Spatio-temporal modelling of Larch Bud Moth dynamics in the European Alps: the importance of data resolution

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Abstract

Spatial scale and in particular grain (as an aspect of scale) of input data is likely to influence the behaviour of ecological models considerably. It is well known that coarse spatial resolution limits the usefulness of spatial models. However, it is often overlooked that uncertainty increases with high resolution input data. Thus, there is likely an optimum spatial resolution, which depends on the nature of the input data and the ecological process being modelled. In this study we investigate how spatial grain of input data within the same spatial extent affects the ability of a model in predicting observed population dynamics of larch bud moth within the Upper Engadine valley in the Swiss Alps. Our results demonstrate that modelling larch bud moth at a higher resolution results in minor but insignificant improvements in the accuracy of predicting of observed larval densities. Increasing the resolution of input data of the given model does not improve its ability to predict spatial patterns at the local scale and increases uncertainty. Observed spatial patterns could be predicted most accurately, and with minimised uncertainty with a model with a coarser spatial grain of input data, thereby confirming a postulated optimum spatial grain.

Key words: Upper Engadine valley; larch bud moth; spatial grain; population dynamics; model prediction

1 INTRODUCTION

The larch bud moth, *Zeiraphera diniana* GN. (*Lep., Tortricidae*), is a conspicuous forest defoliator that has caused large-scale defoliation of larch trees across the entire Alpine Arc approximately every 9 years, documented since at least 1854 (Auer, 1969; Auer, 1977; Fischlin, 1982; Baltensweiler & Fischlin, 1988; Baltensweiler & Rubli, 1999). Theory suggests that the cyclic population dynamics result from either an interaction between larch bud moth and its parasitoids (parasitoid-prey hypothesis) (Baltensweiler *et al.*, 1977; Baltensweiler & Fischlin, 1979; Fischlin, 1982; Baltensweiler & Fischlin, 1988), a feedback relationship between the larch bud moth and its host, the European Larch (*Larix decidua* MILLER) (food quality hypothesis), or a tri-trophic relationship combining the food quality hypothesis and the parasitoid-prey hypothesis (e.g. Turchin *et al.*, 2003).

Models of larch bud moth dynamics have already been developed for a variety of spatial scales, ranging from local scales to that of the entire Alpine Arc (Fischlin, 1982; Fischlin, 1983; Bjornstad *et al.*, 2002; Turchin *et al.*, 2003; Johnson *et al.*, 2004). Many larch bud moth models focus on fluctuations over time, and those that do incorporate spatially varying properties have only been able to take advantage of spatial data at a very coarse spatial resolution, or have depended on subjective defoliation map data (Fischlin, 1982; Fischlin, 1983; Johnson *et al.*, 2004; Bjornstad *et al.*, 1999).

Previous studies (e.g. Fischlin, 1982; 1983; Bjornstad *et al.*, 2002; Peltonen *et al.*, 2002; Johnson *et al.*, 2004; Price *et al.*, 2006) have described distinct spatio-temporal dynamics of larch bud moth, and these dynamics appear to change with spatial scale.

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''Scale is characterised by grain and extent. Grain is the finest possible spatial resolution within a given dataset. Extent refers to the size of the overall study area.' (Turner *et al.*, 2001). Most ecological studies are faced with a decrease in spatial grain as extent increases. However, it is in general unclear whether this can be justified or whether it occurs

5   at the expense of relevant information. To study this question it would be of advantage to investigate the same population system at several spatial scales. This study considers such a case of an increase in spatial grain within the same spatial extent.

Spatial scale and in particular the spatial grain (as an aspect of scale) of input data are likely to influence results produced by an ecological model considerably (Turner, 1989;

10   Wiens, 1989; Levin, 1992). While high resolution input data may be required to make predictions and model processes at high spatial grains, sampling and observational constraints, such as number of weather stations, tend to increase the uncertainty associated with these input data. Moreover, interpolation techniques, introduce further uncertainties through parameterisation and approximation of modelled processes. Such effects have been

15   studied in other contexts, such as climate modelling (e.g. Henderson-Sellers, 1996; Gyalistras & Fischlin, 1999; O'Neill & Steenman-Clark, 2002), hydrology (Cotter *et al.*, 2003), or geostatistics (Kyriakidis & Yoo, 2005), but little in ecology (Landis, 2003).

The required spatial resolution and accuracy of model results depend on the ecological processes being modelled (Levin, 1992; Allen & Holling, 2002). For certain ecological

20   processes it may no longer make sense to use input data at a higher spatial grain as this may complicate computations with propagation of uncertainties or, at the worst, produce results that no longer make sense. However, using input data at low resolution only allows models to make broad predictions across large geographical areas. Moreover, small-scale processes of importance for understanding the ecological process at a large scale may become disregarded.

Therefore, it is likely that for each ecological process being modelled there is a distinct optimum spatial grain for the input and model variables. That spatial grain should allow for highest accuracy in model predictions while being as coarse as possible to minimize uncertainty, yet still include any important small scale process. Beyond that spatial grain (at lower or higher spatial grains) accuracy of results may not improve or perhaps even decline (Mac Nally & Quinn, 1998).

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To investigate this idea we have studied larch bud moth population dynamics at the scale of the Upper Engadine valley, in particular looking at migration and local dynamics. This case study satisfied all requirements: (i) input data with differing spatial grains within the same extent, (ii) observed output data at a high spatial grain, and (iii) a family of validated models capable of generating spatio-temporal patterns of population dynamics comparable to the patterns observed. We used Fischlin's (1982) spatially explicit model of larch bud moth migration throughout the Engadine with coarse spatial resolution coupled with a local dynamics model describing local population fluctuations. We combined this model with a GIS system (GRASS Neteler & Mitasova, 2002) to allow integration of spatial data at several spatial resolutions. Using the GIS and a wind model (NUATMOS) (Ross *et al.*, 1988), we generated the spatially explicit input data as required by the model and simulations were run at three different levels of spatial grain: the entire Upper Engadine valley, the 'site' ($\sim$3.5km^2) and the forest compartment ($\sim$25 ha).

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We determined how an increase in spatial resolution affects the migration patterns of the larch bud moth and the predicted population dynamics within the Upper Engadine. We address the following questions: Does an increase in spatial grain of model input data increase the accuracy of modelled larch bud moth dynamics? Can we better predict spatial patterns across a region by increasing the spatial grain of input data and model?

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2   MATERIAL AND METHODS

2.1 Study area

The Upper Engadine valley is a sub alpine valley in the Swiss part of the European Alps (Figure 1) forested with mixed larch (*Larix decidua* MILLER) - Swiss stone pine (*Pinus cembra* L.) forests. Forests within the Upper Engadine valley were previously divided into 420 'Forst-Abteilungen' (forest compartments) designated according to the needs of forestry management. Thus their delineation is based on a mixture of political, practical, and ecological criteria. The forest compartments have an average area of 25 ha and an average forested area of 16.5 ha. From 1949 to 2005 larval surveys have been carried out within the Upper Engadine valley including recording of the forest compartment in which each surveyed tree was located (A. Fischlin in prep.).

#Figure 1 approximately here#

2.2 Models

Fischlin (1982) developed a model of the local dynamics of the larch bud moth in the Upper Engadine valley based on the food quality hypothesis known as LBM-M8. The model considers the relationship between the larch bud moth and its host, the larch. Larch bud moth feeding causes an increase in raw fibre content of the larch needles, the chosen food quality indicator, which has negative implications for larch bud moth survival of larvae, pupal weight, and in turn determines female fecundity. Low food quality causes a decrease in the following year's larch bud moth population. The model deals with local dynamics only, and treats an entire valley as a homogeneous area with no spatial structure (Fischlin &

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Baltensweiler, 1979). The local dynamics model is a deterministic mathematical model, i.e. a second order, discrete time system of coupled, non-linear equations.

