

A pioneering pest: the winter moth (*Operophtera brumata*) is expanding its outbreak range into Low Arctic shrub tundra

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Abstract: Climate warming allows generalist boreal consumers to expand into Arctic ecosystems. We present experimental and observational field data showing that a generalist boreal insect pest—the winter moth (*Operophtera brumata* Linnaeus, 1758)—is expanding its outbreak range out of the northern boreal mountain birch forest in northeast Fennoscandia and into the adjacent Low Arctic shrub tundra. This is the first documented example of an outbreaking boreal insect pest expanding into a tundra ecosystem. The expansion has coincided with a long-term advancing trend in the expected hatching date of moth eggs in spring for the study region. We show that the winter moth can complete development on Low Arctic willows and that the density of winter moth larvae in willow thickets is unrelated to the amount of mountain birch (the main host plant in northern boreal forest) in the thickets. However, we also demonstrate that larval densities on willows show a regional-scale spatial decline when moving away from the birch forest and into the shrub tundra. Continued monitoring is needed to establish whether the outbreaks will spread farther into the tundra. The expansion of outbreaking boreal pests into the tundra could alter conventional expectations of increasing vegetation productivity and shrubification in tundra ecosystems.

Key words: *Salix*, climate tracking, defoliation, range expansion, generalist consumer, phenology.

Résumé : Le réchauffement climatique permet aux consommateurs boréaux généralistes de s'étendre aux écosystèmes arctiques. Les auteurs présentent des données expérimentales et d'observation sur le terrain montrant qu'un insecte nuisible boréal généraliste — l'arpen-teuse tardive (*Operophtera brumata* Linnaeus, 1758) — est en train d'étendre son aire de répartition boréale-nordique hors de la forêt de bouleaux de montagne du nord-est de la Fennoscandie et dans la toundra arbustive aride adjacente du Bas-Arctique. Il s'agit du premier exemple documenté d'un insecte nuisible boréal en pullulation dans un écosystème de toundra. Cette expansion a coïncidé avec une tendance à long terme à l'avancement de la date d'éclosion prévue des œufs d'arpen-teuse au printemps dans la région étudiée. Les auteurs montrent que l'arpen-teuse tardive peut achever son développement sur les saules du Bas-Arctique et que la densité des larves de l'arpen-teuse tardive dans les fourrés de saules n'est pas liée à la quantité de bouleau de montagne (l'hôte principal dans la forêt boréale nordique) dans les fourrés. Cependant, ils démontrent également que les densités de larves sur les saules montrent un déclin spatial à l'échelle régionale lorsque l'on s'éloigne de la forêt de bouleaux et que l'on entre dans la toundra arbustive. Une surveillance continue

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est nécessaire pour déterminer si les pullulations s'étendront plus loin dans la toundra. L'expansion des ravageurs boréaux dans la toundra pourrait modifier les attentes conventionnelles d'une augmentation de la productivité de la végétation et de l'arbustification dans les écosystèmes de la toundra. [Traduit par la Rédaction]

Mots-clés : *Salix*, suivi climatique, défoliation, expansion de l'aire de répartition, consommateur généraliste, phénologie.

Introduction

The ongoing climate warming in Arctic ecosystems is currently allowing many thermophilic boreal species to expand their ranges northwards (i.e., “climate tracking” sensu Urban 2020 (Fossheim et al. 2015; Kortsch et al. 2015; Norén et al. 2015; Tape et al. 2016; Neukermans et al. 2018; Tape et al. 2018; Pecuchet et al. 2020)). Current evidence suggests that generalist consumers with high mobility often expand poleward in response to warming before more specialized species (Lurgi et al. 2012; Kortsch et al. 2015; Sunday et al. 2015; Bartley et al. 2019). The flexible diets of these generalists may alter Arctic food web dynamics in unexpected ways and, thus, potentially modify the predicted impacts of climate warming on resident Arctic communities (Gilman et al. 2010; Lurgi et al. 2012; Pecl et al. 2017).

For Arctic tundra ecosystems, one of the most basic expectations under a warmer climate is that vegetation productivity will increase (Myers-Smith et al. 2020). However, this is also an expectation that may be modified by northwards expansion of boreal consumers. Boreal forest herbivores are frequently forceful drivers of vegetation dynamics (Côté et al. 2014; Hidding et al. 2013; Leroux et al. 2020). This is especially evident for outbreaking insect herbivores, which tend to surpass all other biotic disturbance agents in terms of the intensity and spatial scale of their impacts on forest vegetation (Barbosa et al. 2012; Weed et al. 2013). By contrast, in tundra ecosystems, invertebrate herbivory rates are typically low (Kozlov et al. 2015; Barrio et al. 2017; Rheubottom et al. 2019) and outbreaks are very rare. Indeed, there is only a single documented example of a native outbreaking insect herbivore acting as a strong driver of vegetation dynamics in a tundra ecosystem, namely that of the great brocade (*Eurois occulta* Linnaeus, 1758, Lepidoptera, Noctuidae) in southwest Greenland (Lund et al. 2017; Dahl et al. 2017; Prendin et al. 2020). Accordingly, the expansion of boreal insect herbivores into the tundra could lead to strongly altered herbivory regimes, which may counteract the expected warming-induced increase in vegetation productivity and plant biomass. As several outbreaking boreal insect pests are already expanding their ranges northwards within the boreal biome (Pureswaran et al. 2018), and may eventually expand into tundra ecosystems, this consideration should not be overlooked when making predictions about future vegetation dynamics in tundra ecosystems.

In this paper, we report what is, to our knowledge, the first example of an outbreaking boreal insect herbivore expanding out of the boreal forest and into the tundra, and exerting a strong impact on a resident Arctic plant community. Our case study concerns the winter moth (*Operophtera brumata* Linnaeus, 1758, Lepidoptera, Geometridae), which is a widespread and highly polyphagous herbivore in boreal and temperate forest ecosystems in Eurasia. Outbreaks are particularly well documented in the northern boreal mountain birch (*Betula pubescens* var. *pumila* Govaerts, 1996, Fagales, Betulaceae) forest of northern Fennoscandia (Tenow 1972; Bylund 1999), which borders on the Low Arctic tundra in the European high north (Wielgolaski et al. 2005). Outbreaks by the winter moth and the related autumnal moth (*Epirrita autumnata* Borkhausen, 1794, Lepidoptera, Geometridae) are the main drivers of stand-level mortality events in the northern boreal mountain birch

Fig. 1. Examples of willow thickets that have suffered mortality following winter moth defoliation (*a* and *b*), an example of a branch enclosed in an experimental mesh bag (*c*), and willow leaves that are heavily infested with winter moth larvae (*d*). Photo credits: Ole Petter Laksforsmo Vindstad (*a*, *b*, *d*) and Helge Molvig (*c*).



forest (Jepsen et al. 2013; Vindstad et al. 2019a). Outbreaks of varying intensity and spatiotemporal extent occur at roughly decadal intervals (Bylund 1999; Ruohomäki et al. 2000). The winter moth has exhibited a northeast expansion of its outbreak range in the mountain birch forest during the last half of the 20th century (Jepsen et al. 2008), coinciding with a pronounced warming climatic trend in the region. By 2005, winter moth outbreaks occurred in the mountain birch forest on the outskirts of the Varanger peninsula in far northeast Norway (Klemola et al. 2008; Jepsen et al. 2013). This represents the last outpost of forest before entering the Low Arctic shrub tundra in the eastern and interior parts of the peninsula (Ims et al. 2013).

