ECOLOGICAL MODELLING 199 (2006) 433–441

available at www.sciencedirect.com

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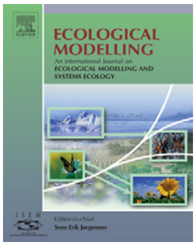

# Synchrony and travelling waves of larch bud moth? Time series analysis with changing scale

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ARTICLE INFO

*Article history:*
Received 29 December 2004
Received in revised form
28 November 2005
Accepted 28 November 2005
Published on line 1 August 2006

*Keywords:*
Larch bud moth
Synchrony
Travelling waves
Time series
Spectral analysis

ABSTRACT

Spatio-temporal patterns of cyclic larch bud moth population densities, for instance synchrony (valley scale) and travelling waves (Alpine arc scale), have been observed at different scales and may be related to distinct causes. In this study, quantification of population data through cross-correlation analysis and spectral analysis revealed that larch bud moth population cycles at the valley scale could be considered to be in close synchrony with one another. At the Alpine arc scale the presence of travelling waves could generally be confirmed. These results have implications for the understanding of the causal mechanisms behind the observed spatio-temporal patterns, suggesting that at the valley scale synchrony depends not only on distances between subpopulations, but is also affected by environmental/habitat characteristics that vary in space. At the Alpine scale, distance between populations is of greater importance in shaping spatio-temporal patterns than at the valley scale.

## 1. Introduction

The larch bud moth, *Zeiraphera diniana* Gn. (*Lep.*, Tortricidae), is a conspicuous forest defoliator that exhibits distinctly regular population cycles peaking approximately every 9 years. These cyclic population dynamics are considered to result from a relationship between the larch bud moth and its host, the European Larch (*Larix decidua* MILLER) (food quality hypothesis), or an interaction with its parasitoids (parasitoid–prey hypothesis) (Baltensweiler et al., 1977; Baltensweiler and Fischlin, 1979, 1988), or a tri-trophic relationship combining the food quality hypothesis and the parasitoid–prey hypothesis (e.g. Turchin et al., 2003).

Previous studies (e.g. Fischlin, 1982, 1983; Bjørnstad et al., 2002; Peltonen et al., 2002) have described distinct spatio-temporal dynamics of larch bud moth, and these dynamics appear to change with scale. Synchrony of population cycles (non-linear phase-locking) in spatially separated locations within valleys—in particular the Upper Engadine valley, has been observed qualitatively (Auer, 1977; Baltensweiler and Fischlin, 1979, 1988; Fischlin, 1982). Synchrony of larch bud moth populations along the Alpine arc has been investigated first by Fischlin (1983) and recently by Peltonen et al. (2002). The possible existence of travelling waves of larch bud moth along the Alpine arc, has also been hypothesised by several authors (Ranta and Kaitala, 1997; Baltensweiler and Rubli, 1999; Feltham and Chaplain, 2000; Bjørnstad et al., 2002; Johnson et al., 2004).

Perfect synchrony would result in standing waves, whereas lagged peaks from one location to another define travelling

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doi:10.1016/j.ecolmodel.2005.11.048

waves. Spatial synchrony can be considered to result from spatial correlations in the environment (the Moran effect)—where all sub populations have identical density dependant dynamics and are subjected to density independent factors that are correlated across large distances such as synchrony in weather patterns (Moran, 1953), and/or dispersal (Fischlin, 1983; Kendall et al., 2000; Liebhold and Kamata, 2000). Additionally, mobile natural enemies can cause regional synchronisation (Ydenberg, 1987; Ims and Steen, 1990).

Recognising spatial scale explicitly is important when studying synchrony of populations and the causal mechanisms of such synchrony. At local scales dispersal may be the dominant factor, whereas at regional to global scales the role of dispersal diminishes and environmental correlations may play a stronger role (Hudson and Cattadori, 1999; Peltonen et al., 2002). Notably, Peltonen et al. (2002) have concluded that the Moran effect is the dominant factor explaining regional scale synchrony for six forest defoliators including the larch bud moth. However, their conclusion contrasts with that of an earlier study of larch bud moth, where dispersal, not the Moran effect dominated the observed synchrony in data and behaviour of models (Fischlin, 1983).

At the valley scale, Fischlin (1982, 1983) found synchrony with few time lags, but without quantifying its parameters. At the Alpine arc scale, Fischlin (1983) found stable synchrony among valleys using a model resembling a metapopulation model, which consisted of several independent subpopulations linked through dispersal. Bjørnstad et al. (2002) have demonstrated waves travelling from west to east along the Alpine arc. Whereas, Johnson et al. (2004) argue that larch bud moth dynamics fit the epicentre hypothesis, spreading out from two different epicentres in the centre of the Alps and the south-west of the Alps respectively. Each of these findings have been based on defoliation data, recorded by a variety of foresters in four qualitative categories (no defoliation (0% of crown defoliated), light defoliation (1–33%), medium defoliation (34–66%) and heavy defoliation (>66%), Baltensweiler and Rubli, 1999). This categorical data may be subjective and is more likely to be inconsistent than larval census data, although it does offer the advantage of covering a critically larger area, which would be prohibitively expensive for larval census data. Peltonen et al. (2002) have investigated larch bud moth synchrony along the Alpine arc with a focus on distinguishing the Moran effect from that of dispersal. However, they have also used defoliation data and have not taken into account temporal lags, therefore not considering the possibility of a travelling wave.

