Spatiotemporal predation patterns of insect herbivores in the Subarctic

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Abstract

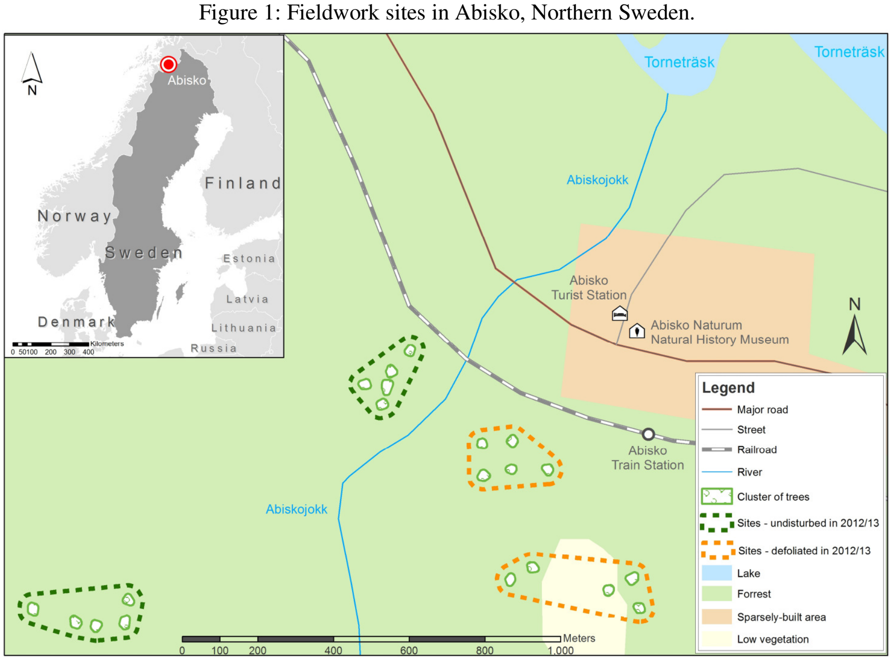
Artificial caterpillars are increasingly used in studies of predator-insect interaction. In this pilot study, we used 3D-georeferenced plasticine caterpillars to study spatio-temporal autocorrelation of predator attacks on caterpillars in Subarctic birch forests. Overall, the results showed that about 49% of the caterpillars were attacked, the majority of which by birds. Spatially, the results suggest that predation follows a clustered pattern, with attacks being spatially correlated within the radius of 5m. The temporal pattern shows that >90% of the attacks occurred between day 6 and the end of the season, which highlights the need to implement a more frequent monitoring schedule to capture the temporal variation of insect predation. This study demonstrates a novel approach for quantifying spatio-temporal autocorrelation in insect predation on a fine scale, which is essential for understanding population dynamics and ecosystem consequences of insect disturbances.
Keywords: Climate change, forest defoliation, plasticine caterpillars, geocoding, 3D spatial analysis, Subarctic

1 Introduction

Higher atmospheric concentration of CO_2 is one of the key contributing factors to global warming (IPCC 2013), hence productive ecosystems are important for climate change mitigation (Goodale et al. 2002). Particularly in the Arctic, global climate change has affected the frequency and intensity of naturally occurring disturbances, such as insect herbivore outbreaks, which can turn forests from carbon sinks to sources (Jepsen et al. 2008).

In Subarctic birch forests, geometrid moth outbreaks lead to severe defoliation resulting in up to 90% reduction in net primary productivity (Olsson et al. 2016). The changed outbreak dynamics are often attributed to the bottom-up control by milder winters, increasing the egg survival rate of the forest-defoliating moth caterpillars *Epirrita autumnata* and *Operopthera brumata* (Nilssen and Tenow 1990; Babst et al. 2010). However, it may also be top-down controlled by predator dynamics (Wauchope et al. 2017).

Figure 1: Fieldwork sites in Abisko, Northern Sweden.



Source: National Land Survey of Sweden (Lantmäteriet); Natural Earth; Fieldwork data.

Plasticine caterpillars have been used to assess insect herbivore predation rates in local studies (Howe and Nachman 2009) and in global studies (Roslin et al. 2017). However, no studies have previously applied accurate georeferencing in studying small-medium scale autocorrelation in predation monitoring. In this pilot study, we develop a novel method for studying spatiotemporal patterns in the predation of moth larvae in Subarctic birch forests.