In recent years, there has been an increasing number of observations to suggest that the long-term range expansion of the winter moth in the northern boreal mountain birch forest is now being followed by a further expansion into the shrub tundra. The first warnings of this new development were detected in 2006, when local forest authorities found winter moth larvae in thickets of willows (*Salix* spp., Malpighiales, Salicaceae) several km east of the birch forest on the Varanger peninsula (H. Molvig, personal observation, 2006). The first major outbreak in the shrub tundra was recorded in 2017 and 2018, when the authors observed that winter moth larvae caused severe defoliation and substantial mortality of willow thickets as much as 15–20 km northeast of the birch forest (Fig. 1a, b and d). These observations of moth outbreaks far from the birch forest are unprecedented, and suggest that the winter moth is expanding its outbreak range into a new ecosystem in the form of Low Arctic willow shrub tundra. Willows have a circumpolar distribution and are functionally important in the tundra, as willow thickets constitute hot-spots of primary productivity and biodiversity, and shape fundamental ecosystem processes like albedo and nutrient cycling (Den Herder et al. 2004; Ehrich et al. 2012; Ims and Henden 2012; Ims et al. 2013). Thicket biomass is also expected to increase

under climate warming, leading to shrubification of tundra ecosystems (Myers-Smith et al. 2011a). The advent of winter moth outbreaks in shrub tundra could, therefore, have negative consequences for many other species and potentially alter the expected future trajectory of this ecosystem type. At present, however, inference about the potential ecological impacts of the winter moth in shrub tundra is hampered by a lack of quantitative population data describing the spatial distribution and intensity of outbreaks in this ecosystem. There is also a need to develop a better understanding of factors that may limit or facilitate the spread of outbreaks in the tundra.

In this paper, we summarize the results from experimental and observational studies that aimed to address the most pressing knowledge gaps concerning the expansion of the winter moth into the shrub tundra. First, we report from a field experiment that was designed to determine whether the winter moth can complete its life cycle exclusively on Low Arctic willows. If this is not the case, outbreaks on willows are likely to be a “spillover” phenomenon that occurs because larvae migrate from mountain birch to willows in mixed thickets. Hence, the spread of outbreaks in the shrub tundra would be limited by the presence of mountain birch in thickets. Second, we present the first two years of data from regional monitoring of winter moth larval densities in willow thickets along a gradient from mountain birch forest to tundra. Thus, we are able to assess the distribution of outbreaks in the novel tundra habitat, with reference to the distance from the original habitat in the birch forest. As part of this monitoring, we have also quantified the amount of mountain birch in the thickets. Thus, we are able to complement the experiment by testing for a relationship between winter moth densities on willows and the amount of birch in thickets. Finally, we describe the recent climatic trends of the study region in terms of known temperature thresholds for the hatching of winter moth eggs in spring, to illustrate that the expansion into the shrub tundra may have been facilitated by a distinct advancing trend in spring phenology in recent decades.

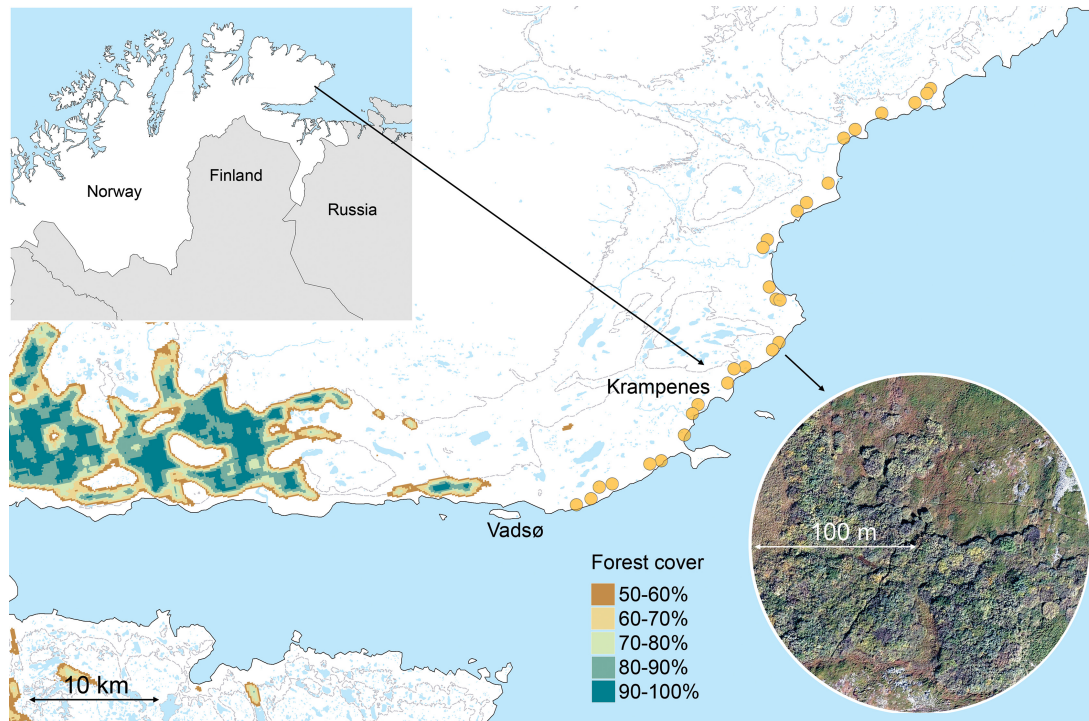
Materials and methods

Study system

The Varanger peninsula (70–71°N, 30°E) in the northeast of mainland Norway represents the western edge of the Eurasian Arctic tundra (Ims et al. 2013). The climate of the peninsula is oceanic, with relatively mild winters, especially in the coastal areas. The lowlands in the southern and western parts of the peninsula harbor forests composed almost entirely of mountain birch, which give way to tundra when moving inland and towards the eastern and northern coasts (Fig. 2). Productive willow thickets (mainly composed of *Salix glauca*, *Salix lanata* and *Salix phylicifolia*, Linnaeus, 1753) are present in the interior in river valleys and on moist ground in tundra close to the coast. Even at distances of several km from the main birch forest line, these willow thickets are often intermixed with patches of shrub-like mountain birch.

The winter moth is an obligate univoltine insect herbivore. Winter moth larvae are highly polyphagous and will feed on a wide variety of deciduous and evergreen plants (Tenow 1972). In northern Fennoscandia, the larvae feed mainly on mountain birch. Moths overwinter as eggs, which are deposited on the branches of host plants in late autumn. In northern Fennoscandia, the eggs hatch in approximate synchrony with birch budburst, which usually occurs in mid to late May. The larvae subsequently feed on foliage and develop through five instars, before pupating in the soil in late June to early July. Adult moths emerge throughout September and October to mate and oviposit (Bylund 1999). Adult female winter moths are flightless, but newly hatched larvae can disperse by wind with the aid of silken threads (“ballooning”). This can probably carry the larvae over distances of several km (Leggett et al. 2011; Vindstad et al. 2019b).