Using quantitative data (larvae per kilogram larch branches) from five valleys along the Alpine arc, one would expect significant spatial autocorrelation or lagged cycle peaks e.g. from west to east, if the hypothesized synchrony or travelling waves were to be present. However, the presence of such patterns is not obvious and requires careful analysis using the various kinds of larch bud moth data available (Fig. 1).

While identification of spatio-temporal patterns, be it synchrony or travelling waves, is indeed only the first step in understanding spatio-temporal dynamics of a population system, it is a vital one. It enables one to speculate on causal mechanisms behind population dynamics, since we believe recognising patterns is a prerequisite for understanding their causes. This research focuses on the analysis of time series of larch bud moth population census data (larvae per kilogram larch branches) in spatially disjunct locations in order to determine quantitatively the spatio-temporal patterns of larch bud moth population dynamics at different spatial scales. In particular, this work aims to determine whether synchrony and/or travelling waves are present in larch bud moth dynamics with a view to distinguishing between migration and the Moran effect as causal mechanisms.

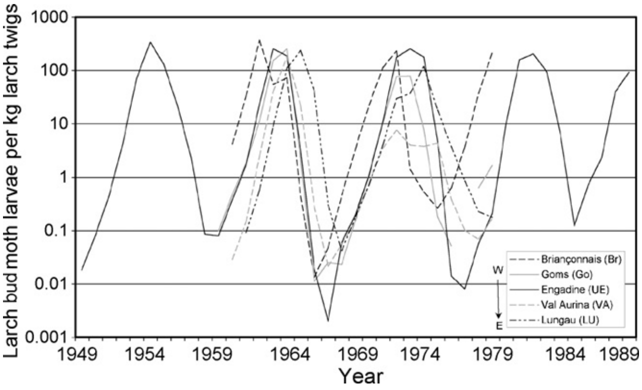

**Fig. 1 – Larval densities in five valleys along the Alpine Arc from 1949 to 1989. 1949–1978, all sites (Auer, 1975, 1977). 1979, all sites: (Auer et al., 1981). 1980, Lu (Baltensweiler and Rubli, 1999). 1980 Br, VA (Hoffmann and Auer, 1989; Baltensweiler and Rubli, 1999). 1980–1981, UE (Baltensweiler and Rubli, 1999). 1982–1989, UE (Fischlin, unpublished).**

A common method to determine synchrony is the use of zero-lag pair-wise cross-correlation (Bjørnstad et al., 1999). Employing (time-) lagged, pair-wise cross-correlation between time series of abundance data from spatially disjunct locations permits to investigate synchrony among populations allowing for a temporal lag and a lag distance (i.e., travelling waves). In addition cross-spectral allows us to demonstrate whether series in separate locations fluctuate similarly and whether series are phase shifted from one another.

With this approach we demonstrate that distinct spatio-temporal patterns are present in the larval census data of larch bud moth and that they may be explained by the dispersal capabilities of larch bud moth without being able to rule out some contribution from the Moran effect entirely. In this sense, because of the wealth of larval census data available, the population system of the larch bud moth can serve as a case study to tackle more general questions of theoretical value relating to the relative roles of the Moran effect and dispersal in causing spatial synchrony as found in many systems (e.g. Peltonen et al., 2002).

## 2. Material and methods

### 2.1. Study area and census data

The Upper Engadine valley is a sub-alpine valley located in the Swiss part of the European Alps (Fig. 2) forested with larch (*L. decidua* MILLER)—Swiss stone pine (*Pinus cembra* L.) forests.

