The Influence of Orography on Larch Bud Moth Migration at the Valley Scale

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Abstract

Spatio-temporal patterns of insect population densities, for instance, spatial synchrony in population cycles, have been observed at different scales for several species and appear to be related to distinct phenomena of spatial and/or biological nature. In this study we investigated the hypothesis that migration processes determine the observable spatio-temporal synchrony in population dynamics of larch bud moth at the valley scale. We explored the effect of orography at a finer resolution on modelled potential dispersal ranges of larch bud moth by incorporating a high resolution GIS based migration model with a coarse resolution population dynamics simulation model. Modelled migration paths were affected considerably by inclusion of orography compared to predecessor models that ignored orographical effects. Our results demonstrate that geographical features such as orography are of importance for determining larch bud moth migration paths and resultant spatio-temporal population dynamics.

KEYWORDS: larch bud moth, migration, modelling, GIS, spatial dynamics, synchrony

1 INTRODUCTION

The larch bud moth, *Zeiraphera diniana* GN. (*Lep., Tortricidae*), is a univoltine, conspicuous forest defoliator exhibiting cyclic population dynamics across the entire Alpine Arc with population peaks every 8-10 years (Auer 1969, Auer 1977, Baltensweiler, et al. 1988, Baltensweiler, et al. 1999, Fischlin 1982). During peaks of population cycles, crowding causes larvae to interrupt each other's feeding, which usually leads to partially eaten needles drying out and resulting in highly visible, large scale defoliation (Baltensweiler, et al. 1988).

Spatio-temporal dynamics of larch bud moth appear to change with scale of observation (spatial extent and resolution). Some studies have noted the synchrony of population cycles within valleys – in particular the Upper Engadine valley (Fischlin 1982, Fischlin 1983), or travelling waves of larch bud moth across the Alpine Arc (Bjornstad, et al. 2002).

Spatial synchrony occurs when populations in spatially separate locations fluctuate in a similar manner (Liebhold, et al. 2000). Spatial synchrony is considered to be a result of either dispersal or spatial correlation in the environment (the Moran effect) – such as synchrony in weather patterns (Kendall, et al. 2000, Liebhold, et al. 2000). With a few exceptions (e.g. Clark 1979, Fischlin 1983) spatial synchrony has only come to be quantified in recent years, and identification of processes causing such synchrony is considered to be a great challenge to population ecologists (Liebhold, et al. 2000).

Fischlin (1983) has found that dispersal may well explain the synchronised cycles of larch bud moth among Alpine valleys. Recent research into synchrony further suggests that dispersal or regional environmental correlation could result in patterns of synchrony as has been observed for larch bud moth (Hudson, et al. 1999, Kendall, et al. 2000, Liebhold, et al.

2000). Peltonen et al. (2002) have shown that dispersal may well be a causal mechanism of synchrony at local scales for several species, including larch bud moth.

If dispersal is a driver for synchrony among population cycles, the physical distance between sub-populations and migration ability of the species is of importance (Peltonen, et al. 2002). The further apart the sub populations relative to the typical migration distance, the less likely that dispersal can cause synchrony. Therefore, knowledge of how far a species can migrate in given conditions is vital to understanding whether dispersal can be a driver for population synchrony.

While we know a great deal about migration behaviour of larch bud moth (Baltensweiler, et al. 1999, Vaclena 1977, Vaclena, et al. 1978) and can successfully model that behaviour at coarse spatial scales (Fischlin 1982, Fischlin in prep.), we know little about how larch bud moth migration is affected by landscape features at fine spatial resolution. Moreover, constructing population models at a high spatial resolution is challenging, since it requires site-specific values for a large number of model parameters.

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 (Bjornstad, et al. 2002, Fischlin 1982, Fischlin 1983, Johnson, et al. 2004, Turchin, et al. 2003). While the focus of many existing larch bud moth models is on fluctuations over time (Auer 1971, Fischlin 1982, Fischlin, et al. 1979, Kälin, et al. 1954, Turchin, et al. 2003, Van den Bos, et al. 1976), some models incorporate spatially varying properties such as wind conditions, distances between sub-populations, habitat connectivity and forested area in order to examine spatio-temporal dynamics (Bjornstad, et al. 2002, Fischlin 1982, Johnson, et al. 2004). However, such models have only been able to take advantage of spatial data at a very coarse spatial resolution or subjective categorical defoliation data (Bjornstad, et al. 2002, Johnson, et al. 2004), and often assume that spatial data is constant over time (e.g. Fischlin 1982).

This research is based on Fischlin's (1982) spatially explicit model of migration throughout the Upper Engadine valley. This model is derived from species specific characteristics and thus lends itself well to consideration of spatial features such as orography at a high resolution. The model was initially formulated with a coarse spatial resolution of input data. Using this model, a GIS based larch bud moth migration model was developed at a higher spatial resolution. The research aims to determine how an increase in spatial granularity would influence the migration patterns of the larch bud moth within the Upper Engadine valley and whether features of the landscape are important in determining migration paths. We show that migration is likely a relevant driver of synchrony and that incorporation of topographical features at an increased spatial granularity in the migration model influences synchrony within the same spatial extent.