2 Method

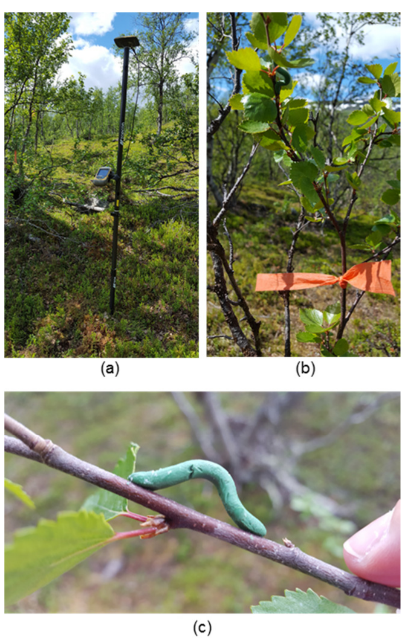
2.1 Fieldwork

During the summer of 2016 four study sites of Subarctic birch forest were selected close to Abisko in northern Sweden (68°20′ N, 19°02′ E). To control for outbreak legacy effects, two of the sites were located in areas that had been severely defoliated during the most recent outbreak in 2013, and two were located in areas undisturbed by that event (Figure 1).

A total of 400 plasticine caterpillars resembling common geometrid moths were glued to twigs (Figure 2(b), Figure2(c)) and geo-tagged with a high precision RTK-GPS (Figure 2(a)).

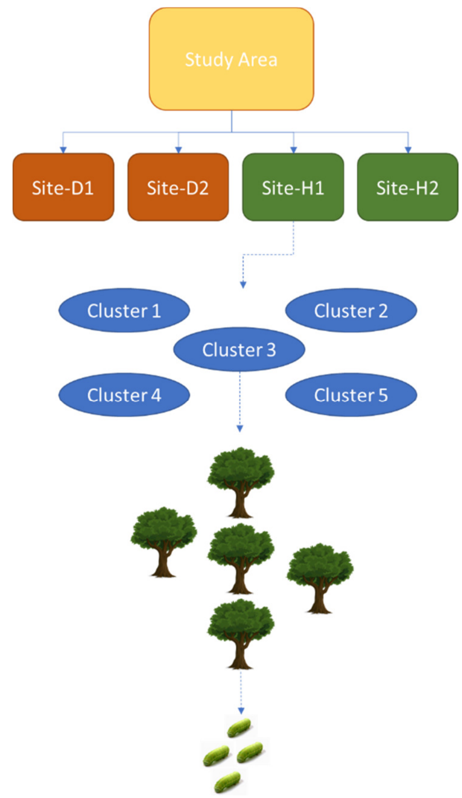
The sampling distribution could be described as a cluster of clusters, within which dummy-caterpillars were placed in a random way (Figure 3). The sampling distribution was dictated by the distribution of canopies.

Figure 2: (a) RTK-GPS, (b) marked caterpillar, (c) attacked caterpillar



Source: Photos from fieldwork sites in Abisko, Sweden. June 28th, 2016.

Figure 3: Diagram depicting the various levels of aggregation of the study area.



Attacks were recorded on day 2, 4, 6, and at the end of the growing season (day 87), and grouped by predator type (ants, bird or unknown). A photographic log was created to store pictures of every attacked larva for future reference.

2.2 Data Processing

The point dataset of attacked caterpillars was tested for complete spatial randomness using the G-function (1), which computes the ratio between the total amount of point pairs whose in-between distance $d_{min}(u_i)$ is less or equal to the cutoff distance d. d contains a list of values that represent the distance between every event and its nearest neighboring event.

$$G(d) = \frac{\#\{d_{min}(u_i) \leq d, i = 1, \ldots, N\}}{N} \quad (1)$$

Some caterpillars were placed at different elevations in locations with similar latitude and longitude. The distance between two such caterpillars in 2D-space is smaller than in reality. Therefore, the distance between all sets of points $A(x_1,y_1,z_1)$ and $B(x_2,y_2,z_2)$ was computed using the 3D Euclidean distance function (2).

$$d(A,B) = \sqrt{(x_2 - x_1)^2 + (y_1 - y_2)^2 + (z_2 - z_1)^2} \quad (2)$$

The G-function was also implemented separately for all attacks recorded by the same predator. We tested for spatial and temporal patterns of attacks per predator type.