We considered it reasonable to use our LBM-M8 larch-larch bud moth model in this study even though a recent study by Turchin et al. (2003) suggests that the parasitoid-larch

5   bud moth interaction was the dominant factor driving the larch bud moth cycle (compared to the larch-larch bud moth interaction). Correlation analysis of the average observed larval densities for the Upper Engadine valley and those predicted by our LBM-M8 model for the same time period as the data analysed by Turchin et al. (2003), resulted in a correlation coefficient of 0.840 (significant at the $\alpha = 0.05$ level). In addition, the formulation of the

10   LBM-M8 model lends itself well to combination with a migration model, which would be more difficult with Turchin et al.'s (2003) model.

To model larch bud moth dynamics in a spatially explicit manner within the Upper Engadine valley, Fischlin (1982) divided the Upper Engadine into 20 spatially discrete regions, known as 'sites'. These sites are homogeneous with respect to aspect, elevation and

15   forest type. The sites have an average area of 3.7km^2 and are between 2 and 30 km apart from site centre to site centre (Fischlin, 1982). This model, known as LBM-M9, incorporates the local dynamics model (LBM-M8) as a sub-model and couples it with another sub-model for flight within the Engadine valley between the 20 sites (see also Baltensweiler et al., 1977; Baltensweiler & Fischlin, 1979; Fischlin, 1982). For a given flight season the flight sub-

20   model simulates the numbers of females emigrating from a given site and the numbers of eggs they oviposit in all the sites to which they immigrate. The flight part of LBM-M9 is also a deterministic mathematical model, and the behaviour of all female moths in a site is defined by a recursive formula involving the current site and all relevant neighbouring sites. Specific site conditions as determined by wind statistics and other site specific characteristics such as

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defoliation, forested area, and number of larch trees determine dispersal rules (Baltensweiler & Fischlin, 1979; Fischlin, 1982). The dispersal rules give the number of moths leaving the site in each flight direction. Moths leave their current site for the neighbouring sites where, on the next recursion level, the dispersal rules are again applied. The recursion continues until all

5   flying moths are dispersed (Baltensweiler *et al.*, 1977; Baltensweiler & Fischlin, 1979; Fischlin, 1982; Baltensweiler & Fischlin, 1988). It is assumed that only mated females become airborne, and thus no interference between moths is considered. Therefore, this recursive formula may be repeatedly computed for the females of all sites in sequence. The abundance of larch bud moth larvae in each site for the next generation is determined by

10   summing the number of eggs oviposited in each site by any female, multiplied by a winter egg survival ratio. Moths are assumed to migrate from the centre of each site (Fischlin, 1982).

The spatially explicit input data required by LBM-M9 are listed in Table 1. Wind statistics (speed and direction) for the flight season July 15th - September 30th were derived for each site from records of the Swiss Federal Office of Meteorology and Climatology

15   (MeteoSwiss) weather stations. Wind was recorded in three speed categories: still (<0.5m/s), gentle (0.5-2.8m/s) and strong (>2.8m/s) in each of eight compass directions. The wind parameters for LBM-M9 were then given as constants, i.e. the average proportion of the total wind behaviour for each wind speed category over time (Fischlin, 1982). At the coarse resolution of the site, applying only eight wind directions yielded ambiguous neighbour

20   relationships. Thus, each direction was further divided into two sub-directions within the LBM-M9 model (Fischlin, 1982).

#Table 1 approximately here#

We introduce in this paper a new higher resolution model known as LBM-M11 (LBM-M10 designates an even coarser spatial resolution, that of an entire Alpine valley. The

model simulates larch bud moth migration along the entire Alpine arc.). LBM-M11 has the same structure as LBM-M9 and requires the same type of input data, but at a finer spatial resolution as it models migration between the 420 forest compartments of the Upper Engadine valley. The mathematical equations are very similar, the only difference being that, due to the

5 coarse spatial resolution of LBM-M9, migration is modelled in 16 directions from each site, whereas, at the higher resolution of LBM-M11 the sub division of wind directions was no longer necessary; shorter distances between forest compartments (as compared to distances between sites) meant there were no longer ambiguous relationships between neighbours. Therefore, migration in LBM-M11 is only modelled in eight directions from each forest

10 compartment.

2.3 Data

2.3.1 LARVAL CENSUS

Larval sampling is timed to take place when larch bud moth is predominately in the larval stages L3, L4 and L5. This timing depends on weather conditions and varies inter-

15 annually (Fischlin, 1993). Within the Upper Engadine valley, during the first phase of the larval survey (1949-1958: A. Fischlin in prep.) between 1000 and 2100 trees were sampled annually and the number of larvae per tree was determined (Auer, 1961). From 1956-1979 the sampling method changed and approximately 400 larch trees were sampled annually according to a statistically sound random sampling scheme (Kälin & Auer, 1954). Sample

20 stratification was according to topographical features (altitude, exposure) and samples were weighted according to host-tree density per unit area (Baltensweiler & Fischlin, 1988). During these annual population surveys approximately 3 kilograms of twigs and foliage (excluding cones) were taken from each tree; 1 kg from each of three levels within the crown.

In 1956 and 1957 both sampling methods were employed to allow compatibility and comparison of the results. The larval censuses provide an average density estimate for the larval population (e.g. Auer, 1969; Auer, 1978) and were converted to an annual absolute population estimate for the site and for the entire Engadine Valley (Fischlin, 1982). The census method within the Upper Engadine changed after 1977, meaning that annual data were no longer available for each of the 'sites' within the Upper Engadine valley (A. Fischlin in prep.). Instead, within three specific sample areas, three trees were randomly chosen. The sampled areas were chosen to be representative of the entire valley and were spread evenly along the length of the valley (Fischlin, 1993). This allowed estimation of a mean population density for the entire valley. Larval census data with larval numbers recorded according to forest compartment ID is available in an electronic database for years 1957-1991(LBM database: A. Fischlin in prep.). Earlier data were not digitised at the forest compartment level. Therefore, annual larval densities per forest compartment could be derived from the database. However, not all forest compartments have been surveyed and density values were not available for every year for every compartment.

2.3.2 TREE DATA

The numbers of larch trees per forest compartment were recorded in management reports of the Upper Engadine Forestry division and prepared for LBM-M9 (Fischlin, 1982). However, tree data was not available for every forest compartment. Therefore, an estimate of larch tree numbers was required for those forest compartments for which the data were missing. Grouping the forest compartments for which tree data were available according to exposure (northern and southern) and plotting forested area versus number of larch trees revealed a linear relationship (Figure 2) from which we estimated the number of larch trees in the remaining forest compartments.

#Figure 2 approximately here#

2.3.3 WIND DATA

NUATMOS is a "physically consistent three dimensional diagnostic model designed to minimize the difference between the initial interpolated wind field and the final wind field subject to a mass-consistent constraint" (Ross *et al.*, 1988). NUATMOS produces a "three dimensional mass-consistent windfield, which bases on arbitrarily located observations" (Ross *et al.*, 1988). The input consists of parameters controlling NUATMOS, specification of the digital elevation model (DEM) on which NUATMOS is applied, and wind observations in the form of horizontal wind components. The wind direction and speed on the surface is calculated from the three dimensional wind field NUATMOS generates (Bachmann, 1998). In this study NUATMOS version 5N (07/31/91) (Ross *et al.*, 1988) has been applied to a DEM with a spatial resolution of 50 m (DHM50 ©, Tydac AG).