2 MATERIAL AND METHODS

2.1 Study Area and Data

The Upper Engadine valley is a sub alpine valley located in the Swiss part of the European Alps (Figure 1) forested with mixed larch (*Larix decidua* MILLER) - Swiss stone pine (*Pinus cembra* L.) forests. During development of a migration model for larch bud moth within the Upper Engadine, the valley was divided into 20 areas known as 'sites', which are considered homogeneous with respect to ecological and orographical characteristics such as aspect and altitude (Figure 1 Fischlin 1982).

From 1949-1979 detailed larval population surveys including recording of parasitism, tree species composition and other area specific data were conducted (e.g. Auer 1975) and have since been stored in a database. Larval densities, climate and other site-specific data for each of the 20 sites have been made available for 1949-1979 by going back to the original raw data with careful re-analysis techniques and using ecological dividing criteria (Fischlin 1982).

Elevation information covering the area of the Upper Engadine valley was taken from a Digital Elevation Model (DEM) with a spatial resolution of 50 m (DHM50 ©, Tydac AG). Slope and aspect information was then derived from this DEM using standard GIS techniques within the GRASS software environment.

2.2 LBM-M8 and LBM-M9 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 (LBM-M8 see also Fischlin, et al. 1979). The model considers the relationship between the larch bud moth and its host, the larch. Grazing by the larch bud moth causes an increase in raw fibre content of the larch needles, which has negative implications for larch bud moth fecundity and thus causes a decrease in the larch bud moth population. The model deals with local dynamics only, and treats an entire area such as a valley as a homogeneous area with no spatial structure (Fischlin, et al. 1979). The local dynamics model is a deterministic mathematical model, i.e. a second order, discrete time system of coupled, non-linear equations. The two state variables represent first the food quality, using the raw fibre content per needle fresh weight as an indicator, and second the population density given as the number of larch bud moth eggs per study area.

A spatially explicit Upper Engadine valley model also developed by Fischlin (1982), known as LBM-M9, incorporates the local dynamics model (as in LBM-M8) as a sub model and couples it with another sub-model for migration between the 20 sites within the Upper Engadine valley. The migration part of this model is also a deterministic mathematical model, and the behaviour of all female moths within a site is defined by a recursive formula relative to specific site conditions as determined by wind statistics and other site specific characteristics such as defoliation, forested area, or number of larch trees (Baltensweiler, et al. 1979, Fischlin 1982, Fischlin in prep.). State variables are the number of flying females and the distance flown. Oviposition takes place as sites are visited. By the end of the flight season accumulated egg masses determine site-specific population sizes of the next generation (Baltensweiler, et al. 1979, Fischlin 1982).

Immigration and emigration determine the numbers of larvae in a given area, while wind speed and direction determine where and how far moths migrate. The spatial arrangement and distances between areas of forest (nearest neighbour) determine to which areas larch bud moth migrate. Once at a site, moths are assumed to continue dispersal from the centre of gravity (determined in planar projection) of the current site (Fischlin 1982).

Wind speed and direction for each site was derived from evening measurements taken at weather stations run by the Swiss Federal Office of Meteorology and Climatology between July and September (Bantle 1989). There are three wind speed categories: still (<0.5m/s), gentle (0.5-2.8m/s) and strong (>2.8m/s) in each of 8 compass directions. The wind parameters for LBM-M9 are then defined as a proportion of the total wind behaviour for each wind speed category as an average over time, and are considered constant over time (see also Baltensweiler, et al. 1979, Fischlin 1982).

Fischlin (1982) derived categories of larch bud moth flight behaviour: upwind flyers for moths that fly against gentle down slope winds (see above), calm flyers that fly in still wind conditions, downwind flyers that fly with strong winds. The proportion of moths in each behaviour category is equal to the average proportion of wind speeds in the corresponding wind speed category, see Table 1. Based on these data the LBM-M9 model calculates maximum flight distances from each 'site' in each of 16 compass directions for each type of moth flight behaviour.

LBM-M9 models migration based on average wind conditions at the centre of a site and does not take into account any topographical features nor any within site variations, such as within site varying wind conditions.

In this study we also used a variant of the LBM-M9 model, where migration was suppressed by forcing all females from a site to oviposit all eggs within their home site (LBM-M9a).

2.3 LBM-GIS

In this study we consider the influence of orography on larch bud moth flight and enhance the model LBM-M9 by developing a simplified migration model within the GRASS open source GIS environment (Neteler, et al. 2002) and designate the new model 'LBM-GIS'. It simulates larch bud moth dispersal from individual sites with assumptions derived from Fischlin's LBM-M9 (1982) according to the rules described below.

The mountainous topography of the Upper Engadine valley gives rise to a diurnal wind system, where cold air drains down slope during the evening and night, and during the day warm air flows upslope (Baltensweiler, et al. 1999, Fischlin 1982, Urfer-Henneberger 1964). Upwind flyers fly against this down slope air drainage (in response to pheromones from the larch) and thus we can assume that upwind flyers fly uphill, or across flat areas but not downhill (we define here 'flat' areas as those with slopes between 0° and 5°). Downwind flyers fly with strong winds down slope and thus we can assume that downwind flyers fly downhill, or across flat areas (defined in the same way as above) but not uphill. These assumptions allow us to determine some simple rules for the influence of orography on larch bud moth flight.