Fig. 2. Map of the study region. The location of the study region in northeast Norway within northern Fennoscandia is shown on the small insert map, whereas the larger map shows the location of the sampling stations along the regional transect (orange circles) and the experimental site at Krampenes. The distribution of the birch forest (source: AR50; Heggem et al. 2019) is shown as % forest cover within a 1 × 1 km neighborhood to illustrate the transition from more or less continuous coastal birch forest west of the town of Vadsø, towards treeless tundra east and north of Vadsø. The round aerial photo shows the distribution of shrub cover within the sampling area at one station. Source of topographical map layers: Norwegian Mapping Authority (2016). Source of forest map layer: Norwegian Institute of Bioeconomy Research (2017); Heggem et al. (2019). Source of aerial photo: Norwegian Mapping Authority (2014).



The northeast expansion of the outbreak range of the winter moth in the Fennoscandia mountain birch forest is relatively well characterized. The first observation of the species from Tromsø (69°40'N, 18°55'E) stems from 1892. This was soon followed by records of outbreaks in that area (Tenow 1972). Analysis of qualitative records subsequently shows a northeast expansion of the area experiencing outbreaks during the last half of the 20th century (Jepsen et al. 2008). The first quantitative record of a winter moth outbreak on birch on the Varanger peninsula stems from 2005 at the location Hana (70°14'N, 28°27'E; Klemola et al. 2008). By 2015, the outbreaks had spread even farther east to the town of Vadsø (70°04'N, 29°44'E), which is located in the transition zone between the birch forest and the tundra (Climate Ecological Observatory for Arctic Tundra (COAT), unpublished data, 2015). Although winter moth outbreaks on mountain birch are a recent phenomenon on the Varanger peninsula, outbreaks by the autumnal moth have been reported from the region as far back as available records go (Tenow 1972). However, there are no records of autumnal moth outbreaks in the tundra.

Experimental assessment of winter moth development on willows

Our field experiment was conducted in 2019 at the location Krampenes (70°06'N, 30°11'E) on the coast approximately 15 km east of the main birch forest line on the Varanger peninsula (Fig. 2). The landscape in the area is dominated by willow thickets, but there is substantial intermixing of shrub-like mountain birch in these thickets. High densities of winter moth larvae had been observed by the authors in the thickets at Krampenes during the summer of 2018. Hence, we expected that the thickets at this location would have a high density of naturally occurring winter moth eggs in the spring of the following year.

Three conditions must be fulfilled for the winter moth to successfully complete its life cycle on Low Arctic willows. (1) Female moths must use willows for oviposition, (2) moth eggs deposited on willows must overwinter successfully, and (3) moth larvae must be able to complete development (reach pupation) by feeding exclusively on willow leaves. To test these conditions in situ, we deployed mesh bags to enclose a sample of 50 willow branches. The bags were mounted on 7–8 May, which is well in advance of the hatching of moth eggs in spring. The presence of winter moth larvae in the bags would confirm that eggs had been deposited on the experimental branches in the preceding autumn (condition 1) and had survived the winter (condition 2). Moreover, the larvae would be restricted to feed on willow leaves throughout their development (condition 3). The density of winter moth eggs on the branches were not manipulated in any way before the bags were mounted. Hence, the experiment was expected to reflect the natural variation in the presence and density of eggs on the branches. An additional 50 bags were deployed on birch branches to provide a comparative treatment on a host plant that is known to be favorable for winter moth development. The length of the enclosed branches varied by between 50 and 70 cm, as natural variation in the size and shape of the branches made it difficult to achieve a strict standardization of branch size. However, to avoid consistent differences in branch size between host plants, we tried to ensure that the selection of a branch of smaller or larger than average size on one of the host plants was followed by the selection of a similarly sized branch for the other host plant. The distribution of bags in the landscape was determined by the natural occurrence of thickets, subject to the constraint that there should be a minimum distance of 10 m between bags mounted on the same plant species. Thus, typically, a set of 2–3 bags would be mounted on the same plant species within a large thicket, before moving on to a new thicket a few tens of metres away. This resulted in the bags being distributed across an area of approximately 400 × 400 m. Due to a lack of foliage in the early spring, the species identity of willows could not be reliably established when the bags were mounted. Hence, the bags were expected to provide a sample of the three dominant willow species in proportion to their occurrence in the landscape.

All experimental bags were removed over a 3 day period from 12 to 14 July, which corresponds to the late larval to early pupal stage for the winter moth. At this time, we cut down the branches and collected all winter moth larvae, prepupae, and pupae in the bag and on the branch. Individuals were stored in individual Eppendorf tubes and frozen. In the laboratory, the individuals from each bag were counted and individually weighed to the closest 0.1 mg. The instar of each larva was also determined visually by an experienced researcher (OPLV).

The experiment was conducted in accordance with the Norwegian national guidelines for the use of animals in research. Permission to conduct the experiment was obtained from the local landowner (permit 19/709–2 from the Finnmark Estate).

Regional monitoring of moth outbreaks on willows

The monitoring of winter moth outbreaks on willows commenced in 2019 along a regional transect that was designed to provide a gradient running from the original habitat

of the winter moth in mountain birch forest and into the novel Low Arctic shrub tundra habitat. Hence, the transect was initiated at the approximate eastern border of mountain birch forest on the Varanger peninsula, and extended along the coast in a northeast direction for about 40 km into the Low Arctic tundra (Fig. 2). Willow thickets occur patchily along the entire transect. To select thickets for sampling, we used high-resolution aerial photographs captured during the summer of 2014 (Norwegian Mapping Authority 2014). These photos were available for a corridor extending approximately 1 km inland from the coast along the entire transect. From the photos, we manually selected a sample of 30 thickets that had a minimum continuous extent of approximately 30×30 m and that were spaced as regularly as possible along the transect. A thicket was defined as an area of ground where the photos showed a dense and largely continuous canopy of tall-growing woody vegetation. Such areas can be reliably delineated based on a combination of the shadows cast by the tall-growing vegetation at the edge of the thicket and the contrasting color of the thicket compared with the surrounding ground vegetation (Fig. 2). The approximate centre point of each thicket was marked with a GPS coordinate. All of the selected thickets were visited during 15–20 July 2019. Thickets that were found to be very low-growing (<1.3 m tall) or predominantly dead were rejected from sampling. For most of the locations, the pre-selected coordinates were either suitable for sampling or a suitable spot could be found by moving the sampling point a short distance (up to a maximum of about 300 m). Two locations had to be rejected altogether, resulting in a final sample of 28 thickets.