The wind observation data used as input to NUATMOS was retrieved from the Swiss Federal Office of Meteorology and Climatology. The six meteorological observation stations chosen to provide initial conditions were within and around the Upper Engadine valley (Bever, Bivio, Corvatsch, Robbia/Poschiavo, Sils Maria, and St.Moritz). As topographical effects largely drive wind patterns within the Upper Engadine valley, average summer wind speed and direction values are considered constant through time by the LBM-M9 and LBM-M11 models (Fischlin, 1982). Therefore, a period for which all of the relevant meteorological observation stations provide data, 1980 to 1982, was chosen from which to take data to drive NUATMOS. Since NUATMOS requires observations from at least one observation station not located on the surface, wind observations from the troposphere (ca. 5500 m.a.s.l.) were also taken.

The goal was to produce wind fields in the Upper Engadine required as input for the models LBM-M9 and LBM-M11, as described in section 2.2. Larch bud moth flight occurs only during a seasonal window of mid July to September in the early evening when temperatures are above 7°C (Fischlin, 1982; Baltensweiler & Rubli, 1999). Therefore only

5   evening (19h30) wind measurements between July 15th and September 30th at temperatures above 7°C were retrieved.

This data was used to generate 200 wind observation input files for NUATMOS. Based on these wind observations, NUATMOS interpolated wind direction fields and wind speed fields for 200 points in time. These wind fields were then applied to generate the wind

10   statistics for each cell as required by the larch bud moth models (see section 2.2).

The accuracy and the usefulness of the wind fields generated by NUATMOS were tested through evaluation of the generated wind fields against values from the meteorological observation station of Samedan, located in the centre of the Upper Engadine. The difference in average wind direction was 62.9 degrees and the observed average wind speed was 3.79

15   m/s compared to simulated average wind speed of 1.63 m/s. An evaluation of NUATMOS by Connell (1989) has shown that the best agreement between modelled and observed values is achieved at mountain tops whereas poor agreement occurs at low wind speeds (i.e. 2m/s) and when re-circulating flow occurs on the lee side of mountains.

While the differences between modelled and observed wind speeds were considerable,

20   the deviations in wind direction were less critical for modelling larch bud moth since the average difference of 62.9 degrees was less than the difference between major wind directions (north, south, east, west) of 90 degrees. Before the final decision on whether to use the NUATMOS results, we performed a sensitivity analysis of the LBM-M9 model to wind statistics. Simulating the model without wind, i.e. where all moths migrate randomly

regardless of wind speed or direction, produced results with very little variation from the results simulated using MeteoSwiss wind data. Calculation of a similarity index:

$$1 - \frac{\sum r1 - r2}{\sum r1 + r2}$$ between the sets of results gave a mean similarity index of 0.9729 (min: 0.9344,

max: 0.9978, sd: 0.0025) suggesting the model is not sensitive to wind. Therefore, we decided

5   it was reasonable to use the NUATMOS wind fields for the LBM-M11 model.

The models LBM-M9 and LBM-M11 require wind statistics representing the entire site, respectively forest compartment. Both models assume that female moths take-off from the centre of the site or forest compartment. Therefore, the wind statistics were computed from the values at the centre point (centre of gravity of planar projection) of each site or forest

10   compartment.

2.3.4 NEIGHBOURHOOD DATA

To obtain the neighbourhood data for each forest compartment required as input to the LBM-M11 model, the forest compartments were first digitised and stored as a vector data layer within a GIS. The model requires knowledge of the nearest neighbours for each forest

15   compartment in each of the eight compass directions. Therefore, forest compartments that are spatially separated and not sharing any borders are still neighbours as long as no other forest compartments are located between them. This meant that neighbours could not be determined by standard GIS neighbourhood analysis functions, which require adjoining borders. Based on the centroid coordinates of each compartment, a list of closest neighbours was determined for

20   each compartment. It was then necessary to manually determine which of those were or were not actual neighbours. Once the neighbours were assigned, a vector containing eight sectors, one for each of eight compass directions, was created for the centre of each compartment. By adding the vectors containing sectors with the forest compartment vector it was possible to

determine (i) in which direction each neighbour is located, (ii) the area of each neighbour in the given compass sector and (iii) the distance to each neighbour centre.

2.4   Comparison of Models Performance

In order to compare the results of our higher resolution model LBM-M11 with the coarser spatial resolution models LBM-M9 and LBM-M8, mean square error (MSE) statistics were calculated for standardised modelled time series of larval density compared with standardised observed time series of larval density for each forest compartment (where observation data existed).

The forest compartment observation data was compared to the standard LBM-M11model run data, LBM-M11 output with only random flight (not dependant on the wind field), the LBM-M9 output for the associated site and the LBM-M8 output (average of the entire Engadine valley). The series were standardised using a $\ln(x+1)$ transformation, due to the presence of many zero observations.

In LBM-M11, the initial larval density in each forest compartment was determined from the mean larval density per tree over the entire Engadine valley and multiplied by the number of larch trees in each compartment. Thus the initial larval density per kg of tree branches is the same in each forest compartment (the model assumes that the number of kilograms of branches per larch tree is constant regardless of spatial location). However, when we examine field data (cf. Figures 3a and 4a) we see that observed larval density varies considerably from one forest compartment to another in some years. Thus we run the model over a long period (>80 years) so that the model approaches a steady state, where the relationship between the forest compartments remained similar and the initial conditions no longer influenced the modelled results. We considered this to be a steady state with respect to

spatial variance. Thus we simulated larch bud moth densities for at least 100 years and compared modelled densities at steady-state with an average cycle of observed densities to gain an understanding of the accuracy of the modelled results. The average cycle of observed larval densities is determined by averaging over all available, overlapped cycles (overlapping

5   is obtained by temporal shift till peak years match Fischlin, 1982).

#Figure 3(a and b) approximately here#

#Figure 4 (a and b) approximately here#

We calculated the same MSE statistics as described above for standardised observed and steady state modelled time series.

10   While the MSE statistics inform us about how well our modelled data fits the observed data, they do not tell us much about how well the spatial patterns are modelled. In order to determine if our higher resolution model can predict observed spatial patterns we performed linear regression for each year of an average observed cycle versus each year of a steady state modelled cycle, for modelled and observed values at the 'site' resolution and at

15   the forest compartment resolution. Finally we categorised both observed and modelled larval densities from one cycle into 4 groups: 0-1, 1-10, 10-100 and 100-1000 larvae/kg tree branches. We then mapped these values for each year in one cycle and compared maps by calculating coincidences between the maps.

Another measure of whether a higher spatial grain model is needed to define spatial patterns

20   would be to determine if larval density values are highly variable over space. Once we have classified the densities as described above we can measure landscape pattern through calculation of landscape metrics. Contagion enables us to distinguish whether area with the same category value are clumped together across the landscape or dissected (O'Neill *et al.*, 1988; Li & Reynolds, 1993; Turner *et al.*, 2001). A measure of contagion for modelled and

observed density maps will also give us an indication of whether the model predicts more or less spatial variability than is observed. We calculated a contagion index for modelled and observed density maps for each year of a single cycle using the contagion metric as described by Li and Reynolds (1993) (adapted from O'Neill et al. (1988)):

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$$C = \frac{1 + \sum_{i=1}^{n} \sum_{j=1}^{n} (P_{ij}) \ln(P_{ij})}{2\ln(n)}$$

where P_{ij} = the probability that patch type i is adjacent to patch type j, and n is the number of patch types on the landscape.