We assume that as calm flyers fly randomly in any still wind conditions they are not affected greatly by orography. The behaviour of downwind and upwind flyers allows for easy construction of a simple model describing the influence of landscape features. The LBM-M9 model simulates downwind flyers as migrating short distances only (0-5km), whereas upwind flyers fly distances up to 30km in response to pheromones. Thus the influence of an increase in spatial granularity is likely to be greater in the case of upwind flyers.

Possible flight direction is determined by average wind conditions measured in each site and maximum flight distance from each site for each year is simulated with the LBM-M9 model, dependant on the wind conditions. Starting from the centre of gravity of a site, the migration distances and directions given by LBM-M9 are applied to calculate a maximum migration area in LBM-GIS from the centre of each site.

Taking into consideration the behaviour of upwind and downwind flyers as described above, simple rules are used to calculate a possible migration area from the centre of each site in the direction(s) given by the LBM-M9 model.

LBM-GIS states that moths are able to fly in the 22.5° sector of their favoured direction (defined by average wind direction) to a maximum distance calculated by LBM-M9 from the centre of each site. Upwind flyers are able to traverse areas with a positive slope and flat areas, and downwind flyers were able to traverse areas with a negative slope and flat areas.

Positive and negative slopes were determined dependant on aspect and the flight direction of larch bud moth. For example, for moths flying north, positive slopes are those with southern exposure and negative those with northern exposure (Figure 2).

Raster (or grid) layers of slope were constructed for each of the 16 flight directions and combined with raster layers of the maximum distance sector for each direction to determine possible flight areas for both upwind and downwind flyers.

Maximum flight distance changes little from year to year, since it is dependant mostly on average wind conditions, which are assumed to remain constant over time. LBM-M9 gives two different sets of maximum flight distances due to increased flight occurring during population peak years, when high defoliation makes sites less attractive and causes more moths to emigrate in search of more attractive habitat. The first set of maximum distances are for the 1st- 4th and 7th-9th years of a cycle and the second set for the 5th and 6th years of a cycle. Therefore only two sets of maximum distance raster layers were constructed.

The raster layers showing possible flight areas allowed us to determine to which sites moths migrated from each site. The numbers of migrating females in each direction was calculated with LBM-M9. We assumed that each target site could be reached with equal probability, thus the numbers of moth migrating to a site was calculated as the total number of moths flying in the given direction divided by the total number of possible target sites. We then added and subtracted emigrating and immigrating moths from each site to gain new population density values following dispersal as modelled by LBM-GIS.

2.4 Comparison of Results

In order to compare the outputs of LBM-GIS and LBM-M9 we calculated mean square errors of log transformed times series for each site between observed and modelled larval densities.

We also compared observed densities with densities modelled with no dispersal process occurring (LBM-M9a). To determine how the models prediction ability changed with spatial location we calculated correlation coefficients for time series of each site separately. To compare the ability of the models to predict spatial patterns between the sites we calculated mean square errors between observed and modelled data at each site for each year of a single cycle (1949-1958).

To determine if modelling migration at a higher resolution gives us more insight into the behaviour of the larch bud moth in the Upper Engadine valley on average, we calculated the correlation coefficient between the modelled and observed values averaged over the entire valley and compared it to correlation coefficients between the observations and averaged LBM-M9 values and the results of LBM-M8, which simulates average values for the entire valley.

2.5 Sensitivity analysis

The sensitivity of the model to slope was tested by running the model with flat areas defined with cut-off at 1° and 15° instead of 5°. In addition, we tested the sensitivity of size of the flight sector by allowing moths to fly within a 45° sector of their favoured wind direction (LBM-GIS-45 in comparison to the 22.5° sector, and decreasing the sector size to 15° (LBM-GIS-15).

3 RESULTS

Mean square error values for comparisons between observed and modelled time series of larval densities for the models LBM-GIS, LBM-M9 and LBM-M9a (no migration) are shown in Figure 3. There is no significant difference between the mean square error values although the larval densities simulated for the model with no migration (LBM-M9a) are lowest.

Figure 4 shows a box plot of mean square error values between observed and modelled larval densities across space. Here we again observe no significant differences between the three models. However, for this comparison the model LBM-GIS produces the slightly lowest mean square error values suggesting this model might be best in reproducing the spatial pattern of larch bud moth across the Upper Engadine valley.

Correlation coefficients between time series of observed and modelled time series for each site are displayed in Table 2. Correlation is significant at the α=0.05 level in all cases. The model results with highest correlation to observed data vary depending on site, however, on average the results of LBM-GIS are best correlated with observed values.

The correlation analysis between modelled times series averaged over the entire Upper Engadine valley and the average observed values showed an increased correlation with incorporation of orography in the LBM-GIS model. The correlation coefficients were 0.843 for LBM-M8, 0.861 for LBM-M9 and 0.925 for LBM-GIS.