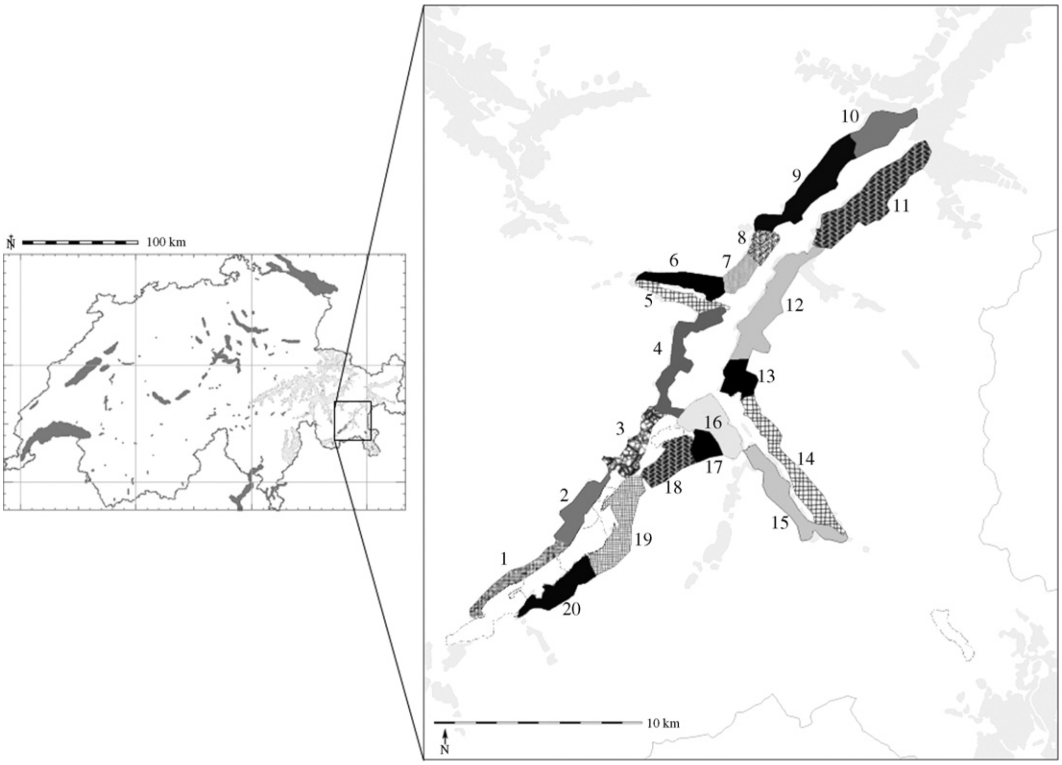

Fig. 2 – Location of the 20 sites within the Upper Engadine valley, Swiss Alps. Sites were delineated to be homogeneous with respect to forest type, exposure, altitude and aspect within site (Fischlin, 1982).

During development of a model for migration of larch bud moth within the Upper Engadine, the valley was divided into 20 ‘sites’, which are considered homogeneous with respect to forest type, aspect and altitude within each site (Fig. 2; Fischlin, 1982). The sites have an average area of 3.7 km$^2$ and are between 2 and 30 km apart (from site centre to site centre) (Fischlin, 1982). Larval sampling is timed to take place when larch bud moth is predominately in the larval stages L3–L5, dependent on weather conditions (Fischlin, 1993). Within the Upper Engadine valley, during the first phase of the larval survey (1949–1958) between 1000 and 2100 trees were sampled annually and the number of larvae per tree was determined (Auer, 1961). From 1956 to 1979 the sampling method changed and approximately 400 larch trees were sampled annually according to a statistically sound random sampling scheme (Kälin and Auer, 1954). Sample stratification was according to topographical features (altitude, exposure) and samples were weighted according to host–tree density per unit area (Baltensweiler and Fischlin, 1988). During these annual population surveys approximately 3 kg 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 of the results. The larval censuses provide an average density estimate for the larval population (e.g. Auer, 1969, 1978) and were converted to an annual absolute population estimate for each site and for the entire Engadine Valley (Fischlin, 1982). Thus 20 time series for spatially disjunct populations (up to 30 km apart) are obtained (Fig. 3; Fischlin, 1982). The census method within the Upper Engadine changed after 1977, meaning that detailed data were no longer available for each of the sites within the Upper Engadine valley. Instead, three trees were randomly chosen within each of three specific sample sites. The sampled sites were chosen to be representative of the entire valley and were spread evenly along the length of the valley (Fischlin,

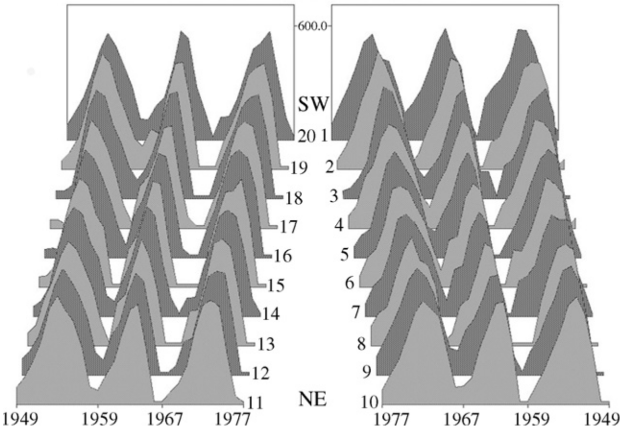

Fig. 3 – Observed larval densities in the 20 sites of the Upper Engadine valley for the period 1949–1977 (Fischlin, 1982). The right-hand side of the graph represents site 1–10 along the east side of the valley with mostly south-eastern exposure. The left-hand side of the graph sites 11–20 with mostly north and north-western exposure. The observer therefore looks down the valley to the south-west. Cycles at this valley scale are in very close synchrony for the period 1949–1977.

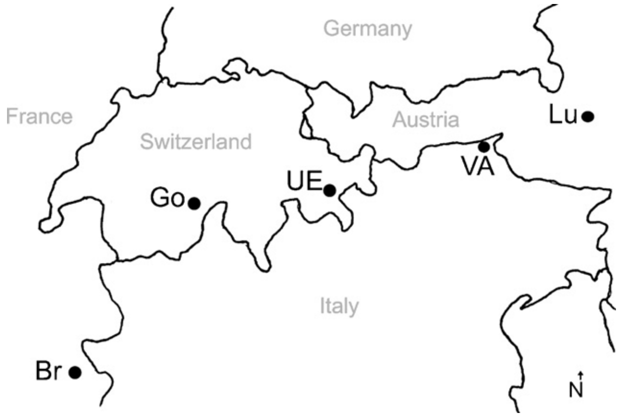

**Fig. 4 – Locations of five studied valleys along the Alpine Arc. Br = Briançonnais (Vallée de la Guisane, Val Névache), France, Go = Goms, Switzerland, UE = Upper Engadine, Switzerland, VA = Val Aurina, Italy, Lu = Lungau, Austria (Auer, 1977; Baltensweiler and Rubli, 1999).**

1993). This allowed estimation of a mean population density for the entire valley.