3   RESULTS

Comparison of the modelled time series with the observed time series for each forest

10   compartment for the LBM-M8 model run, the LBM-M9 model run, the steady-state LBM-M11 run and the LBM-M11 model run with uniform wind conditions, reveal that the average value of MSE for the steady state cycle of LBM-M11 is the lowest by a small margin (Figure 5). This result suggests that LBM-M11 has the best fit to the observed data although the range of values suggests there is no significant (α=0.05) difference between the fit of LBM-M11

15   compared to all other model runs.

#Figure 5 approximately here#

The results of linear regression at the spatial grain of the 'site' show a linear relationship between observed and modelled values, except for trough years (1, 8 and 9) where R^2 values are low due to zero values in the observations which can not be predicted by

20   the model (Table 2). This suggests that the LBM-M9 model is actually capable of predicting the observed spatial pattern of larch bud moth larval densities. At the spatial grain of the

forest compartment, R^2 values are very low and slopes close to zero across all comparisons (Table 3). This result suggests that the LBM-M11 model is not able to accurately predict the spatial pattern observed in larval densities at the forest compartment resolution. The intercept values increase as larval densities increase, with the highest values at peak years and very

5   small values for trough years.

#Table 2 approximately here#

#Table 3 approximately here#

As we know that there is little difference between the overall predictive ability of the coarse resolution model and the fine resolution model, we are now interested in how well the

10   spatial pattern at the forest compartment spatial grain is modelled: whether high and low values are correctly predicted as high or low values. Given the results of our MSE calculations we surmise that actual larval densities are not better predicted than by a coarser resolution model. One problem is that the observed data shows many instances of zero larch bud moth/kg tree branches, while the model does not predict zero values at cycle troughs

15   (local population extinction).

Calculation of coincidences between the maps of observed and modelled (LBM-M11) larval densities over one cycle suggests that the LBM-M11 model is not capable of predicting spatial pattern well, with only one category predicted well in each year of a cycle (Table 4).

#Table 4 approximately here#

20   There is no pattern between the contagion values for observed maps and those for modelled (LBM-M11) maps, i.e. contagion indices for the observed density maps are neither consistently greater nor smaller than those for modelled density maps over time (Table 5).

Very high contagion values occur in trough years (i.e. 8 and 9) because a majority of forest compartments have recordings of zero larvae per kilogram tree branches.

#Table 5 approximately here#

4   DISCUSSION

5　　　　Calculation of mean square error values between times series of observed larch bud moth densities at the forest compartment level and modelled larch bud moth densities at three different spatial grains revealed that, on average, a higher resolution model achieves a slightly greater accuracy in prediction. However, the improvement in accuracy is not significantly (α=0.05) better than that of the coarser resolution models (Figure 5).

10　　　　Results of linear regression reveal that the LBM-M9 model predicts spatial pattern at the 'site' spatial grain rather well (Table 2). However, low R^2 values and linear regression slopes close to zero at the forest compartment spatial grain (Table 3) suggest a poor relationship between the observed and the predicted values across space.

　　　　When we examine the time series produced by the model in comparison with the 15　observed densities we find that in general the LBM-M11 model over estimates densities at cycle troughs (particularly with respect to zero value observations) and otherwise under-estimates densities. This under-estimation is also revealed through examination of the regression equations (Table 3). These inaccuracies of the modelled densities also bias our correlation and regression analyses, making it unlikely that significant relationships could be 20　detected.

　　　　Calculating the coincidence between two maps of larval densities categorised into 4 categories showed that in any given year more than 50 % of the observed values were

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predicted to be in the correct category for the most commonly occurring category (Table 4). However, other categories were poorly predicted. This result suggests again that the LBM-M11 model does not predict observed spatial pattern well.

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However, the high spatial resolution model, LBM-M11, reproduced some spatial patterns that by eye can be seen to match some of the patterns observed from field data (Figures 3 and 4). Visual examination of maps of observed larval densities across the Upper Engadine valley (Figures 3a and 4a) and calculation of contagion indices reveals that larval densities are not heterogeneous across space. However, considerable clumping of values occurs (Table 5), and can be seen to correspond well to the extent of the 'sites' defined in

10   LBM-M9 (Figures 3a and 4a), particularly during peak years (Figure 4a). Then we find clumping of compartments with similar larval densities to match closely to the site definitions. While a uniform pattern of densities across sites or across the Upper Engadine valley as predicted by LBM-M8 is unrealistic and obviously not applicable for the purposes of determining spatial pattern, the pattern predicted by LBM-M9 fits the observed data well

15   (Table 2, Figures 3a and 4a).

As the local cyclic dynamics for each forest compartment depend on the mechanism driving the model, discrepancies between observed and modelled densities could be caused by an inappropriate choice of local dynamics model. In this study we used the food quality hypothesis model to describe local dynamics (Fischlin, 1982). Turchin et al. (2003) have

20   found that a food-quality hypothesis based model explains the observed larch bud moth cycles less well than a model based on the parasitoid hypothesis or a tri-trophic model combining interaction between the larch bud moth and both parasitoids and the host larch. While the food quality hypothesis fits our data well at the grain and extent of the Upper Engadine valley

treated as a single spatial unit (LBM-M8), this may be the case because an averaging out of the local heterogeneity improves the predictability of the patterns (Wiens, 1989).

The inability of the LBM-M11 model to predict spatial variability at forest compartment spatial grain also suggests that this migration model is not particularly suitable

5   at that resolution. A different migration model may be needed in order to predict spatial patterns given at that or similar spatial resolutions. In addition, it is also possible that larch bud moth populations should no longer be considered as distinct populations which consist of individuals with common properties, in contrast to other populations distinguished at that level. Instead the animals living within any given forest compartment may merely form an

10   arbitrarily designated group of individuals, which all share characteristics with the individuals from neighbouring groups, thus not forming a true population.

Visual analysis of the maps of observed larval densities (Figure 3 and 4) and the contagion indices (Table 5) show considerable clumping across several forest compartments, suggesting that in many cases larch bud moth populations should not be considered to be

15   separate from each other at the forest compartment level. Since forest compartments are not defined only by ecological criteria, let alone criteria that govern the population dynamics of larch bud moth, this result appears plausible.

The variance of any given variable changes in measurement scale. Moreover, the manner in which it changes will depend on whether the grain or extent is altered (Wiens,

20   1989). In estimating larch bud moth densities from tree based samples (Auer, 1969), the extent of the sample size is effectively reduced by averaging measurements per forest compartment as compared to a measurement for the entire Engadine valley. This effect actually causes a change in measurement extent. With fewer observations per sample extent, our values for each forest compartment have a higher probability of differing from the actual

density level than those averaged from observations over the entire Upper Engadine valley, increasing the uncertainty in our modelled results. In addition, the fewer observations per spatial extent also means greater likelihood of zero density values in low density years, although the larch bud moth is not always likely to actually be totally absent from any given

5   area. This makes it difficult to compare observations with modelled predictions.

Due to the relatively small numbers of trees sampled within each forest compartment sample, 95% confidence intervals around the mean observed larval density values are often larger than the difference between modelled and observed values. Some examples of 95% confidence intervals are given in Table 6. This suggests that in many cases modelled values

10   may not deviate as far from the actual values as our MSE results suggest, as the observation data is also uncertain due to very small sample sizes.