The LBM-GIS model was not sensitive to slope. Running the model with flat slope cut-off at 15° did not increase potential migration areas and thus did not change the number of sites that could be reached by migrating moths. To demonstrate this point, simulated potential migration areas for site 19 are shown as an example in Figure 5, where Figure 5a shows the potential migration area with flat area cut-off at 5° and Figure 5b for flat slope cut-off at 15°. There is no visible difference in the sites that can be reached. With flat area cut-off at 1° some migration was prevented, however only in very few cases and of small numbers of moths so as to cause no meaningful difference in results.

Enlarging the potential flight sector from 22.5° to 45° did not influence the ability of the LBM-GIS to predict observed densities overall (Figure 6) but did slightly decrease its ability to produce the observed spatial patterns as can be seen in the box plot of mean square errors for observed values compared to modelled values at each site across each year of a cycle (Figure 7). In addition, correlation coefficients between modelled and observed series were lower for the model with a larger potential flight sector (Table 3). A decrease in flight sector to 15°, restricted migration significantly giving results that were the same as, or very close to, the simulation results without migration (LBM-M9a).

4 DISCUSSION

Landscape features such as slope and altitude influenced simulated migration behaviour of upwind and downwind flyers, however the impact on resultant larval densities was not significant. Using LBM-GIS we were able to determine potential migration paths through the Upper Engadine valley at a high (50m) spatial resolution and consider the effect of orography on migration, which was not possible within the model LBM-M9 alone. Thus we could overcome at least partially the present limitations of the model resolving space coarsely, and were able to investigate the influence of topography on migration patterns of larch bud moth at a much higher spatial resolution than previously possible.

We learned from this study, simulating flight distances at a high spatial resolution within a GIS, how movement through the Upper Engadine valley is in some cases restricted. These constraints resulted from explicitly considering landscape features (i.e. topographical elements) at a higher spatial resolution, which prevented some migration from some sites in some directions that would have occurred if the model were used at a coarser spatial resolution. However, in other cases the finer spatial resolution of LBM-GIS enabled new migration paths. It allowed for more flexible movement of larch bud moth through the landscape where moths flying in a given direction from a given site could now deposit eggs in several sites that were otherwise not visited by moths in the coarser resolution model variant (LBM-M9). Since these effects may offset each other, on average, considering the influence of topographical features at a higher resolution on migration did not greatly impact the ability of the model to predict actual larch bud moth densities, either across space nor time (Figures 3 and 4).

However, some improvement in prediction of spatial and temporal patterns could be observed. In particular, correlation between modelled and observed time series was higher with the higher resolution migration model for many sites and also higher on average (Table 2 and 3).

Sites for which the LBM-GIS migration model was not able to better predict the observed patterns of larch bud moth densities are located at the ends of the Upper Engadine valley: sites 8-12 at the north-eastern end and sites 1 and 20 at the south-western end (Figure 1). These sites would be more affected by immigration into the valley from outside the valley (sites 1 and 20 due to the predominant westerly winds entering the Upper Engadine valley via the Malojapass and travelling along the valley (Baltensweiler, et al. 1999)) and emigration out of the valley (sites 8-12).

The LBM-GIS model does not take migration into and out of the valley into account, instead treating it as a closed system. However, this kind of migration is likely to be important in the Upper Engadine valley larch bud moth system, especially considering that local wind conditions within the Upper Engadine valley and the geographic location of these particular sites does not allow for much migration into and out of these areas. This observation also corroborates the hypothesis that aspects of orography are important in determining larch bud moth migration and associated population dynamics.

It has been qualitatively observed that populations of larch bud moth in areas on the right, northern-exposed sites of the Upper Engadine valley can experience a lag in density behind populations on the south-east exposed site (Baltensweiler, et al. 1999). On the south-eastern side of the Upper Engadine valley (sites 1 to 4, 6 to 10), forests are pure larch whereas on the northern exposed side (sites 11 to 13, 16 to 20) forest coverage contains a large fraction (often > 50%) of Swiss stone pine. However, from current understanding of the ecology of larch bud moth, it is not plausible why these differences in species composition should cause the described lags. In a related study, cross-spectral analysis of larval census data (Price, et al. in press) revealed a trailing phase lag in population densities between 2 and 4 months for sites 15, 16, 17 and 19 when compared to most other sites, whereas other northern exposed sites did not show such a lag. The time series of observed larval densities from these sites were better correlated with the LBM-GIS and LBM-M9a model than with the LBM-M9 simulating migration only at a coarse spatial resolution. This suggests that topographical features restricting migration may cause the phase lags observed in population cycles at these sites.

Comparison of the average observation values with the average modelled values over the entire valley showed that including the effect of orography on modelled migration as done in LBM-GIS allows us to improve our ability to predict the temporal patterns of larch bud moth as observed at a relatively coarse spatial resolution of the valley (resolution of 20 sites, cf. Fischlin 1982). Moreover it increased our understanding of the spatial temporal dynamics within the valley.

The results of this study have general implications for modelling dispersal as a driver of spatial synchrony in populations at large scales. As orography at higher spatial resolution was shown to influence migration patterns, it is likely also to influence the synchrony of sub populations at large distances from each other inasmuch as it is caused by migration.