When the centre point of a thicket had been established, we walked 10 m in a straight line from this point in each of eight equally spaced compass directions. At the endpoint of each line, we recorded the proportion of canopy cover of mountain birch in a 5×5 m square centred on the endpoint. In addition, we cut down a single willow branch of about 80 cm length from the most common willow species in the square. Apart from the length and species identity, the branch was chosen at random, in the sense that no other selection criteria were applied. The same procedure was repeated 5 m from the centre point in the northern and southern direction, to obtain ten squares per thicket. The collected branches were thoroughly shaken in a large plastic box, until all moth larvae had detached. The larvae were subsequently sorted to species (winter moth or autumnal moth) and counted. This procedure is a modified version of the standardized protocol for estimating moth larval density on mountain birch described by Ims et al. (2004). Densities of more than 100 larvae/10 branches are enough to cause easily visible defoliation of birch forest and can thus be interpreted as a high-amplitude outbreak (Vindstad et al. 2019b). We regard this definition of an outbreak to be meaningful also for our density estimates on willows.

We also quantified the abundance of birch in a 50 m radius around the centre point of each thicket. To do this, we identified the three closest birch stems to the centre point up to a maximum distance of 50 m. Distance was measured as a straight line from the centre point to the base of the stem with a handheld GPS. Around each chosen stem, we recorded the proportion canopy cover of birch in a 5×5 m square, as described above. To prevent multi-stemmed birches from yielding overlapping squares, the minimum distance between selected stems was set to 5 m. Based on the aerial photographs (see above) we also quantified the overall spatial extent of the thickets. To do this, we defined buffer zones with 50 and 100 m radii around the selected centre points of the tickets. The buffer zones were divided into polygons with an area of 100 m^2 , yielding 78 and 314 polygons for the 50 and 100 m buffers, respectively. Each polygon was visually scored to one of three classes of thicket canopy cover, namely ≥ 50 percent cover, <50 percent cover, or no cover. It was not possible to reliably distinguish willow and birch canopy from the photos. Accordingly, these measurements only quantified the overall extent of thicket canopy cover within the

buffer zones. Although thicket biomass in the study region can be relatively labile (Henden et al. 2013), we expected that the canopy cover estimated for images from 2014 would show a strong correlation with the actual canopy cover during our field measurements five years later.

In early July 2020, we revisited the thickets to estimate moth larval density again. As for 2019, the density measure was defined as the number of larvae on ten standardized willow branches. However, for logistic reasons, we could not implement the full protocol from 2019, which was relatively time-consuming due to entering the dense thickets. Thus, in 2020, we approached as close to the thicket centre points as we could get without entering the thickets. For most thickets, this took us to within 20 m of the original centre points. The ten branches were then haphazardly collected within a 20 m radius of the new sampling point. Based on observations we had made during fieldwork in 2019, we had no reason to think that moth densities would differ strongly between the edges and interior of the thickets. Hence, the data collected with the simplified protocol for 2020 was expected to be comparable with the data from 2019. This protocol will be implemented annually after 2020 to monitor moth outbreak activity along the sampling transect.

Climatic context

The recent range expansions of outbreaking geometrid moths in the mountain birch forest of northern Fennoscandia have been attributed to improved overwinter survival of eggs due to reduced occurrence of extreme winter cold (Jepsen et al. 2008; Ammunet et al. 2012), or improved phenological matching between hatching larvae and birch budburst due to warmer springs (Jepsen et al. 2011). Reduced winter cold is unlikely to explain the current expansion of the winter moth outbreak range into the coastal Low Arctic shrub tundra on the Varanger peninsula, as winter temperatures in this area do not attain the approximately $-35\text{ }^{\circ}\text{C}$ that represents the cold tolerance limit of winter moth eggs (Ammunet et al. 2012). Hence, we describe the climatic context in which the range expansion has taken place in terms of spring phenology.

We lack the data to establish a mechanistic link between spring phenology and the expansion of the winter moth into shrub tundra. However, we know from laboratory experiments that the eggs of north Fennoscandian winter moth populations need to accumulate a temperature sum of about $250\text{ }^{\circ}\text{C}$ (daily means with a base temperature $0\text{ }^{\circ}\text{C}$) after January 1 before hatching (Jepsen et al. 2011). The day of the year on which this temperature sum is reached (hereafter DOY_{250}) can thus be interpreted as a proxy for the expected winter moth hatching date. To assess long-term trends in DOY_{250} in the study region, we used gridded climate maps with a 1 km resolution provided by the Norwegian Meteorological Institute (<https://www.met.no/>). Yearly DOY_{250} values were calculated from daily mean temperatures for all grid cells on land in the Varanger peninsula and the surrounding region. This area, thus, included the tundra on the peninsula (including the monitoring transect) and a substantial area covered by birch forest. The yearly DOY_{250} were grouped into three time periods corresponding, respectively, to the decade preceding the first winter moth outbreak on birch on the Varanger peninsula (1991–2000), the decade with the first outbreak on birch (2001–2010), and the decade with the first outbreak in the shrub tundra (2011–2017).

Statistical analysis

The analysis of the mesh bag experiment aimed to detect differences in winter moth occupancy and phenology between bags on willow and birch branches. Accordingly, host species was taken as a categorical predictor variable in all models. For moth occupancy, we considered a binary variable indicating if a bag contained winter moth individuals or

not, and a count variable giving the number of individuals per bag. These variables were analyzed with generalized linear models, employing binomial and negative binomial error distributions, respectively. For moth phenology, we considered three response variables, namely body mass, larval instar, and pupation status. Body mass was treated as a continuous variable. For instar, the larvae in the bags were distributed almost exclusively among fourth and fifth instars. Thus, instar was treated as a binary response variable with instar four and five as the two possible outcomes. A single third instar larva was included with the fourth instars. Pupation status was also treated as a binary variable, with the outcomes defined as pupating (prepupae and pupae) or still feeding (all larvae). The phenology variables were defined on the level of individual moths, but could not be assumed to be independent among individuals within bags, as all larvae within a bag will originate from the same limited number of clutches. For the response variable of body mass, we accounted for this by employing a mixed model taking bag as a random effect. However, such models failed to converge for larval instar and pupation status. Hence, for these variables, we employed standard generalized linear models taking the proportion of fifth instars and pupating larvae per bag as the response variables; hence, treating the bag as the replicate rather than the individual. We assumed a normal error distribution for the model of body mass and a binomial distribution for the models of instar and pupation status. A quasi-likelihood correction was employed for the two binomial models to correct for overdispersion.

The regional larval abundance data consisted of highly aggregated counts, and was, therefore, analyzed with a generalized linear model employing a negative binomial error distribution. A mixed model using site as a random effect was considered, but was abandoned due to convergence failure. The first question addressed by the modelling was whether larval abundance on willows was positively related to the amount of mountain birch in the thickets. The amount of birch for a given thicket was represented by the total area (m^2) of mountain birch canopy cover recorded across all of the 5×5 m sampling squares employed for that thicket in 2019 (i.e., the ten squares around the thicket centre point, plus up to three additional squares within a 50 m radius of the centre point). Birch canopy cover for a given square was calculated as the estimated proportion cover multiplied by the total area of the square ($25 m^2$). Birch canopy cover showed a skewed distribution, with many zeros and a few large values. Hence, this variable was log +1 transformed to linearize its effect in the model. Dead birch was excluded from the birch canopy cover variable. We also defined a covariate that represented the overall spatial extent of the thickets. This covariate was defined as the proportion of $100 m^2$ polygons that were fully or partially covered by thicket canopy in the high-resolution aerial photographs of the thickets (see above). Covariates based on the 50 and 100 m buffer zones were strongly correlated ($r = 0.88$). Hence, we retained the covariate for the 50 m buffer, which had a spatial scale that was closest to the scale of the birch canopy cover covariate. Both of the canopy cover covariates were expected to change little between 2019 and 2020, and we, therefore, assumed constant values of these covariates across the two years.