#Table 6 approximately here#

5   CONCLUSION

Our results show that while a higher resolution model of larch bud moth dynamics

15   across the Alpine Arc predict larch bud moth densities slightly but not significantly better than a coarse spatial resolution model, it is not capable of reproducing well a spatial pattern similar to that observed.

We find that the inaccuracies in the model predictions are likely due to joint effects of increased variance in the observed data, due to smaller sample sizes per extent, and the

20   inappropriateness of defining distinct larch bud moth populations and thus use of the spatial dynamics flight sub model at a higher resolution. These effects increase the uncertainty in the input data as well as the observational data.

21

In order to determine spatial patterns of larch bud moth, our results suggest that a coarser spatial grain such as that of the 'site' ($\sim$3.7km^2) appears to be optimum with minimum uncertainty given the available data and the characteristics of the modelled processes. Incorporating greater spatial detail into existing models did not produce spurious results or

5   unexplainable behaviour, but also did not enhance our ability to predict larch bud moth dynamics and introduced uncertainties.

Further comparisons using a similar method but incorporating a parasitoid hypothesis as the local dynamics sub-model and/or a different migration model would likely glean more insights into the causal mechanisms of larch bud moth dynamics and help distinguish the

10   parasitoid hypothesis and food quality hypothesis as appropriate candidates.

6   ACKNOWLEDGMENTS

7   TABLES

Table 1

Spatially explicit data required as input to model LBM-M9 and LBM-M11 with sources

Constant	Source (LBM-M9)	Source (LBM-M11)
Frequency of turbulence in site i	SMA, 1901-1990	SMA, 1901-1990
Frequency of still winds (0-0.5m/s) in site i	SMA, 1901-1990	NUATMOS
Frequency of calm winds (0.5-2.8m/s) in site i	SMA, 1901-1990	NUATMOS
Frequency of strong winds in site i	SMA, 1901-1990	NUATMOS
Frequency of calm winds in site i in direction j	SMA, 1901-1990	NUATMOS
Frequency of strong winds in site i in direction j	SMA, 1901-1990	NUATMOS
Area of neighbouring site n in direction j in sub-sector A resp. B	SMA, 1901-1990	n/a
Area of neighbouring site n in sector j	n/a	Calculated in GRASS
Air distance from site i to neighbouring site n in sub-direction A resp. B	SMA, 1901-1990	n/a
Air distance from site i to neighbouring site n in direction j	n/a	Calculated in GRASS

where: for LBM-M9 i = 1-20, n = 1 – 20, j = NE,E,SE,S,SW,W,NW, N

   for LBM-M11 i = 1-420, n = 1-420, j = as above

Table 2

Linear regression results between modelled (LBM-M9) and observed larval densities at the 'site' spatial grain across space for each year of a single cycle

Cycle year	Regression equation	R-squared
1	x = 0.17142 - 0.1157y	0.0082
2	x = -0.014 + 1.466y	0.6783
3	x = 0.03913 + 0.6953y	0.3147
4	x = 1.2795 + 0.4075y	0.3591
5	x = 42.7218 + 0.3204y	0.2
6	x = -22.464 + 1.523y	0.1479
7	x = 64.057 + 1.124y	0.63
8	x = 27.264 - 1.967y	0.06882
9	x = 3.2745 - 0.8120y	0.0428

where x is observed larval density, and y is modelled larval density. Year 1 is a trough year and years 5 and 6 peak years.

25

Table 3

Linear regression results between modelled (LBM-M11) and observed larval densities at the forest compartment spatial grain across space for each year of a single cycle

Cycle year	Regression equation	R-squared
1	x = 22.205 + 0.0316y	0.0006
2	x = 41.129 + 0.06428y	0.0009
3	x = 58.8813 - 0.1483y	0.0013
4	x = 50.458 - 0.0165y	0.0003
5	x = 99.157 - 1.027y	0.006
6	x = 55.267 - 0.063y	0.0034
7	x = 43.867 - 0.0091y	0.0043
8	x = 47.3624 - 0.591y	0.0001
9	x = 49.8715 - 0.4717y	0.0011

where x is observed larval density, and y is modelled larval density. Year 1 is a trough year and years 5 and 6 peak years.

Table 4

Coincidence between observed and modelled larval density maps over one cycle (1958-1967)

Larval density (/kg branches)	1958	1959	1960	1961	1962	1963	1964	1965	1966
0-1	87.8	25.51	0	NA	NA	NA	2.33	0	69.1
1-10	0	77.32	65.57	6.95	0	NA	79.08	57.76	0
10-100	NA	NA	0	61.88	25.89	32.81	32.12	NA	NA
> 100	NA	NA	NA	33.75	60.5	64.52	NA	NA	NA

Numbers denote the percentage of cells in the observed map that were correctly categorised by the model for each of 4 categories of larval density

Table 5

Contagion value for modelled (with LBM-M11) and observed maps of larval densities

for each year of an average cycle.

Year	Observed	Modelled
1	0.7966	0.7815
2	0.5126	0.5845
3	0.6184	0.6641
4	0.6166	0.4878
5	0.6047	0.6620
6	0.6054	0.6620
7	0.6123	0.5890
8	0.9430	0.6314
9	0.9632	0.4878

Larval densities were categorised as 0-1, 1-10, 10-100 and over 100 larvae per

kilogram of tree branches

Table 6

95% confidence intervals for observed mean larval densities per forest compartment

Compartment I.D.	Sample size	Year	Larval density (/kg tree branches)	95% confidence interval
167	2	1960	1.3542	±0.6125
292	2	1960	1.3334	±2.6133
342	13	1963	117.675	±43.857
132	2	1963	375.261	±257.036

8   FIGURE CAPTIONS

Figure 1: Location of the Upper Engadine Valley in Switzerland

Figure 2: Number of larch trees per forest compartment plotted against forested area

5   seperated into forest compartments on northern and southern exposed slopes.

Figure 3a: Observed larval densities (larvae/kilogram tree branches, retrieved from LBM database: A. Fischlin in prep.) per forest compartment 1960 (trough year of the larch bud moth cycle). The darker the colour, the greater the larval density. Lines indicate 'site' borders.