Our results suggest that a consideration of orography and topographical features at fine spatial resolution are important for migration patterns and resultant larch bud moth dynamics also at coarse spatial scales. In addition, the effects we found due to a change in spatial resolution and the inclusion of topographic features, provides further evidence for the basic hypothesis that migration is causing the observed synchrony within the Upper Engadine valley (e.g. Baltensweiler, et al. 1979, Baltensweiler, et al. 1999, Fischlin 1982) and lags in synchrony for certain sites (Price, et al. in press).

5 CONCLUSIONS AND OUTLOOK

The results show how an increase in spatial resolution impacted the behaviour of a set of dynamic larch bud moth models. Indeed, actual dispersal may be more sensitive to orography and topography than has been assumed previously. The ability to predict mean larval densities for large areas such as an entire valley did not improve through inclusion of topographical features at a finer spatial resolution. In fact this ability decreased, but not significantly. However, the ability to predict within valley spatio-temporal patterns was increased through inclusion of topographical features at a finer spatial resolution. This is in particular true with respect to observed lags in densities for some sites in the Upper Engadine valley.

This suggests that geographical features, in particular those related to orography, at a fine scale are important for larch bud moth migration. Our results are consistent with the basic hypothesis that migration is an important driver of spatio-temporal patterns in the Upper Engadine valley, but in no way conclusive as the Moran effect was not investigated here. Yet, to distinguish between the two synchronizing mechanisms, explicit inclusion of migration at a fine spatial resolution may be relevant generally and in the case of the larch bud moth.

We can conclude that a fully integrative temporal-spatial modelling at a high spatial resolution will help to gain important new insights into the population dynamics of a key species such as larch bud moth. Only tighter coupling of temporal and spatial modelling, will enable further investigation of the implications of changes in spatial resolution for migration appropriately. This study demonstrated the sensitivity of dispersal to the degree in which additional landscape characteristics are incorporated. In the past, modelling efforts simulating larch bud moth dynamics, such as that with which LBM-M9 was developed (Fischlin 1982), were hampered by lack of availability of highly resolved spatio-temporal data. Linking temporally explicit simulation models to a GIS, reveals many new insights into the population dynamics of highly vagile species such as larch bud moth, particularly with respect to the influence of orography on dispersal.

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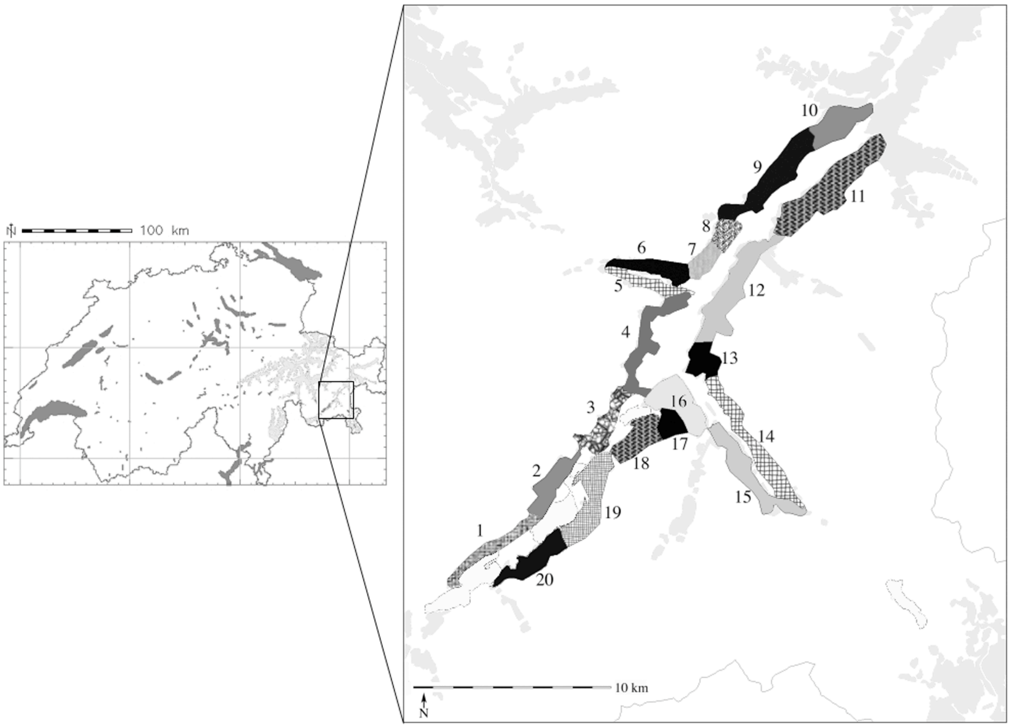
8 FIGURES