In addition to the canopy cover covariates, we needed to account for the regional-scale spatial gradient running from the original habitat of the winter moth in the birch forest and into the novel shrub tundra habitat. The spatial gradient was represented by the Euclidian distance in km between each sampling site and the first site in the transect (close to the forest). This covariate was modelled as a linear term, as plots of partial residuals against distance revealed no indications of strong non-linearity in the effect of distance. Finally, we included year as a categorical predictor variable. The effects of the canopy cover covariates were not expected to differ between 2019 and 2020. Hence, these covariates were represented only by their main effects, without interactions with year. However, for the distance covariate, an ongoing expansion of the outbreaks into the tundra could cause the

effect of distance to differ between years. We, therefore, included the interaction between year and distance in the model. The residuals from the model were checked for spatial autocorrelation with the Moran I autocorrelation index, as implemented in the Moran.I function in the ape library in R. A two-sided test for the null hypothesis of no spatial autocorrelation was non-significant for the residuals of both 2019 ($p = 0.92$) and 2020 ($p = 0.70$).

All analyses were conducted in RStudio, running R version 4.0.3 (R Development Core Team 2020). Models were fitted with the functions glm (library stats), glm.nb (library MASS) and lmer (library lme4). Plots of residuals were inspected to detect potential outliers and departures from model assumptions. The cook's distance measures provided by the stats and influence.ME libraries were also inspected to detect observations with an unduly large influence on model parameter estimates. None of these diagnostics indicated problematic observations or violations of assumptions. We summarized the results of the modelling by deriving the predicted values from the models across the range of variation in the predictors. All predictions are presented with 95% confidence intervals (CI). The explanatory power of all fitted models were assessed with the pseudo- R^2 statistics calculated by the r.squaredGLMM function in the MuMIn library in R. We employed the delta method for deriving the observation-level variance. This can be used to calculate a pseudo- R^2 for all error distributions and link functions (Nakagawa et al. 2017). An overview of all response variables and predictors is provided in Table 1.

Results

Experimental assessment of winter moth development on willows

Most of the experimental mesh bags on willows contained winter moth larvae; thus, confirming that winter moth females had used willow branches for oviposition and that the eggs had survived the winter (conditions 1 and 2). The winter moth occupancy rate for bags on birch (0.87 (CI: 0.73, 0.94)) was slightly, but not statistically significantly, higher than for willow (0.75 (CI: 0.61, 0.85); Table 2, Fig. 3a). Bags that contained larvae generally showed a somewhat higher larval count for willow (9.4 larvae (CI: 7.1, 12.3)) than for birch (6.9 larvae (CI: 5.3, 9.0); Table 2, Fig. 3b), although this difference was not statistically significant. Thus, the experiment revealed no evidence for preferential oviposition on either host plant.

Concerning larval development, there was no evidence for differences in body mass between larvae feeding on different plant species. Predicted masses were 33.0 mg (CI: 14.9, 51.2) and 31.8 mg (CI: 13.6, 49.9) for willow and birch, respectively and this did not amount to a statistically significant difference between host plants (Table 2, Fig. 4a). The phenology of the larvae (proportion instar 5) was slightly more advanced on willows (0.77 (CI: 0.69, 0.84)) than on birch (0.69 (CI: 0.60, 0.76)), but again, without a statistically significant difference (Table 2, Fig. 4b). However, a significantly higher proportion of larvae on willows (0.12 (CI: 0.08, 0.18)) had completed development (i.e., pupated) compared with larvae on birch (0.01 (CI: 0.00, 0.06); Table 1, Fig. 4c). Importantly, the finding of pupating winter moth larvae in bags mounted on willow branches (43 pupae or prepupae in total) showed that the larvae could successfully complete development despite being restricted to feed only on willow leaves (condition 3).

Regional monitoring of moth outbreaks on willows

The count data for 2019 documented high densities of winter moth larvae on most of the surveyed willow thickets located within 20 km of the starting point of the regional monitoring transect (Fig. 5). The majority of thickets in this area had counts of more than 30 larvae per 10 branches, and some thickets had densities exceeding 100 larvae per 10 branches, i.e., the equivalent of a high-amplitude outbreak in birch forest (see Materials and methods

Table 1. Overview of response variables, predictor variables, and error distributions for the statistical models fitted in the study.

Study design and response variables	Predictor variables	Error distribution
Mesh bag experiment		
1. Proportion of bags occupied by larvae or pupae	Host plant (willow or birch)	Binomial
2. Number of larvae and pupae per bag	Host plant (willow or birch)	Negative binomial
3. Body mass of larvae and pupae in bags	Host plant (willow or birch)	Normal
4. Proportion of fifth instar larvae per bag	Host plant (willow or birch)	Binomial
5. Proportion of pupae or prepupae per bag	Host plant (willow or birch)	Binomial
Density monitoring transect		
6. Number of larvae per ten willow branches	Square m of birch canopy in 50 m radius around site (log-transformed) Proportion of polygons with thicket canopy (birch and willow) in 50 m radius around site Euclidian distance (km) to first site in transect (close to forest) Year (2019 or 2020)	Negative binomial

Note: The numbering of response variables corresponds to the numbering in Table 2. All models are generalized linear models, except the model for body mass, which is a linear mixed model. The study design that generated the data is given in italics in the first column, with response variables listed below.

section). This resulted in complete defoliation of parts of the willow thickets (Fig. 1). Larval densities generally decreased when moving farther northeast into the tundra, but a small number of winter moth larvae (1–5 larvae per 10 branches) were, nevertheless, also recorded on most of the surveyed thickets in this part of the transect. The spatial distribution of larval densities for 2020 largely conformed to the overall pattern for 2019, although with much lower densities along the entire transect. Autumnal moth larvae were practically absent, with a total of six larvae found over both years.

In the statistical model for the larval count data, the interaction between year and distance to the first sampling site was not statistically significant ($p = 0.39$) and was, therefore, removed from the model. However, the spatiotemporal patterning of larval densities (see above) produced highly significant and negative additive effects of both predictors. Meanwhile, the amount of birch in the thickets and the overall thicket extent were non-significant and did not contribute to the explanatory power (pseudo- R^2 statistic) of the model (Table 2).