Aside from the Upper Engadine valley, population surveys were also carried out in four other valleys along the Alpine Arc (Fig. 3) in a very similar manner to that described above for population surveys between 1956 and 1979. Time series of annual numbers of larch bud moth larvae per kilogram of larch branches averaged across the valley are available for each of the following valleys (Fig. 4): Briançonnais (Vallée de la Guisane and Val Névache, France, 1960–1979), Goms (Western Switzerland, 1959–1979), Upper Engadine (Eastern Switzerland, 1949–2004), Val Aurina (Italy, 1960–1979), and Lungau (Austria, 1961–1979).

### 2.2. *Time series analysis*

Spectral analysis examines a time series in the frequency domain, exploring cyclical patterns by reducing them to underlying sine and cosine functions with particular wavelengths (Wolfram, 1996; Grover et al., 2000). Cross-spectral analysis would then allow us to determine the correlations between series at different frequencies.

Each of the 25 log-transformed time series (20 at the within valley scale and 5 at the Alpine Arc scale) were subjected to non-parametric spectral analysis. Log transformed data were used to render measurement errors additive, and to reduce skew and the correlation between the mean and the variance (Koenig, 1999; Grover et al., 2000). During spectral analysis, relying on Fourier decomposition, cyclical components were mapped to sine and cosine functions. The periodograms calculated summarise in graph form estimated spectral density in function of frequency (Wolfram, 1996; Grover et al., 2000). Spectral analysis assumes a stationary process (constant mean, variance and autocorrelation structure in time) (Priestley, 1981; Grover et al., 2000). Thus all time series were also de-trended prior to performing spectral analysis. A raw periodogram is not a consistent estimator of the spectrum, as it may fluctuate strongly and often has a large variance; therefore, we reduced fluctuations with weighted average smoothing using a Daniel window (moving average) with a width of 3 years (Wolfram, 1996).

Using pair-wise cross-correlation, each of the 20 within valley time series were compared to one another, as were the 5 series along the Alpine arc. Cross-correlation coefficients were calculated at temporal lags from 0 to 5 years for each pair of time series.

We estimated co-variation between the time series as a function of frequency using cross-spectral analysis (Platt and Denman, 1975; Priestley, 1981). The squared coherence and associated phase were derived from the cross-spectrum. Squared coherency—the squared correlation of cyclical components of two series for a given period (Platt and Denman, 1975; Puckridge et al., 2000), served as a measure of explained variance. Squared coherence and phase spectra provided further information about the maximum cross-covariance function and the corresponding lag for each frequency (cyclic period) (Platt and Denman, 1975).

The coherence and phase spectra showed us which time series were correlated with one another at which phase lag. According to Platt and Denman (1975), the behaviour of the phase function is an indicator for the accuracy of the coherence spectrum. Therefore, if the phase spectrum was a smooth function of frequency, we considered the squared coherence to be significantly different from zero, but when the phase spectrum oscillates rapidly with frequency, we assumed the squared coherence to be inaccurate (Platt and Denman, 1975).

## 3. Results

### 3.1. *Valley scale*

As the area under a spectrum is proportional to the total variance in the time series, the highest peaks in a spectrum correspond to cyclic periods (or frequencies) that are of greatest importance in accounting for variation in the series (Haydon et al., 2002). The spectral analysis of our 20 series results in spectra with a maximum peak at frequency $\sim 0.11\,a^{-1}$, corresponding to a 9-year cycle for all time series (Fig. 5).

The cross-correlation analysis revealed highest significance for correlations between series at lag zero, where cross-correlation coefficients significant at the $\alpha = 0.05$ significance level ranged between 0.806 (sites 3 and 5) and 0.996 (sites 16 and 17). The exception was for site 3, which exhibited maximum correlation at a lag of −1 year (leading) with three other sites, 1, 6 and 7 (cross-correlation coefficients of 0.854, 0.852 and 0.786, respectively).