Figure 1



B.Price, ETH Zurich

Figure 2

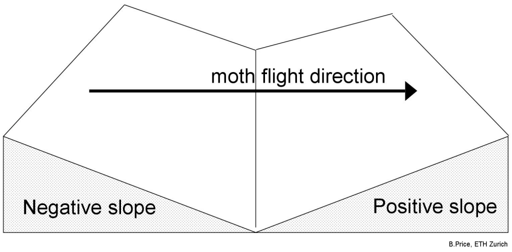

moth flight direction
Negative slope
Positive slope
B.Price, ETH Zurich

Figure 3

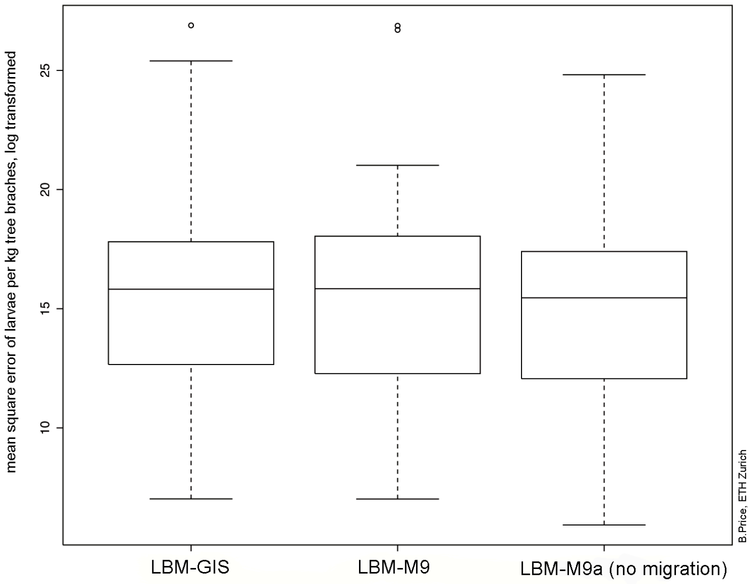

mean square error of larvae per kg tree braches, log transformed
10
15
20
25
LBM-GIS
LBM-M9
LBM-M9a (no migration)
B.Price, ETH Zurich

Figure 4

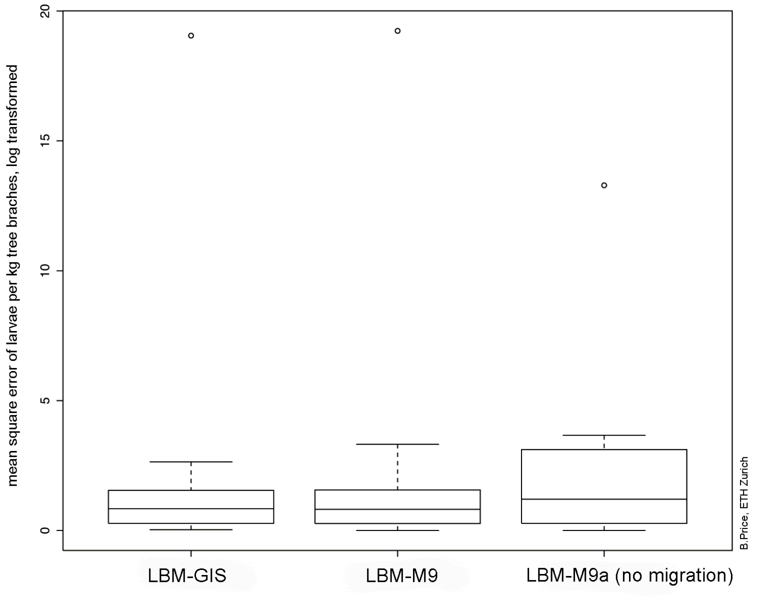

mean square error of larvae per kg tree braches, log transformed
0
5
10
15
20
LBM-GIS
LBM-M9
LBM-M9a (no migration)
B.Price, ETH Zurich