Climatic context

The mean DOY_{250} , which serves as a proxy for the expected hatching date of winter moth eggs, advanced by roughly five days per decade across most of the study region between 1991 and 2017 (Fig. 6). This was also the case for the sampling sites in the regional monitoring transect, where the mean DOY_{250} value was 173 (22 June) for 1991–2000, 166 (15 June) for 2001–2010 and 161 (10 June) for 2011–2017 (Fig. 7). However, the yearly DOY_{250} values from the transect showed extensive inter-annual variation in all three periods, with as much as 4 weeks difference between years. Accordingly, although an overall advancing phenological trend was clearly discernable, the yearly DOY_{250} values overlapped extensively among the three periods.

Table 2. Parameter estimates for the statistical models fitted in the study. All models are generalized linear models, except the model for body mass, which is a linear mixed model.

Parameter	Estimate [95% CI]	R ²	Figure
1. <i>Bag occupancy</i>		0.02	Fig. 3a
Intercept (birch)	1.90 [1.04, 2.76]***		
Willow	-0.80 [-1.88, 0.28]		
2. <i>Individuals per bag</i>		0.02	Fig. 3b
Intercept (birch)	1.93 [1.66, 2.19]***		
Willow	0.31 [-0.07, 0.69]		
3. <i>Body mass</i> (mixed model)		0.00 (0.36) ^a	Fig. 4a
Intercept (birch)	31.77 [28.39, 35.15]***		
Willow	1.25 [-3.6, 6.10]		
4. <i>Proportion instar 5</i>		0.07	Fig. 4b
Intercept (birch)	0.78 [0.39, 1.16]***		
Willow	0.44 [-0.12, 1.00]		
5. <i>Proportion pupating</i>		0.43	Fig. 4c
Intercept (birch)	-4.22 [-5.61, 35.15]		
Willow	2.29 [0.83, 6.10]**		
6. <i>Larvae per 10 branches</i> (Intercept)	4.27 [1.93, 6.60]***	0.83 (0.83) ^b	Fig. 5
Birch canopy cover	-0.05 [-0.29, 0.18]		
Total canopy cover	1.52 [-0.95, 3.99]		
Distance to forest	-0.16 [-0.20, -0.13]***		
Year (2020)	-2.43 [-3.13, -1.74]***		

Note: Response variables are listed in italics in the first column, with parameter estimates for the respective predictors below. The numbering of response variables corresponds to the numbering in Table 1. R² gives the approximate proportion of variance explained by the models according to a pseudo-R² statistic (see main text for details). Parameter estimates are given with 95% confidence intervals, whereas asterisks denote statistical significance (**p ≤ 0.001. **p ≤ 0.01. *p ≤ 0.05). Significant terms (except intercepts) are highlighted in bold. See the listed figures/figure panels for visualization of model predictions.

^aThe figure in parentheses is the total variance explained by both fixed and random effects.

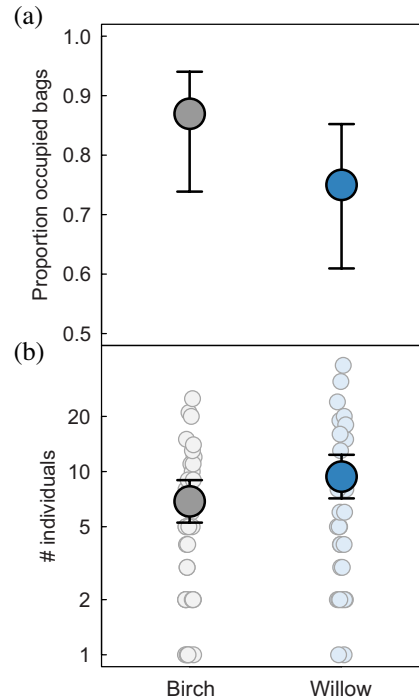
^bThe figure in parentheses is the variance explained only by year and distance to forest.

Discussion

The current study provides the first quantitative documentation of an outbreak by a range-expanding defoliating forest insect in the Low Arctic shrub tundra. Our regional monitoring design documented high densities of winter moth larvae on willows up to 20 km away from the birch forest, and the densities in some thickets were comparable with those observed during outbreaks on birch. Substantial mortality of thickets was also evident at several monitoring sites. Moreover, our experiment demonstrated that the winter moth can successfully complete its life cycle stages from eggs to pupae on Low Arctic willow shrubs.

Our results stress that range-expanding boreal insect herbivores should not be ignored when making predictions about future vegetation dynamics in Arctic ecosystems. Outbreaking herbivores like the winter moth can have extremely powerful impacts on their host plants (Barbosa et al. 2012; Jepsen et al. 2013; Karlsen et al. 2013), and the expansion of such herbivores into the Arctic could substantially modify the classic expectation of increased vegetation productivity and shrubification under a warmer climate. Outbreaks represent pulsed disturbances of high intensity, which can suppress plant

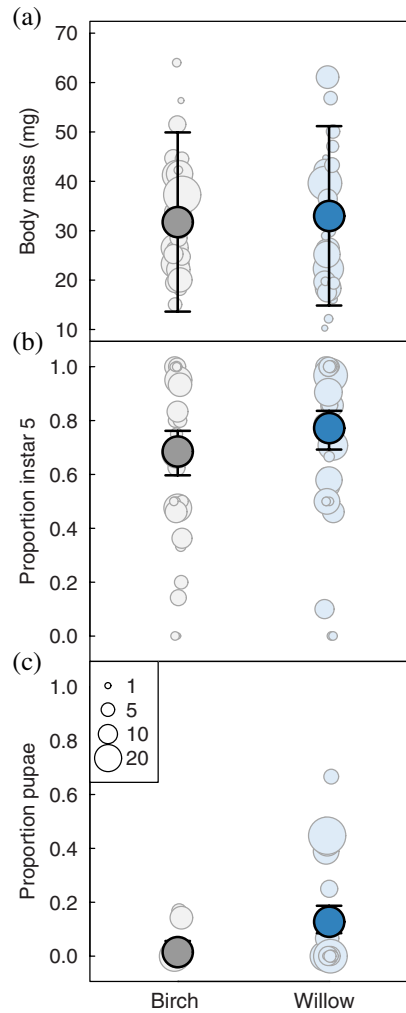
Fig. 3. Winter moth occupancy of experimental mesh bags, expressed as the proportion of bags with at least one winter moth individual (a) and the number of individuals per bag (b). The bold symbols in the foreground give predicted proportions and individual counts for mesh bags on birch (grey) and willow (blue), based on generalized linear models. Error bars represent 95% confidence intervals for the predictions. The symbols in the background represent observed individual counts for each mesh bag. See Table 2 for model parameter estimates.



growth in outbreak years and cause extensive mortality of established woody structures. Accordingly, outbreaks could counteract climatically facilitated increases in shrub growth rate and potentially wipe out long-term gains in shrub biomass. We hope that our present case study will lead Arctic ecologists to become more alert to the potential arrival of boreal insect pests in Arctic tundra ecosystems. Willows merit special attention in this respect, because they are palatable to many herbivores and are focal to predictions of climate change impacts on tundra vegetation (Myers-Smith et al. 2011a). Indeed, two of the willow species included in our study have already been implicated in climatically facilitated increases in primary productivity and shrub biomass in the tundra of North America (*S. glauca*; Myers-Smith et al. 2011b) and Eurasia (*S. lanata*; Forbes et al. 2010). The role of vertebrate herbivory as a top-down control on climatically facilitated shrubification of tundra ecosystems has already received considerable attention (Christie et al. 2015; Bråthen et al. 2017; Verma et al. 2020). However, several recent studies have shown that the impacts of native invertebrate herbivore species on tundra plants tend to increase with temperature in both space and time (Barrio et al. 2017; Rheubottom et al. 2019; Virtanen et al. 2020; Finger-Higgins et al. 2021). These studies have all stressed that we need to pay greater attention to the role of invertebrate herbivores in the tundra in the context of climate warming. Our current findings reiterate this point, with the added aspect that range-expanding boreal species also need to be considered.