The Join Count Statistics method for point pattern analysis (Rosenberg and Anderson) was used to test for spatial and temporal autocorrelation. This method is used for categorical point datasets. It creates pairs of points that display the same nominal variable-value and are within a certain distance. In this case, a distance matrix was used containing the shortest 3D-distances between all points in combination with an inverse distance weighting scheme. Next, this number of pairs were compared to the expected by chance number of pairs in a random distribution. A permutation test (999 repetitions) was used to test the significance of the results.

3 Results

An absolute number of 197 (49%) caterpillars were attacked over the course of the experiment, the vast majority by birds (~75%), of which >90% were attacked between day 6 and the end of the season. No results of the temporal point pattern analysis are included, as most of the attacks occurred between day 6 and day 87 with no kept records in between. There were no differences between the site outbreak history. The G-function values based on the 3D Euclidean distance between all the attacked caterpillars suggest a clustered pattern of attacks within a distance of ~2.5 m (Figure 4).

Figure 4: G-function diagram over total # of attacks with distances computed in 3D.

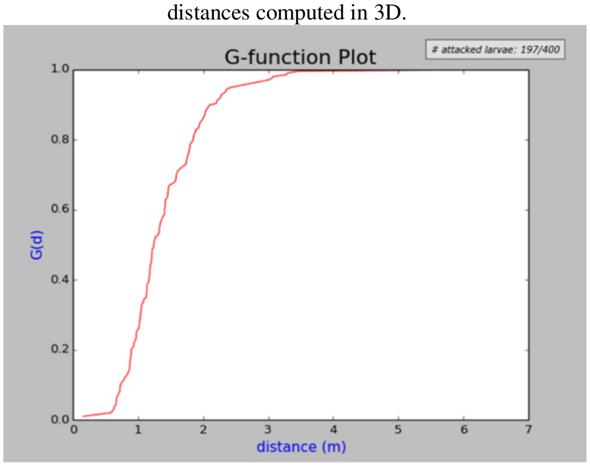


Table 1: Joint Count Statistics results for bird-predators (BxB)

Distances classes (m)	Expected Join Counts	Join Counts	SD	T-score	Prob.
0-5	67.88	84.03	5.58	2.89	0.004
5-10	37.37	38.04	2.34	0.28	0.777
10-25	15.54	15.16	1.34	0.27	0.781
25-100	17.50	18.01	1.31	0.38	0.699
100-500	15.69	16.88	0.80	1.48	0.140
500-1000	3.86	4.29	0.30	1.43	0.152

Attacks by bird: 147

The results of the join counts statistic for bird predators (Table 1) suggest a significant spatial autocorrelation effect between attacks on dummy-caterpillars placed within 5m from each other. The conclusion is based on the higher number of occurring join counts compared to the lower number of expected join counts recorded for this distance along with a high t-score. The dependency is lost for longer distances.

4 Discussion

Conducting 3D spatial analysis over point datasets of study areas that consist of several non-adjacent locations can be a challenge. There is a lack of tools dealing with significance-tests over this kind of study areas in 3D. The next step would be to develop a tool in R that would compute the G-function and its envelope for point datasets of study areas that consist of more than one location. Every such location could then be represented as the minimum bounding 3D-object of the points within it.

The temporal monitoring frequency of the caterpillars should be increased to document when the attacks peek and when they seize to occur in correlation to the life circle of the moths and their predators.

The experiment needs to be repeated for a sequence of years over the same areas, using the same placement method. This way, data from the time series could be used to spot potential fluctuations in the herbivore predator populations as well as differences in predation patterns.

5 Concluding remarks

Given the severe ecosystem disturbances defoliator moth outbreaks constitute, it is important to understand top-down control of insect population dynamics to make realistic predictions of future outbreak risks. This pilot study presents a novel methodology for obtaining detailed understanding of the small-intermediate scale spatiotemporal patterns of insect predators using a unique 3D-georeferenced dataset and geostatistics. The results should be interpreted with careful consideration of potential artefacts from the spatial caterpillar distributions, and biological factors, such as predator phenology, but it is nonetheless a first step towards the development of a new quantitative method for studying predator-herbivore interaction in complicated forest ecosystems.

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