The results of the cross-spectral analysis of the 20 time series within the Upper Engadine valley showed that all spectra are in high coherency with one another, with coherency values in the range of 0.768–0.995, all significant at the $\alpha = 0.05$ significance level. The phase spectra were smooth functions at lower frequencies, below 0.2, allowing us to consider the coherency spectra accurate at our frequency of interest $\sim 0.11\,a^{-1}$, but inaccurate at higher frequencies where the phase spectra oscillate considerably. The corresponding phase lags were often not significantly different from zero, with some

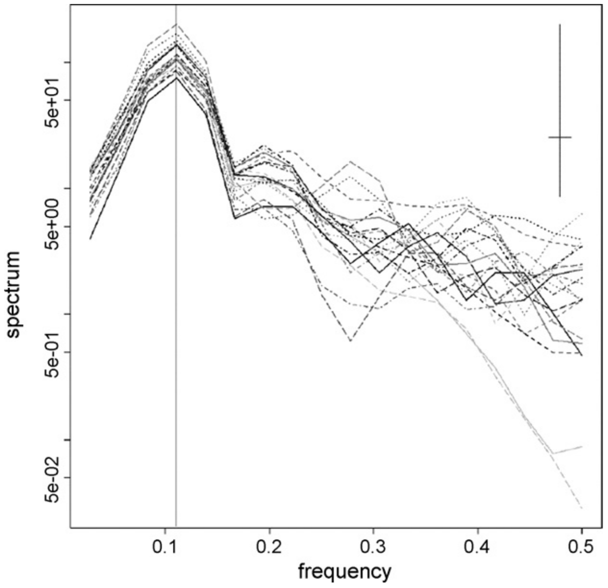

**Fig. 5 – Spectrum for each of the 20 sites within the Upper Engadine valley. Maximum spectral peak is at ~0.11 a$^{-1}$ (indicated by the vertical line) for each site and corresponds to a 9-year cycle. The blue line at the top right demonstrates the 95% confidence interval with the centre mark indicating the bandwidth of the Daniel window.**

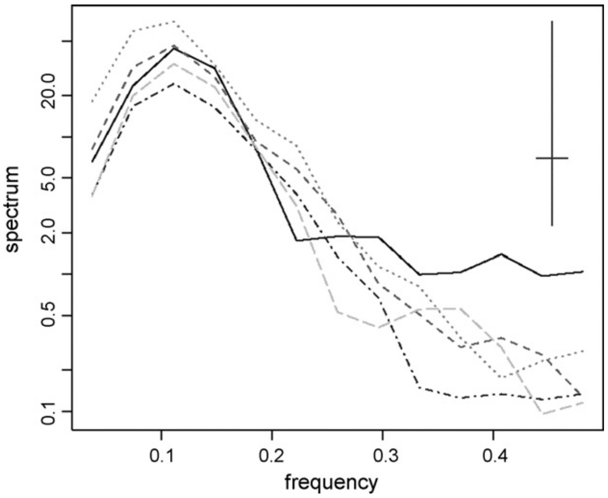

**Fig. 6 – Spectrum for each of the five valleys within the Upper Engadine valley. Maximum spectral peak at ~0.11 a$^{-1}$ for each valley corresponds to a 9-year cycle. The blue line at the top right demonstrates the 95% confidence interval with the centre mark indicating the bandwidth of the Daniel window.**

exceptions. Site 3 was found to be out of phase with all other sites at negative (leading) phase lags corresponding to values between 2 and 6 months. Such lags would correspond to an average lag over the entire time series, meaning that in some years the series peak in the same year and in some years with a 1 year lag. Sites 15, 16, 17, 19 and 20 are out of phase with almost all other sites (although in phase with one another) at lags corresponding to values between 2 and 4 months (trailing).

The cross-correlation method used calculates correlation coefficients only for whole integer values of lag, i.e. integer years, which partly explains the discrepancies between the results of the two analyses.

### 3.2. Alpine arc scale

The results of the cross-correlation analysis are presented in Table 1. We observed a general pattern of increase in temporal lag for maximum correlation with distance along a west-east axis.

The spectral analysis yielded a maximum spectral peak at ~0.11 a$^{-1}$ corresponding to a 9-year cycle for all series along the Alpine arc (Fig. 6).

Cross-spectral analysis revealed high coherency between all pairs of series for a 9-year cyclic peak (Fig. 7). Examination of the phase spectra (Fig. 8) showed that these high levels of coherency occur for phase lags increasing with distances in a west-east direction across the Alpine arc as summarised in Table 2. Again at lower frequencies the phase spectra were quite smooth, indicating accuracy of the coherency spectra at the ~0.11 a$^{-1}$ frequency.

## 4. Discussion

Spatio-temporal dynamics of larch bud moth at the valley scale and the Alpine arc scale were quantified using cross-correlation and spectral analysis. The results reveal that at the valley scale (Upper Engadine), subpopulations have very

**Table 1 – Cross-correlation results Alpine arc**

| | Br | Go | UE | VA | Lu |
|---|---|---|---|---|---|
| Brianconnais (Br) | 0 | 0.8 | 0.46 | 0.63 | 0.77 |
| Goms (Go) | 1 | 0 | 0.64 | 0.87 | 0.84 |
| Upper Engadine (UE) | 1 | 0 | 0 | 0.61 | 0.56 |
| Val Aurina (VA) | 2 | 1 | 1 | 0 | 0.9 |
| Lungau (Lu) | 2 | 1 | 1 | 1 | 0 |

Above the diagonal are maximum cross-correlation coefficients, all significant at the $\alpha = 0.05$ level, for each of the five valleys along the Alpine arc and below the diagonal the corresponding temporal lag (years).