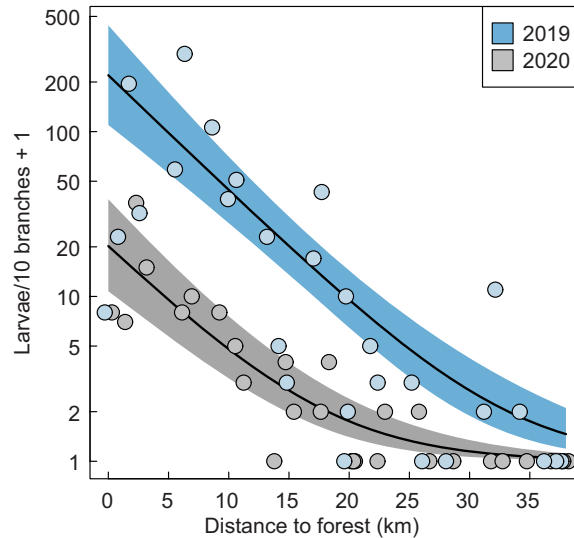
The expansion of the winter moth into the shrub tundra conforms to expectations from empirical and conceptual works that highlight dietary generalism and high dispersal

Fig. 4. Developmental status of winter moth larvae and prepupae found in the experimental mesh bags, expressed as body mass (a), proportion of fifth instar larvae per bag (b), and proportion of pupating or pupated larvae per bag (c). The bold symbols in the foreground give predicted masses and proportions for mesh bags on birch (grey) and willow (blue), based on a linear mixed model (a) and generalized linear models (b and c). Error bars represent 95% confidence intervals for the predictions. The symbols in the background represent observed mean masses and proportions per mesh bag. Symbol sizes are proportional to the total number of individuals found in each bag (see legend). See Table 2 for model parameter estimates.



capacity as strong predictors of a consumer’s ability to expand poleward under climate warming (Lurgi et al. 2012; Kortsch et al. 2015; Sunday et al. 2015; Bartley et al. 2019). The winter moth is a textbook example of a generalist insect herbivore and neonate larvae can probably disperse by wind over long distances (Leggett et al. 2011; Vindstad et al. 2019b). Hence, the winter moth is exactly the kind of species that might be expected to expand rapidly into the Arctic under climate warming. The fact that the association between certain traits and poleward expansion appears to be repeatable across a wide range of taxa may be helpful for the monitoring of Arctic ecosystems, as it can make it easier to figure range-expanding species into the a priori expectations and conceptual models

Fig. 5. Variation in the density of winter moth larvae on willow thickets along the regional monitoring transect running from the birch forest and into the Low Arctic shrub tundra. Symbols give the observed larval counts for each of the monitored willow thickets. The solid lines represent predicted larval densities along the transect in 2019 and 2020 based on a generalized negative binomial model (holding other covariates constant at their mean values. See Materials and Methods section). The shaded polygons represent 95% confidence intervals for the predictions. See Table 2 for model parameter estimates.



that underpin effective monitoring (Lindenmayer and Likens 2010; Ims and Yoccoz 2017). This could be particularly helpful for taxa that have traditionally been understudied in the Arctic — including invertebrates — as these groups often lack even rudimentary baseline descriptions of their taxonomic and functional composition, leading to difficulties in demonstrating that perceived changes in communities are, in fact, novel developments (Hodkinson 2013; Gillespie et al. 2020).

The future ecological role of the winter moth in the shrub tundra of northeast Fennoscandia has to be ascertained by additional studies. One determinant of future impacts is whether the outbreaks will spread further into the tundra or be restricted to a zone close to the birch forest. Of particular concern are the river valleys in the interior of the Varanger peninsula, where willow thickets are hotspots of primary productivity that provide food and shelter for a host of other species (Henden et al. 2011; Ims and Henden 2012; Henden et al. 2013; Ims et al. 2013). Our experiment showed that the winter moth can complete development on Low Arctic willows as readily as on mountain birch. Moreover, we found no relationship between winter moth larval density on willows and the local amount of birch in thickets. This suggests that winter moth outbreaks may develop even in pure willow thickets far from the forest. Despite this, on a regional scale, our monitoring transect revealed a strong spatial dependency between outbreak intensity on willows and the distance to the birch forest. This dependency has three possible interpretations. First, outbreaks on willows may be partly sustained by wind-driven long-distance dispersal of larvae from ongoing outbreaks in the birch forest, thus creating a regional-scale source-sink dynamic (Bode et al. 2006). Data on wind directions from the airport close to Vadsø (Fig. 2) suggest that the period of potential larval dispersal during spring has a high incidence of winds coming in from the open sea (northeast), but that winds from

Fig. 6. Maps illustrating long-term trends in the first day of year with an accumulated temperature sum of 250 °C (DOY₂₅₀) across the study region over the periods 1991–2000, 2001–2010, and 2011–2017. The colors correspond to the mean DOY₂₅₀ per time period. The maps are derived from gridded climate data with a 1 km resolution. The samplings sites in the regional monitoring transect are represented by grey dots in the maps and the distribution of forest as grey hatching. Source of topographical map layers: [Norwegian Mapping Authority \(2016\)](#). Source of forest map layer: [Norwegian Institute of Bioeconomy Research \(2017\)](#) and [Heggem et al. \(2019\)](#).