10   Figure 3b: Simulated larval densities (larvae/kilogram tree branches, retrieved from LBM database: A. Fischlin in prep.) per forest compartment 1960 (trough year of the larch bud moth cycle). Simulated with model LBM-M11. The darker the colour, the greater the density. Lines indicate 'site' borders.
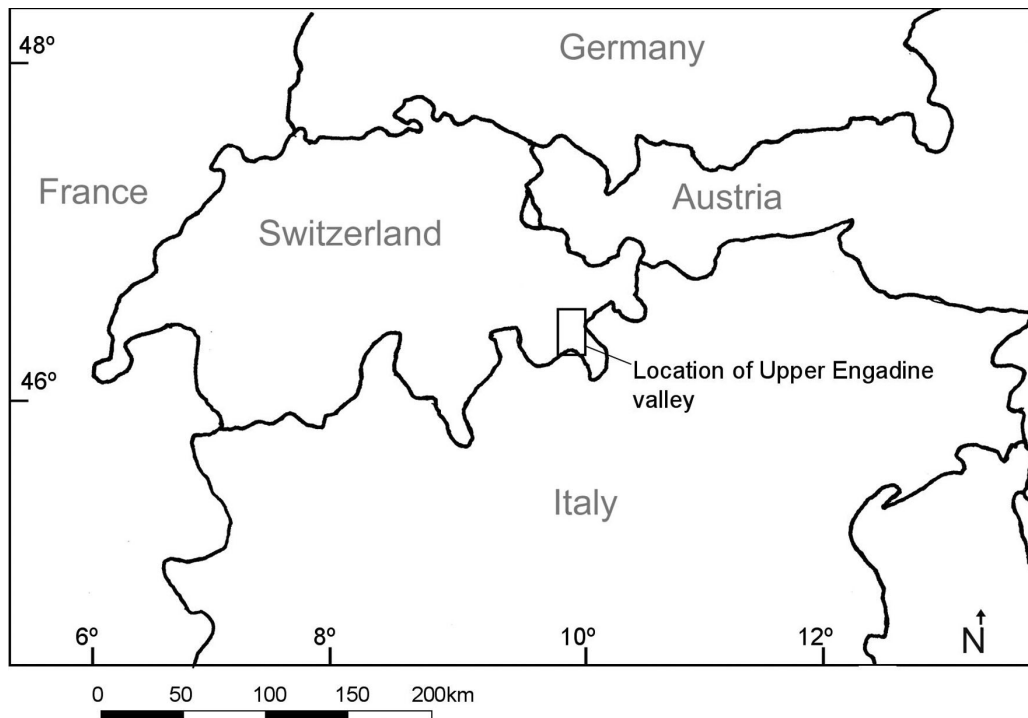
Figure 4a: Observed larval densities (larvae/kilogram tree branches, retrieved from LBM

15   database: A. Fischlin in prep.) per forest compartment 1963 (peak year of the larch bud moth cycle). The darker the colour, the greater the larval density. Lines indicate 'site' borders.

Figure 4b: Simulated larval densities (larvae/kilogram tree branches, retrieved from LBM database: A. Fischlin in prep.) per forest compartment 1963 (peak year of the larch bud

20   moth cycle). Simulated with model LBM-M11. The darker the colour, the greater the density. Lines indicate 'site' borders.

Figure 5: Boxplot of mean square errors for comparisons between log-transformed time

series of observed larval densities per forest compartment (larvae/kilogram tree branches,

retrieved from LBM database: A. Fischlin in prep.) and log-transformed time series of

larval densities simulated by a: LBM-M8 model at the entire valley spatial grain, b:

5   LBM-M9 model at the 'site' spatial grain, c: LBM-M11 model at a steady state with

respect to spatial variance and d: LBM-M11 model with uniform calm wind conditions