**Table 2 – Phase lags (months) relating to cross-spectral analysis results Alpine arc**

| | Br | Go | UE | VA | Lu |
|---|---|---|---|---|---|
| Brianconnais (Br) | 0 | | | | |
| Goms (Go) | 9 | 0 | | | |
| Upper Engadine (UE) | 12 | 3 | 0 | | |
| Val Aurina (VA) | 12 | 5 | 4 | 0 | |
| Lungau (Lu) | 20 | 12 | 10 | 8 | 0 |

All values corresponding to significant values ($\alpha = 0.05$) of coherence resulting from cross-spectral analysis of time series for each of the five valleys along the Alpine arc.

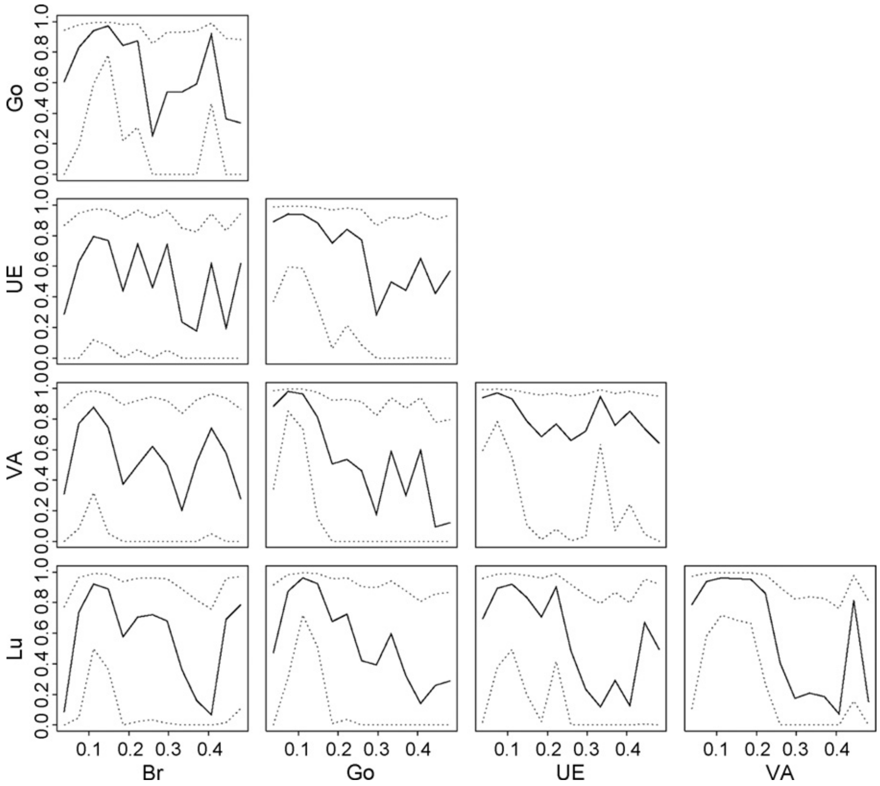

**Fig. 7 – The coherency spectrums resulting from cross-spectral analysis between each of the five valleys along the Alpine arc. High coherency is present between all pairs of times series for spectral frequency representing a 9-year cycle (∼0.11 $a^{-1}$). Dotted lines are 95% confidence intervals. For abbreviations see Fig. 3.**

similar cyclic fluctuations, even at large distances from one another (up to 30 km), and exhibit remarkably close synchrony. However, there are exceptions to this general pattern, in particular the time series for site 3 is out of phase with some other sites for negative temporal lags (leading) of 1 year (cross-correlation analysis), or negative temporal lags (leading) of 2–6 months (cross-spectral analysis). Sites 15, 16, 17, 19 and 20 are also out of phase with most other sites, by lags (trailing) of 2–4 months. Assuming that sites separated by as little as 5 km, are affected in a similar manner by similar conditions (i.e. weather conditions as typical candidates for the Moran effect), the observed temporal lags in synchrony are unlikely to result from the Moran effect. Previous studies (Auer, 1961; Baltensweiler, 1984; Baltensweiler and Rubli, 1999) have reported observed lags in cyclic peaks and attributed this to different physical characteristics of areas. In particular, areas experiencing a lag were northern exposed with a higher proportion of Swiss stone pine (and lower proportion of larch), and thus less attractive to migrating larch bud moth (Vaclena and Baltensweiler, 1978; Baltensweiler and Rubli, 1999). Populations in northern exposed areas also grow slower due to less insulation (Fischlin, 1982). Indeed sites 15, 16, 17, 19 and 20 are northern exposed (Fischlin, 1982) and this may explain the observed lag in synchrony as partly caused by biased dispersal. The key assumption of Moran's hypothesis is that all sub-populations are governed by the same density-dependant dynamics. Consequently, if populations on northern exposed sites experience different dynamics due to climatic or habitat variables, then Moran's hypothesis no longer holds (Moran, 1953; Peltonen et al., 2002). However, not all time series from northern exposed sites showed a lag. Moreover, sites 2 and 4 are south-easterly exposed and also in other respects quite comparable to their neighbouring site 3 and yet lagged behind this site. Thus reasons for the negative lag are currently unclear, but may be due to unmeasured wind-aided dispersal patterns.