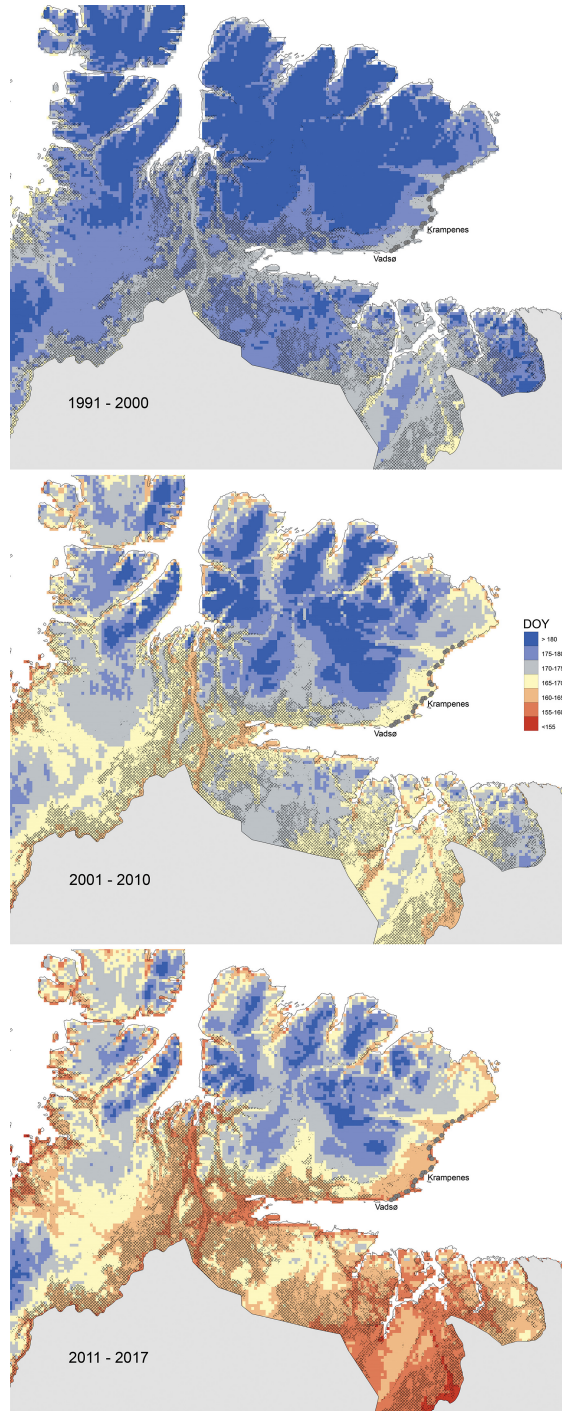
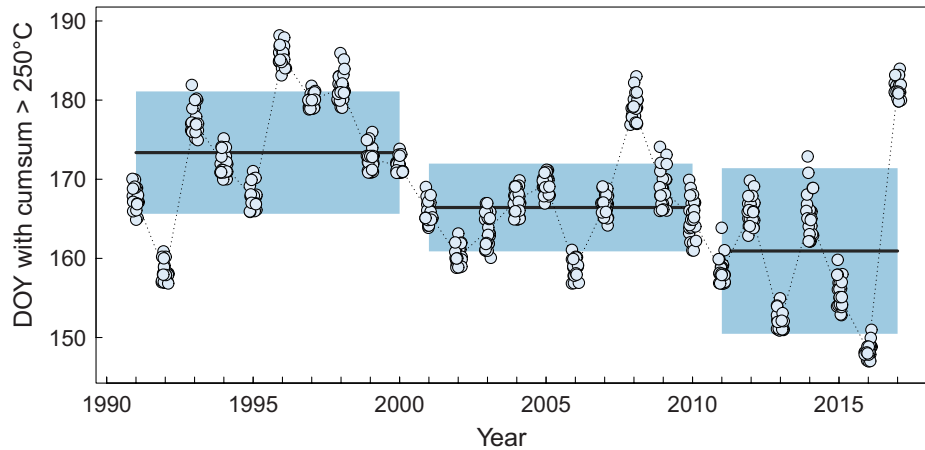


Fig. 7. Yearly variation in the first day of year with an accumulated temperature sum of 250 °C (DOY₂₅₀) for the regional monitoring transect based on gridded climate maps. Dots represent individual samplings sites. The horizontal lines represent mean DOY₂₅₀ for the periods 1991–2000, 2001–2010, and 2011–2017, whereas the shaded areas represent ± 1 SD of the means.



the from the west are also common (Supplementary Fig. S1¹). Hence, there may be ample opportunities for larval dispersal eastward from the forest and towards the transect. Second, the locations farthest away from the forest may, as of yet, be climatically unfavorable for the winter moth. Third, our two years of monitoring data may represent a snapshot of a winter moth invasion front that will gradually move farther into the tundra (Elkinton et al. 2014). Continued monitoring is necessary to resolve this uncertainty. This could take several years, as the outbreak in the tundra appeared to be collapsing in 2020, suggesting that winter moth populations were about to enter the low phase of their population cycle. This coincided with a collapse in the winter moth population at our monitoring site in birch forest at Vestre Jakobselv, which is located about 25 km west of the first site in the willow transect (COAT, unpublished data, 2020). The decline of moth densities on willows in 2020 is, therefore, likely to reflect a regional decline in moth populations, rather than a bias introduced by our change of method in 2020. Hence, inference about a potential spread of the outbreaks farther into the tundra may not be possible until moth population densities start to increase again.

We have shown that the expansion of the winter moth into the shrub tundra has coincided with a distinct advancing phenological trend for the study region, but this does not demonstrate decisively that mechanisms related to phenology have facilitated the expansion. However, we know that warmer springs lead to improved phenological matching between the budburst of mountain birch and the hatching of eggs in another range-expanding geometrid, namely the scarce umber moth (*Agriopsis aurantiaria* Hübner, 1799, Lepidoptera, Geometridae; Jepsen et al. 2011). Similar mechanisms have been suggested to drive range expansions and host plant shifts in the spruce budworm (*Choristoneura fumiferana* Clemens, 1865, Lepidoptera, Tortricidae; Pureswaran et al. 2015; Pureswaran et al. 2019). Hence, it is possible that the expansion of the winter moth into the shrub tundra has been facilitated by improved phenological matching between the budburst of willows and hatching of moth eggs in warmer and earlier springs. Also, according to our analysis,

¹Supplementary data are available with the article at <https://doi.org/10.1139/as-2021-0027>.

winter moth eggs would, on average, not be expected to hatch until mid to late June in our monitoring transect in the two decades preceding the expansion into the tundra. This is roughly a month later than what is typically observed in coastal mountain birch forest (Bylund 1999; Mjaaseth et al. 2005). If this resulted in a corresponding delay in the eclosion of the adult insects in autumn, there would be high risk of premature termination of the flight period due to snowfall and sub-zero temperatures. Thus, phenological advancements may have been necessary for the winter moth to complete its life cycle in the tundra. Indeed, the ability to complete development within the time constraints of seasonal environments is thought to be a key mechanism by which phenology determines species ranges (Chuine 2010).

Conclusion

We have documented an outbreak by a range-expanding boreal insect herbivore in Low Arctic shrub tundra. The advent of outbreaks in this ecosystem is likely to have substantial consequences for the dynamics of resident willow shrubs and associated species. Our findings demonstrate that climate-tracking boreal pests should be taken into consideration when making predictions about future vegetation dynamics in Arctic ecosystems or when designing monitoring programs for these systems. Our case study also adds to a growing body of evidence that successful expansion into the Arctic is often associated with dietary generalism and high dispersal capacity.

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Author contribution statement

OPLV, JUJ, HM, and RAI conceived and designed the study. OPLV, JUJ, and HM collected the data. OPLV and JUJ analyzed the data with contributions from RAI. OPLV wrote the paper with input from all co-authors. All authors contributed to manuscript editing.

Data availability statement

Data for the experimental part of the study are archived at the Dryad Digital Repository at doi: [10.5061/dryad.sxksn0336](https://doi.org/10.5061/dryad.sxksn0336). The rest of the data are available at the data portal of the Climate-ecological Observatory for Arctic Tundra (<https://data.coat.no/>).

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