Figure 5

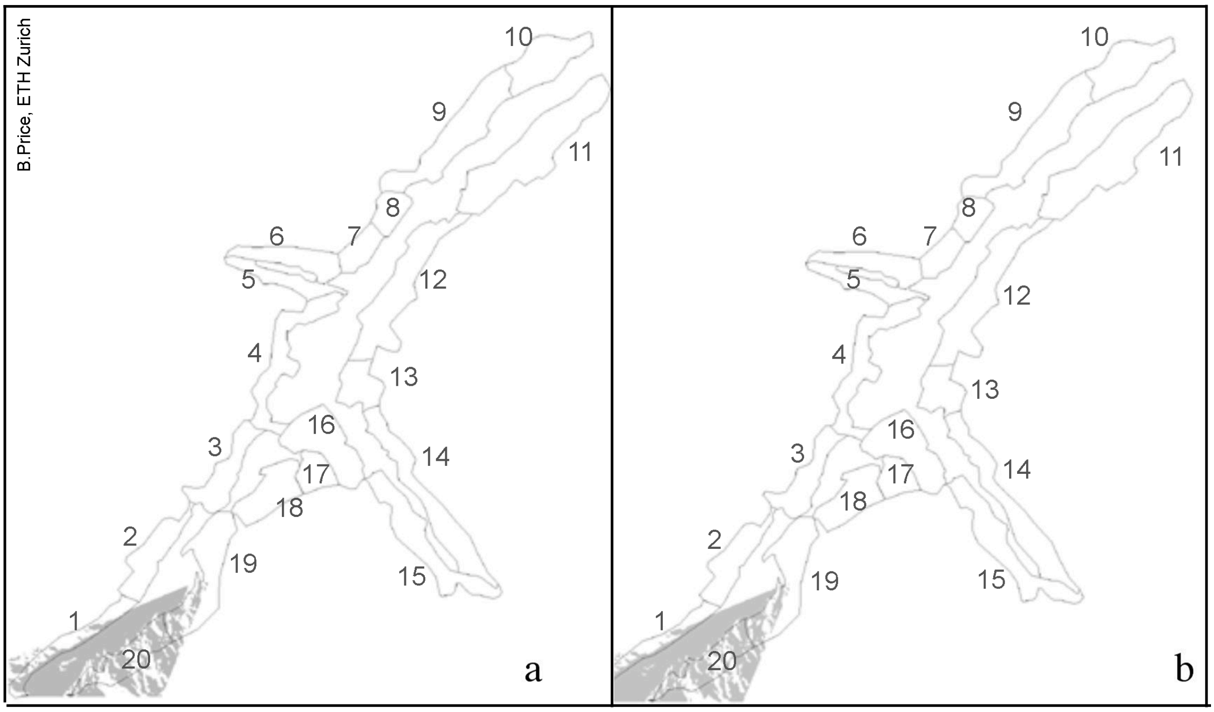

B.Price, ETH Zurich
10
9
11
8
6
7
5
12
4
13
16
3
14
17
18
2
19
15
1
20
a
10
9
11
8
6
7
5
12
4
13
16
3
17
14
18
2
19
15
1
20
b

Figure 6

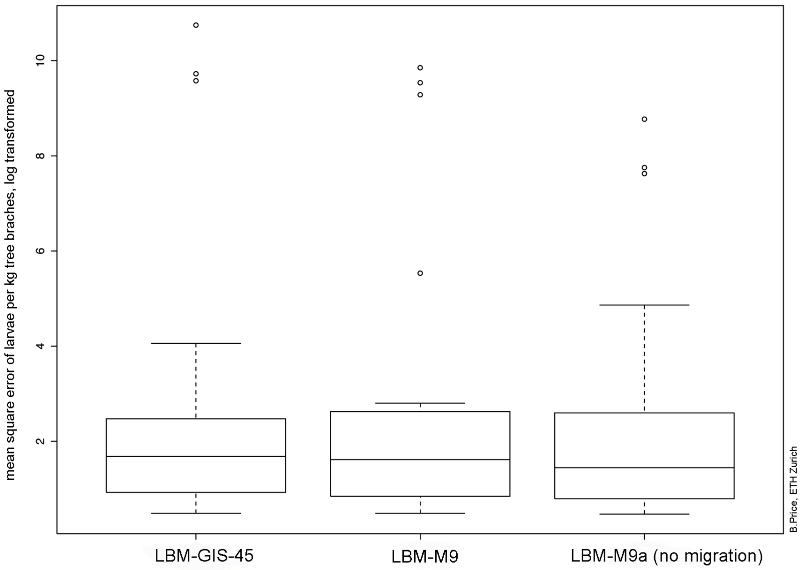
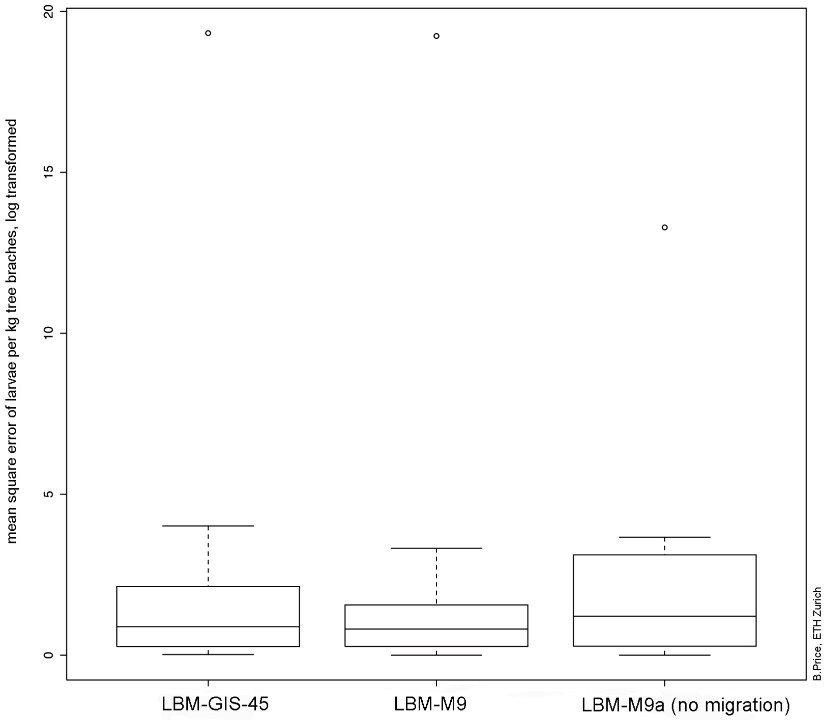

mean square error of larvae per kg tree braches, log transformed
2
4
6
8
10
LBM-GIS-45
LBM-M9
LBM-M9a (no migration)
B.Price, ETH Zurich

Figure 7


mean square error of larvae per kg tree braches, log transformed
0
5
10
15
20
LBM-GIS-45
LBM-M9
LBM-M9a (no migration)
B.Price, ETH Zurich

9 FIGURE CAPTIONS

Figure 1: Location of the 20 sites within the Upper Engadine valley, Switzerland. Sites were delineated by Fischlin (1982) to be homogeneous with respect to exposure, altitude, aspect, and forest structure as well as to remain within a given upper size limit. Light grey coloured polygons depict forested areas.