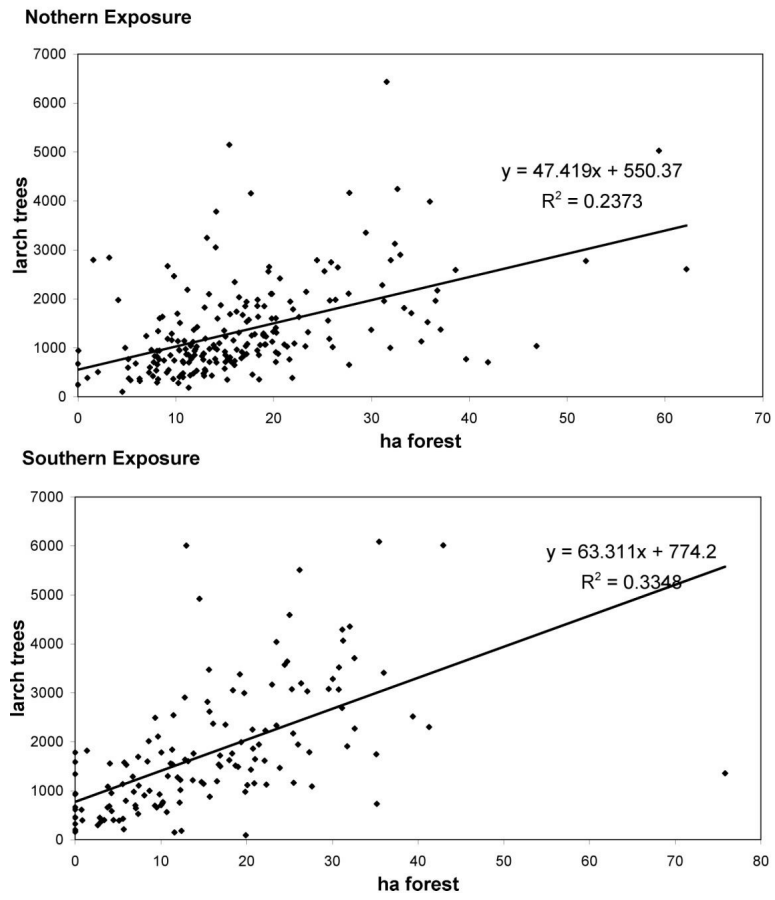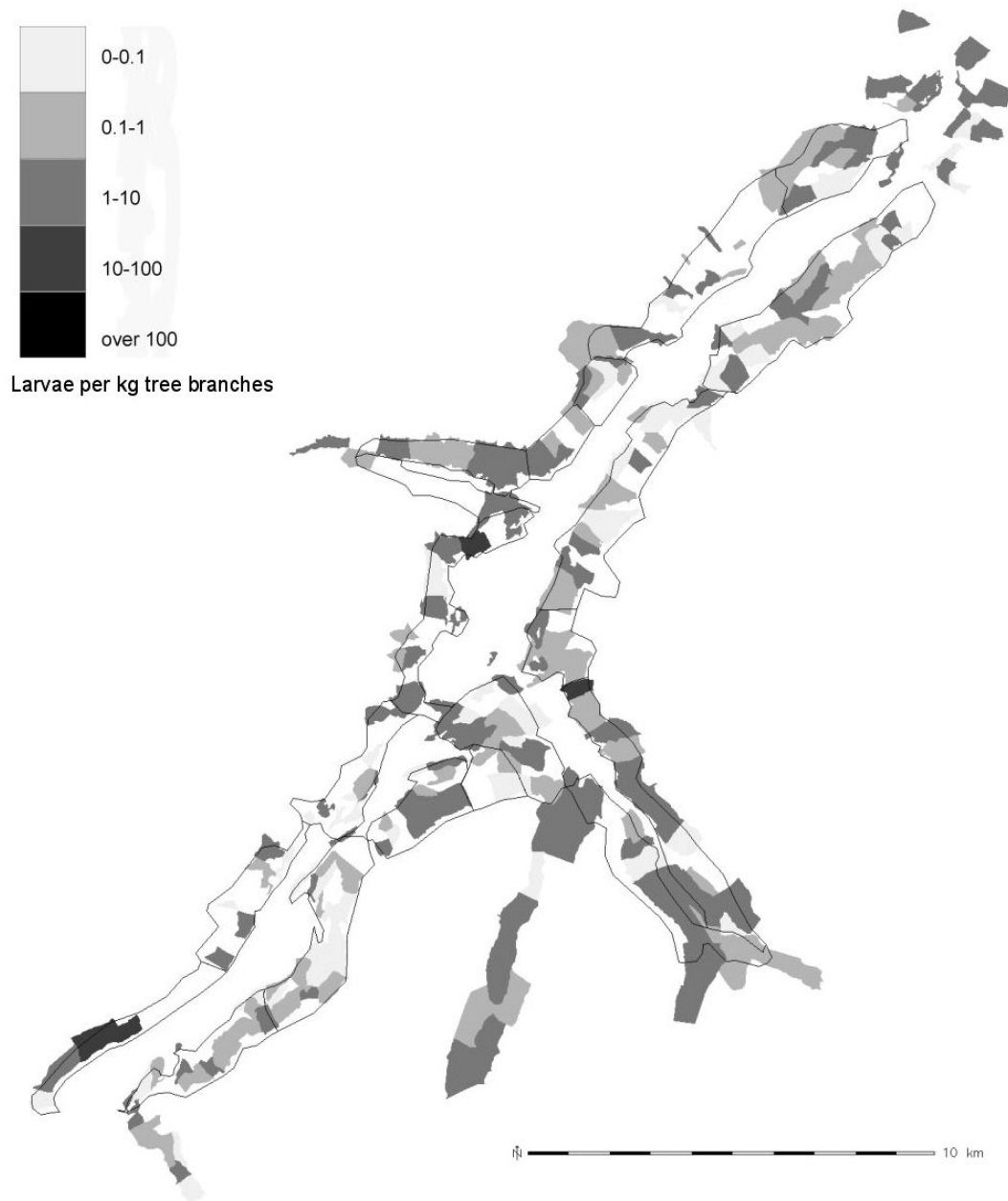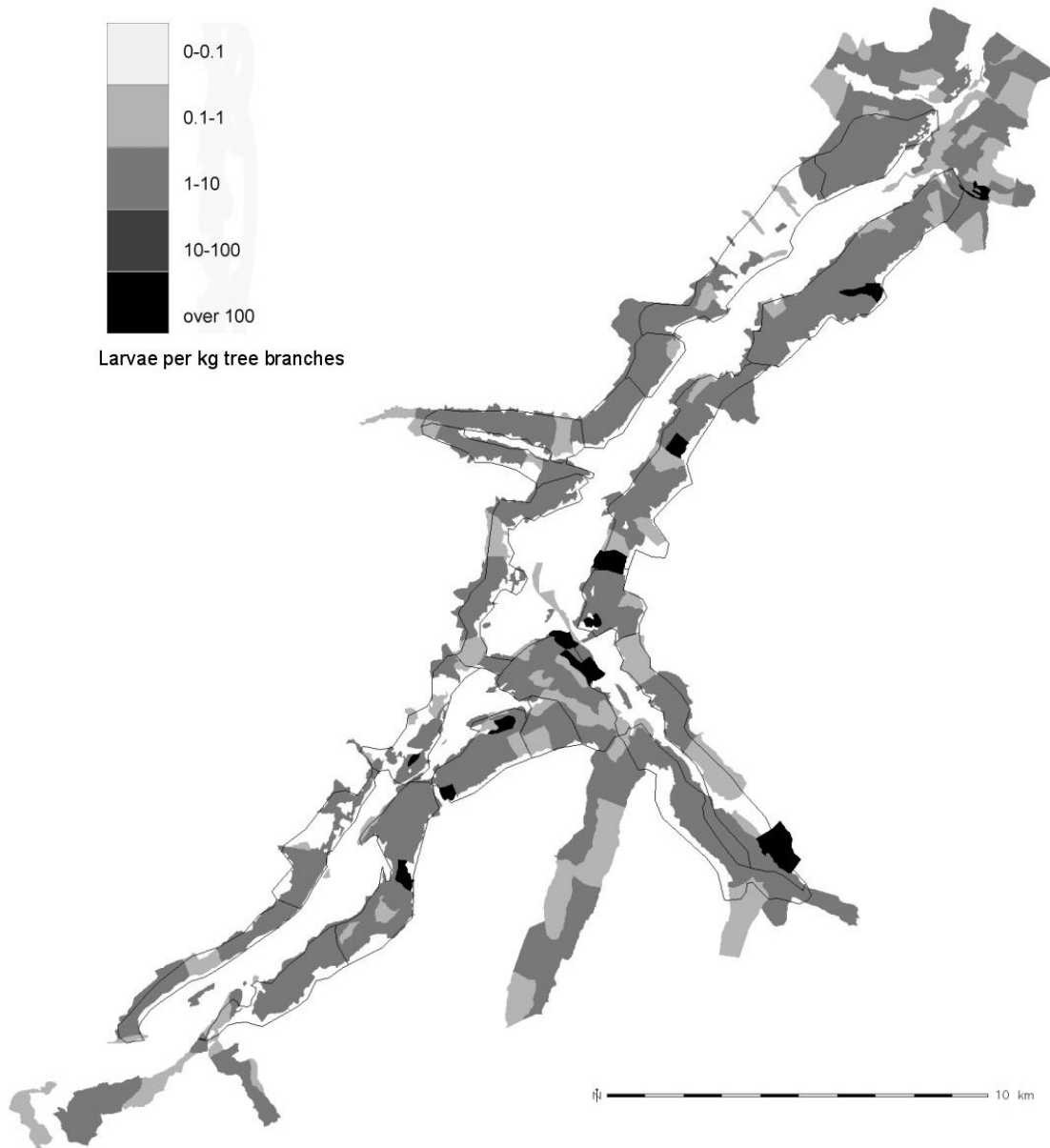(flight occurring randomly, i.e. any wind effects ignored).

9   FIGURES

Figure 1

Location of Upper Engadine valley

5

Figure 2

Nothern Exposure

$y = 47.419x + 550.37$
$R^2 = 0.2373$

Southern Exposure

$y = 63.311x + 774.2$
$R^2 = 0.3348$

Figure 3a

0-0.1

0.1-1

1-10

10-100

over 100

Larvae per kg tree branches

10 km

Figure 3b

0-0.1

0.1-1

1-10

10-100

over 100

Larvae per kg tree branches

10 km

Figure 4a

0-0.1
0.1-1
1-10
10-100
over 100

Larvae per kg tree branches

Figure 4b

Larvae per kg tree branches

Legend:
- 0-0.1
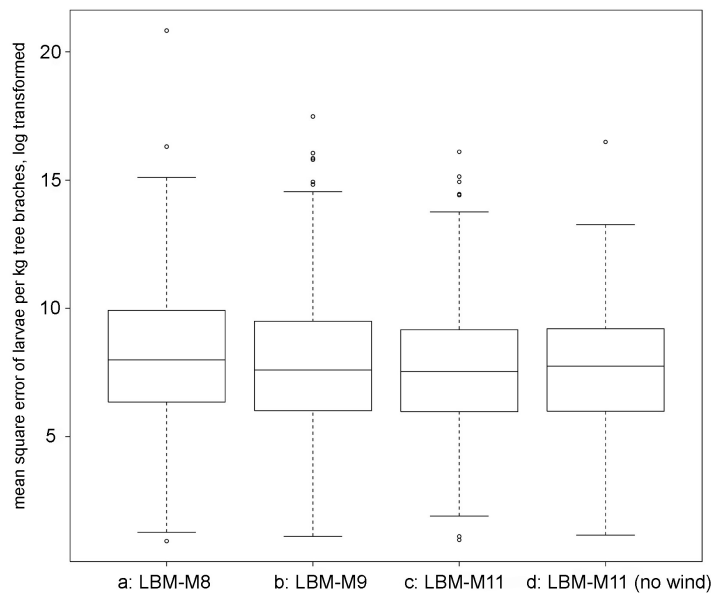- 0.1-1
- 1-10
- 10-100
- over 100