Due to relatively small distances between the sites and the high flight ability of the larch bud moth, the idea presented by Johnson et al. (2004) that habitat connectivity, as a function of inter-quadrat distance and moth dispersal ability, can also determine dispersal routes is of less significance at the valley scale. While long range migration of the larch bud moth is downwind and occurs once moths arriving at mountain ridges and passes are taken up by gradient winds, local and regional flight of larch bud moth is upwind and occurs in response to pheromones (Baltensweiler and Fischlin, 1979). Therefore, habitat connectivity as a function of a moth's ability to traverse a landscape as determined by wind conditions and aspects of the terrain, is important. A recent modelling study (Price, 2006) combining a wind driven dispersal model with a GIS model shows that physical components of the landscape, in particular slope, aspect and altitude, at the valley scale may determine migration paths and this may also affect spatial synchrony of populations.

At the Alpine arc scale, populations in valleys along the Alpine arc exhibit very similar cyclic properties (Table 1;

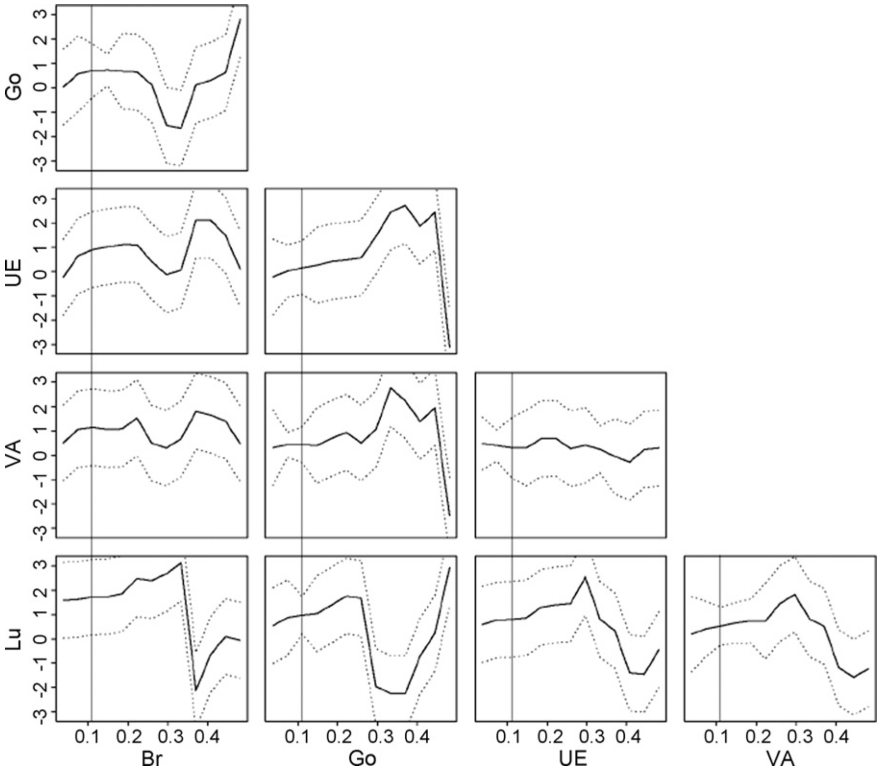

**Fig. 8 – Phase spectrum resulting from the cross-spectral analysis between the five valleys along the Alpine arc. Dotted lines are 95% confidence intervals. The phase spectrum must be viewed in conjunction with the coherency spectrum. Note the phase lag values (years, y-axis) where coherency is highest and significant, here ∼0.11 $a^{-1}$, representing a 9-year cycle. High coherency between the spectra occur at a lag of 9 months. for Briançonnais (Br) and Goms (Go), 1 a (year) for Br and the Upper Engadine (UE), 1 a for Br and Val Aurina (VA), 20 months for Br and Lungau (Lu), 3 months for Go and the UE, 5 months for Go and VA, 1 a for Go and Lu, 4 months for the UE and VA, 10 months for the UE and Lu, and 8 months for VA and Lu.**

Figs. 6 and 7). It would be expected that if travelling waves were present, population cycles would be correlated to each other at increasing time lags with increasing distance. The results of this study (Tables 1 and 2; Figs. 7 and 8) suggest that this is indeed the case, confirming a travelling wave of larch bud moth dynamics similar to that described by Bjørnstad et al. (2002) based on defoliation data. Therefore, at the Alpine scale level, distance between populations appears to strongly influence the level of synchrony.

Baltensweiler and Rubli (1999) have hypothesised that west-to-east travelling waves could be driven by migration with the predominant westerly winds blowing in general along the Alpine arc. However, Bjørnstad et al. (2002) found that models based on the food quality hypothesis with directional dispersal resulted in waves travelling in the opposite direction. Under the parasitoid hypothesis with directional dispersal, they found that modelled directional waves resulted for only narrow ranges of moth and parasitoid mobilities, but when dispersal depended on an east-to-west gradient of habitat quality, directional waves could be modelled for a wide range of model parameters (Bjørnstad et al., 2002).