Figure 2: Definition of positive and negative slopes, depending on flight direction of larch bud moth. This scheme applies for all flight directions and aspects.

Figure 3: Box plot of mean square error values for log transformed times series of observed larval densities versus modelled densities for the models LBM-GIS, LBM-M9 and LBM-M9a (no migration).

Figure 4: Box plot of mean square error values for observed larval densities versus modelled densities across space, i.e. for each year of an average cycle, for the models LBM-GIS, LBM-M9 and LBM-M9a (no migration).

Figure 5: Potential migration areas from site 19 as modelled with LBM-GIS with a) flat-area cut-off at slope = 5° and b) flat-area cut-off at slope = 15°. We observe very little difference between potential migration areas with change in flat-area cut-off slope.

Figure 6: Sensitivity analysis: Box plot of mean square error values for log transformed times series of observed larval densities versus modelled densities for the following models: LBM-GIS-45 with a potential flight sector enlarged to 45°, LBM-M9 and LBM-M9a (no migration).

Figure 7: Sensitivity analysis: Box plot of mean square error values for observed larval densities versus modelled densities across space, ie for each year of an average cycle for the models LBM-GIS-45 with a potential flight sector enlarged to 45°, LBM-M9 and LBM-M9a (no migration).

10 TABLES

Table 1

Proportion (%) of moths in each behaviour category for each site within the Engadine valley.

Site No.	Upwind flyers	Downwind flyers	Calm flyers
1	40	20	40
2	40	20	40
3	20	20	60
4	30	5	65
5	25	15	60
6	25	15	60
7	30	20	50
8	35	20	45
9	40	20	40
10	25	10	65
11	25	5	70
12	30	20	50
13	30	20	50
14	20	20	60
15	20	20	60
16	30	5	65
17	25	20	55
18	30	25	45
19	25	20	55
20	35	15	50

This amount is based on average wind conditions in each site and is assumed to be constant over time (Fischlin 1982)

Table 2

Correlation coefficients between observed and modelled time series (1949-1977) for each of the 20 sites (Fischlin 1982) for each of the models LBM-GIS, LBM-M9 and LBM-M9a (no migration)

Site	**LBM-GIS-45**	**LBM-M9**	**LBM-M9a (no migration)**
1	0.7271	**0.7719**	0.7317
2	**0.8225**	0.6553	0.7219
3	**0.7902**	0.7464	0.7707
4	**0.8083**	0.5882	0.7313
5	**0.7781**	0.6130	0.7293
6	**0.7120**	0.5329	0.7075
7	**0.7496**	0.5828	0.7114
8	0.7356	**0.7624**	0.6067
9	0.5275	**0.7504**	0.6356
10	0.6395	**0.7343**	0.6130
11	0.5370	**0.6328**	0.6225
12	0.6062	**0.6542**	0.6303
13	**0.7321**	0.6066	0.6892
14	**0.8665**	0.7222	0.8040
15	0.7130	0.6795	**0.7233**
16	**0.8160**	0.6764	0.7749
17	**0.9170**	0.6938	0.7850
18	**0.8547**	0.6660	0.7509
19	**0.8240**	0.6605	0.7264
20	0.4529	**0.6681**	0.6156
mean	**0.7305**	0.6699	0.7041

All coefficients significant at the $\alpha=0.05$ level. Bold values represent maximum correlation for a given site.

Table 3

Sensitivity analysis: Correlation coefficients between observed and modelled time series (1949-1977) for each of the 20 sites (Fischlin 1982) for each of the models LBM-GIS-45 with 45° possible flight sector, LBM-M9 and LBM-M9a (no migration)

Site	**LBM-GIS-45**	**LBM-M9**	**LBM-M9a (no migration)**
1	0.7338	**0.7719**	0.7317
2	0.6590	0.6553	**0.7219**
3	**0.7730**	0.7464	0.7707
4	**0.7436**	0.5882	0.73127
5	**0.7396**	0.6129	0.7293
6	**0.7075**	0.5329	**0.7075**
7	**0.7207**	0.5828	0.7114
8	0.5759	**0.7624**	0.6067
9	0.6328	**0.7504**	0.6356
10	0.6130	**0.7343**	0.6130
11	0.6221	**0.6328**	0.6225
12	0.6310	**0.6542**	0.6303
13	0.6862	0.6066	**0.6892**
14	**0.8057**	0.7222	0.8040
15	**0.7247**	0.6795	0.7233
16	0.7695	0.6764	**0.7750**
17	0.7817	0.6938	0.**7850**
18	0.7496	0.6660	**0.7509**
19	**0.7346**	0.6605	0.7264
20	0.6179	**0.6681**	0.6156
Mean	0.7011	0.6699	**0.7041**

All coefficients significant at the α=0.05 level. Bold values represent maximum correlation for a given site.