjord and Storelva, Norway. Error bars correspond to standard errors (SE). Note the different scaling of the y-axis for the two localities.



At Skogsfjord, where altitude did explain some variation in predator abundance, the inter-annual component of the variation was clearly more important than variation across altitudes (Table 1). The temporal analyses showed strong consistency among the different predator groups at both localities, as is reflected by a significant trough in abundance in 2009 and similar levels in 2008 and 2010 (Fig. 4). Predator groups with clear spatial and temporal variation in abundance at Skogsfjord (*i.e.*, harvestmen, rove beetles, and other predatory beetles; see Table 1) showed no indication of any direct or delayed response to the moth outbreak (Fig. 5).

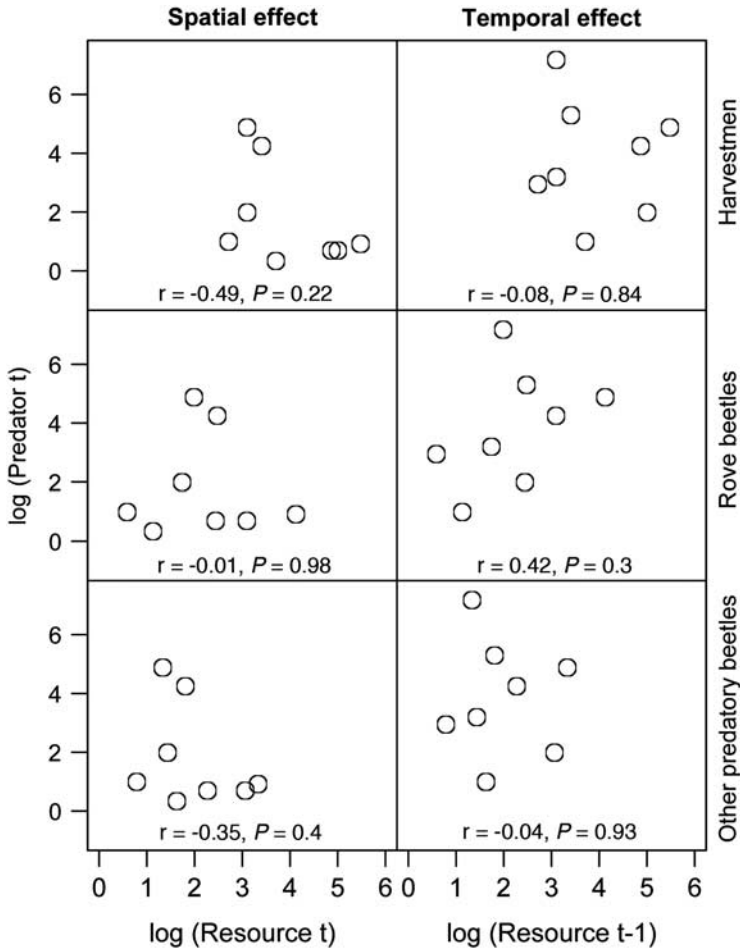
Discussion

In the present study, we found no support for the hypothesis that the studied moth outbreaks close to the altitudinal tree line (Hagen *et al.* 2007) are a consequence of a release from ground-dwelling invertebrate predators. We compared the abundance of predators across altitudes at two localities with outbreaking and nonoutbreaking moth populations, respectively. We failed to reveal the consistent negative relationship between predator abundances and altitude as predicted by the predator-release hypothesis. We acknowledge that pitfall sampling to some extent confounds activity with abundance, and moreover that there are other aspects than

abundance (and activity) that could determine predator impact. Still, based on our results, we are now confident that the sampled ground-dwelling predators cannot be responsible for the hugely different altitudinal population dynamics of sub-arctic birch forest geometrids.