Although synchronisation of mobile natural enemies can theoretically cause region-wide synchrony, larch bud moth parasitoids have relatively low mobility (Delucchi, 1982) and are likely not able to cause such widespread travelling waves. In addition, Bjørnstad et al. (2002) found that the larch bud moth–parasitoid model with isotrophic dispersal could not easily produce travelling waves. Since our results document high degrees of coherency at increasing phase lags with increasing distances between populations in a west-east direction, either the predominant westerly winds or an east-west gradient of habitat quality, e.g. in food quality, fit the evidence well. Both mechanisms require migration to explain the lagged spatial synchrony and contrast with any hypothesized Moran effect.

Moreover, spatial synchrony is expected to drop with distance, either due to exceeding the dispersal capacity of the involved organisms or due to uncorrelated characteristics of the environment. It is well known that variograms of temperature and particularly precipitation show significant declines in autocorrelation with distance, in particular in complex terrain such as the European Alps (e.g. Gyalistras and Fischlin, 1999). Such effects also result in a decline in spatial covariance, e.g. in the Alps, temperature is usually no longer correlated at distances beyond 50 km (e.g. Gyalistras et al., 1997). Although Peltonen et al. (2002) report significant correlation in temperatures at lag distances up to 400 km in the European Alps, more detailed analysis of highly reliable records e.g. from Swiss weather stations (Gyalistras, 2003) contradict these findings. The observed travelling waves also contradicts the assumption of a large range Moran effect covering all of the Alps, e.g. due to June common mean temperatures (Peltonen et al., 2002), as this conflicts with the lags we found increasing with distance in west-east direction, However, directional migration could easily explain those patterns.

The larch bud moth is known as a strong flyer, which can cover flight distances of over 200 km, meaning synchronisation of sites across large regions through dispersal is plausible (Fischlin, 1982). Moreover, Peltonen et al. (2002) found spatial synchrony to decline more rapidly with distance when the environmental heterogeneity is spatially structured than would be expected from the decrease in correlation with distance of some weather variables alone. It follows that even at the regional scale, a mere decline in spatial covariance with distance is not conclusive for distinguishing between the Moran effect and dispersal as causes of synchrony, particularly not in the case of the larch bud moth.

Johnson et al. (2004) propose that larch bud moth dynamics at the scale of the Alpine arc could follow the epicentre hypothesis. They suggest two epicentres: a primary one in the south-western Alps, and a secondary in central north-eastern Alps. According to this hypothesis, larch bud moth is considered to spread from these epicentres via dispersal depending on the habitat density and connectivity. Our results are not conclusive with respect to the hypothesis proposed by Johnson et al. (2004), since there are only five time series available. Nevertheless, the results of our analyses would favour a west-to-east travelling wave, which could be considered to start from the proposed primary epicentre, rather than the two epicentre hypothesis proposed.

The two epicentres described by Johnson et al. (2004) correspond closest to the valleys Briançonnais and the Upper Engadine. Under the epicentre hypothesis, should waves always spread from these valleys, one would not expect a correlation, lagged or otherwise, between populations at these valleys (unless we would assume a strong, superimposed Moran effect correlating only the epicentres, which however, would make it difficult to explain why areas in between should not also be affected by the very same Moran effect). In fact, we found a strong, 1 year lagged correlation between the valleys Briançonnais and Upper Engadine. Dispersal mechanisms can easily explain that finding, whereas a Moran effect faces considerable difficulties.

In addition, as long-range dispersal of larch bud moth occurs when moths are taken up by gradient wind (Baltensweiler and Fischlin, 1979) moths usually lose touch with the canopy during such dispersal. This makes it difficult for them to distinguish 'high quality' from 'low quality' habitats. Nevertheless, both Johnson et al. (2004) and Bjørnstad et al. (2002) using models, which assume dispersal within some kind of habitat quality gradient have been able to reproduce travelling waves. Therefore, dispersal, driven by wind dynamics in conjunction with habitat gradients, could be considered to be an important driver of the spatial dynamics of larch bud moth.

## 5. Conclusions and outlook

Using time series analysis techniques of cross-correlation analysis and spectral analysis of larval census data, this study has been able to demonstrate and quantify the patterns of synchrony at the valley scale and travelling waves at the Alpine arc scale in population cycles of larch bud moth as have been hypothesized previously only from defoliation data. Although these spatio-temporal patterns are present they are not consistent, particularly not across all sites in the Upper Engadine valley. The results of this study suggest that differences in characteristics between sites could help determine the spatio-temporal dynamics of the larch bud moth at the valley scale. Our results indicate that at the Alpine Arc scale spatial synchrony is more likely attributable to synchronising dispersal effects than the Moran effect. However, particularly at the scale of the Alpine arc, further research is needed to identify the relevant environmental characteristics in order to more conclusively distinguish between the Moran effect and migration hypotheses. In addition, previous studies have suggested that dispersal can be driven by wind and/or gradients in habitat quality, therefore it would also be of primary interest to look further into those drivers of larch bud moth migration.

## Acknowledgments

This work was funded by the Swiss National Science Foundation within the National Research Program 48 'Landscapes and Habitats of the Alps' (Grant No. 4048–064432/1). The useful comments of two anonymous reviewers are gratefully acknowledged. Special thanks to members of the Terrestrial Systems Ecology group for their feedback and comments on the paper structure and content, in particular Bernhard Buchter, Sophie Fukutome, Dimitrios Gyalistras and Claude Théato.

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