10 km
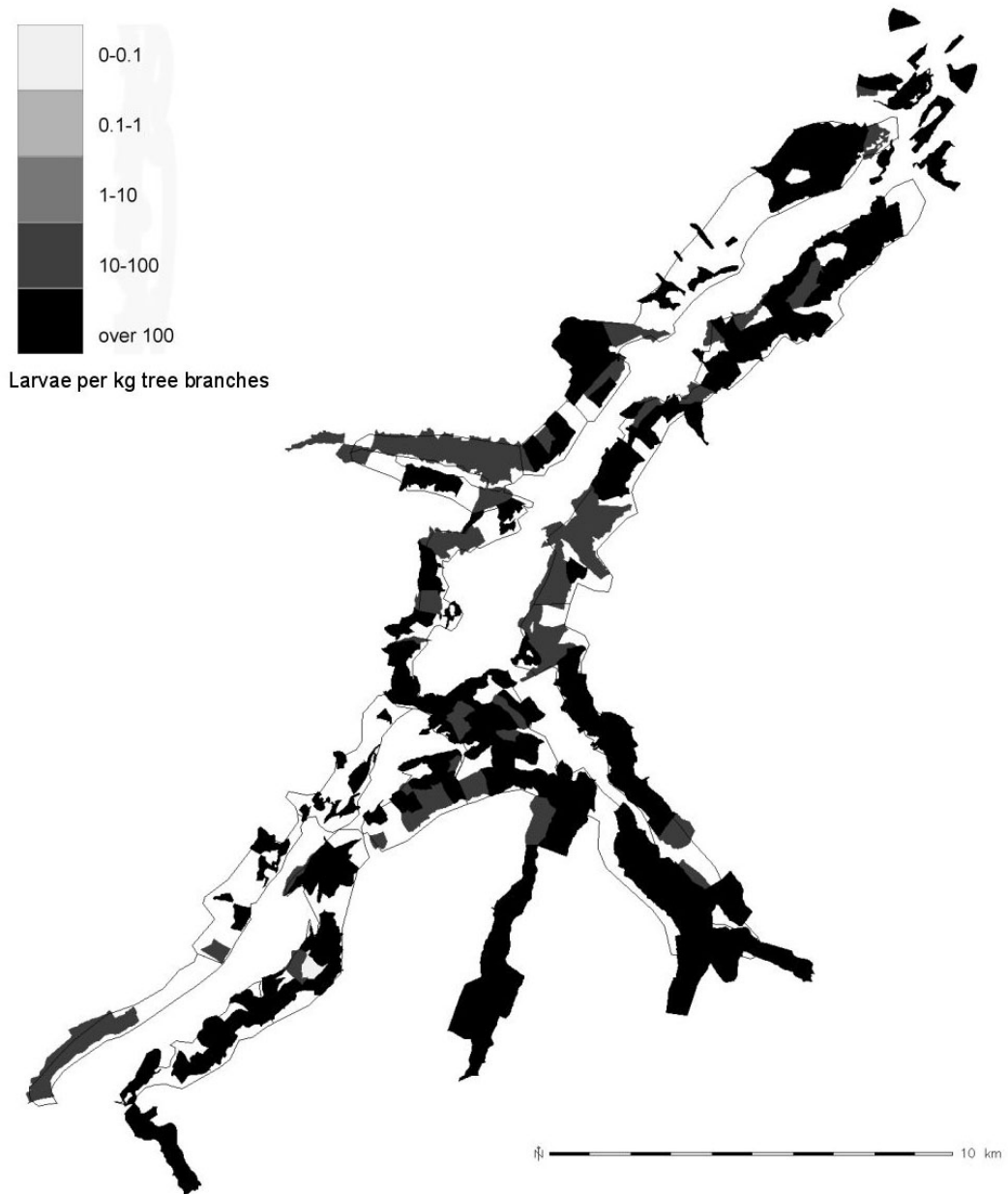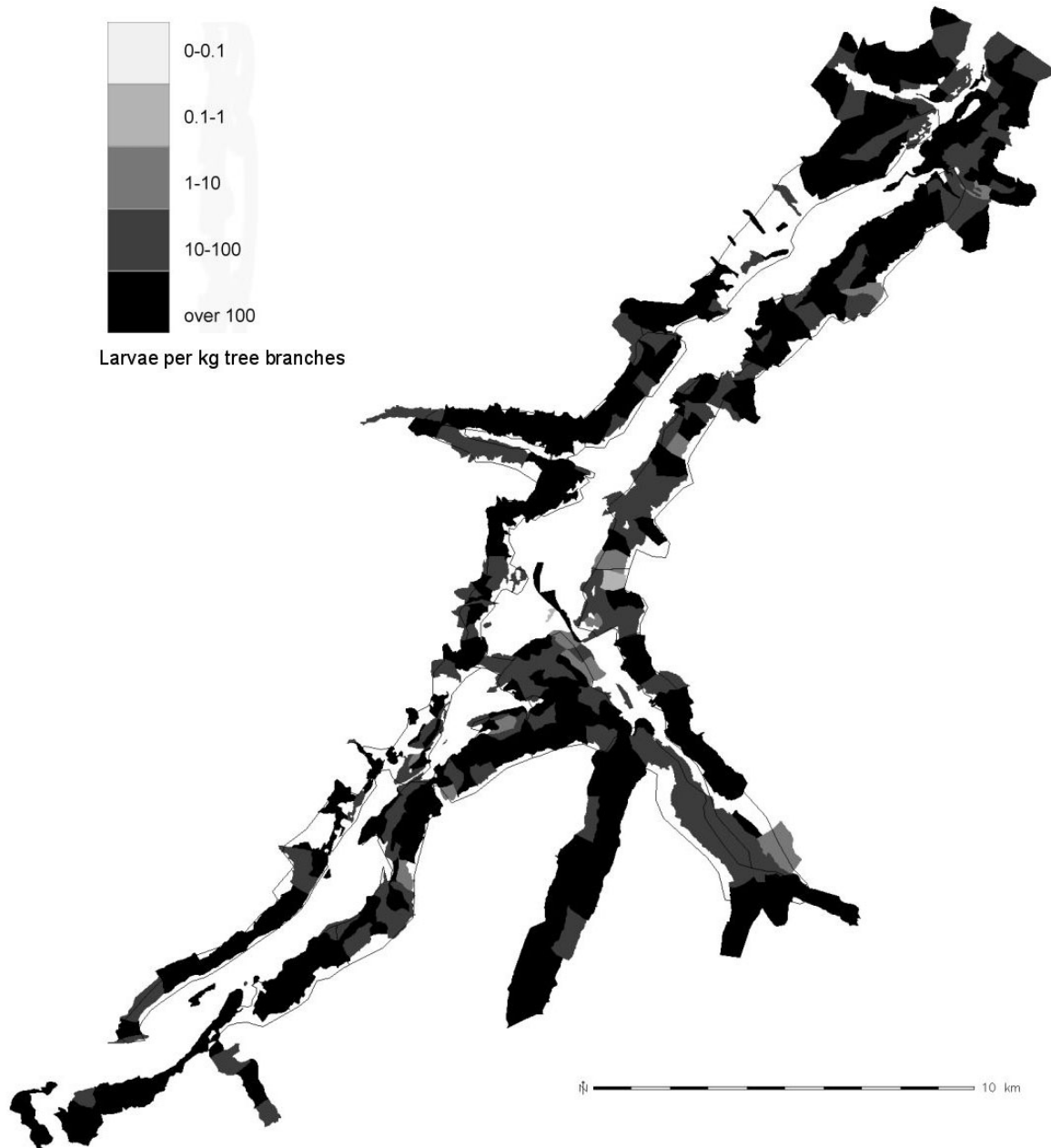
Figure 5

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