Instead, predator abundances seemed to be ruled largely by inter-annual variability at one locality (Skogsfjord), but neither by altitude nor year to any great extent at the other (Storelva). At Skogsfjord, where the abundance variation of some of the predator groups showed some evidence for a systematic altitudinal component (see Table 1), there was no relation to the moth outbreak in terms of direct or (one year) delayed numerical responses (Fig. 5). Indeed, we were surprised to find that the extreme resource pulse caused by the winter moth outbreak had no discernible effects on the assemblages of ground-dwelling invertebrate predators. Although we are not in a position to identify the mechanism underlying the rather strong effect of year (*i.e.*, the trough in the abundance of all predator groups evident for both localities in 2009), it is tempting to propose that a climatic event could have synchronised the dynamics both spatially and inter-specifically (Bjørnstad *et al.* 1999). However, we do not know the natural history of the different predators well enough to know which weather parameter or season to focus on.

Fig. 5. Plots of altitude and year-specific abundances of moth larvae at Skogsfjord, Norway against the corresponding abundance estimates for the predator groups that showed significant effects of both year and altitude (see Table 1). Top panel: harvestmen, middle: rove beetles, and bottom: other predatory beetles. Both direct (spatial effect) and one year delayed (temporal effect) relations are shown. Correlation coefficients (*cor*) with *P*-values are given on the bottom of each plot.



The sampling method employed in the present study does not capture all predators that could be responsible for regulating geometrid moth populations at low altitudes. One group of mammalian generalist predators, namely shrew species (*Sorex* Linnaeus; Mammalia: Soricidae), may potentially have a significant impact on moth abundances through predation on the pupal stage. Negative density-dependent pupal survival in *E. autumnata*, mainly caused by predation from shrews, was reported from experiments conducted by Tanhuanpää *et al.* (1999) at southern non-outbreak locations in Fennoscandia. The lack of such a relationship in northern outbreking

E. autumnata populations (Tanhuanpää *et al.* 1999) suggested that a release from pupal predation in the north might explain the observed outbreak dynamics there (Klemola *et al.* 2002). However, this hypothesis found no support in an experimental field test performed in northern Norway in an altitudinal gradient design identical to the one of the present study (Hansen *et al.* 2009). That study showed that the abundance of the common shrew (*Sorex araneus* Linnaeus) was not structured with respect to altitude and that the predation rate on moth pupae was neither related to altitude nor to the densities of moths or shrews.

The altitudinal distribution of invertebrate predators observed in the present study contrasts with findings from a study investigating invertebrate predators associated with *O. brumata* populations in Scotland, United Kingdom (Raymond *et al.* 2002). Also in that system, the moth outbreak was restricted to high altitudes. Raymond *et al.* (2002) found higher densities of carabid and rove beetles, as well as higher predation rates on moth pupae, at low-altitude nonoutbreak sites compared with moth outbreak sites at higher altitude and interpreted this finding as support for the predator-release hypothesis. However, the ecological context of the subarctic birch forest system in northern Norway and the temperate Scottish system may be so different that the mechanisms behind winter moth outbreaks also differ.

Conclusion

The aim of this study has been to delimitate the number of ecological candidate mechanisms that might play a crucial role in directly or indirectly shaping Fennoscandian moth dynamics. The extremely localised outbreak dynamics along mountain slopes in northern Norway offer a unique opportunity for such an approach. So far, limitation or regulation by shrews and larval parasitoids has been rejected as being important for shaping spatio-temporal moth dynamics (Hansen *et al.* 2009; Schott *et al.* 2010). By testing and rejecting the predator-release hypothesis for invertebrate predators that are efficiently sampled by pitfall traps, we have added one more candidate to that list. The determinants of altitudinally patterned moth outbreaks in the mountain birch forests of northern Fennoscandia consequently remain unknown. With reference to Johnson *et al.* (2010), we suggest that further research might aim at surveying the optimal temperature-mediated altitude of these moths as another determining candidate for spatial moth outbreak patterns in Fennoscandia (Jepsen *et al.* 2009).

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