

# Population synchrony within and among Lepidoptera species in relation to weather, phylogeny, and larval phenology

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**Abstract.** 1. The population dynamics of native herbivore species in central Appalachian deciduous forests were studied by analysing patterns of synchrony among intra- and interspecific populations and weather.

2. Spatial synchrony of 10 Lepidoptera species and three weather variables (minimum temperature, maximum temperature, precipitation) from 12 sites was measured using cross-correlation functions relating levels of synchrony to the distance separating each set of populations. Based on both the pattern of synchrony and the region-wide cross-correlation coefficients, Lepidoptera species appear to be synchronised, at least in part, by local weather conditions.

3. Interspecific cross-correlations were calculated for all sympatric species pairs and trends in interspecific synchrony were related to phylogenetic relatedness, life-history timing, and weather. Interspecific synchrony was highest among species whose larvae were present during the same time of the season, but there was no relationship between interspecific synchrony and phylogenetic affinity.

4. Spatial synchrony of weather variables was significantly related to both species of some interspecific pairs, indicating weather as a potential mechanism involved in synchronising populations of different species.

**Key words.** Cross-correlation, interspecific synchrony, Lepidoptera, spatial synchrony, weather.

## Introduction

Foliage feeding forest insect species that exhibit intermittent outbreaks have often served as useful model systems for studying population dynamics. Despite the voluminous number of studies on the population dynamics of outbreaking species, little research has been conducted on the dynamics of the many non-outbreaking, herbivore species. More information on the population dynamics of non-outbreaking species is needed because it may provide critical information for understanding the dynamics of outbreak species (Cappuccino, 1995), and because it may clarify how management practices targeting the control of outbreaking species result in reductions of non-target species

populations (Reardon & Wagner, 1995; Sample *et al.*, 1996; Wagner *et al.*, 1996). Considering the overwhelming majority of non-outbreaking species (generally >90% of the foliage feeding guild, Markin, 1982) and the potential risk to their populations in management areas, understanding their population dynamics may be valuable in conservation efforts engaged on their behalf.

In the past decade, there has been increasing interest in characterising spatial patterns of animal abundance through time and identifying processes that cause these patterns. An important characteristic of spatial dynamics that is frequently observed is spatial synchrony among geographically disjunct populations (Lande *et al.*, 1999; Paradis *et al.*, 2000), measured as the correlation of temporal fluctuations among localities. The intensity and spatial extent of population synchrony have been characterised in populations of insects (Miller & Epstein, 1986; Pollard, 1991; Hanski & Woiwod, 1993; Sutcliffe *et al.*, 1996; Williams

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& Liebhold, 2000), fish (Ranta *et al.*, 1995a), birds (Ranta *et al.*, 1995a, b; Lindström *et al.*, 1996; Paradis *et al.*, 2000; Koenig, 2001), mammals (Ranta *et al.*, 1995a; Steen *et al.*, 1996; Ranta *et al.*, 1997), and diseases (Bjørnstad, 2000). Synchronous population fluctuations may be a result of dispersal between populations, regional stochasticity (*Moran effect*), or synchronous trophic effects (Bjørnstad *et al.*, 1999); relative roles of these factors may vary among species and spatial scales. While many studies have documented spatial synchrony among populations of a single species, relatively few studies of interspecific synchrony exist.

Intraspecific and interspecific synchrony of 10 Lepidoptera species native to central Appalachia were studied here with two primary objectives. The first objective was to describe the intraspecific spatial synchrony of local native Lepidoptera populations and identify trends in the correlation of weather with local population dynamics. The second objective was to measure the interspecific synchrony within the herbivorous lepidopteran community and relate patterns of synchrony to phylogenetic relations and larval phenology. It was expected that if trophic interactions are the dominant synchronising factor that this would be indicated by greater synchrony among closely related species, which can be expected to share natural enemies. In contrast, if weather is the dominating synchronising agent then species sharing similar phenological timing would be expected to be more synchronised.

## Methods

Six 200-ha plots were established each on the Monongahela National Forest, Pocahontas County, West Virginia and the George Washington National Forest, Augusta County, Virginia (Butler & Strazanac, 2000a, b). Weekly collections of adult Lepidoptera were made during a 15-week sampling period from May to August of each year from 1995 through to 2001 using 12-W black light traps. One trap was hung at a designated location on each plot at a height of approximately 1.5 m and operated throughout one night per week. Photoelectric eyes on each trap assured that they

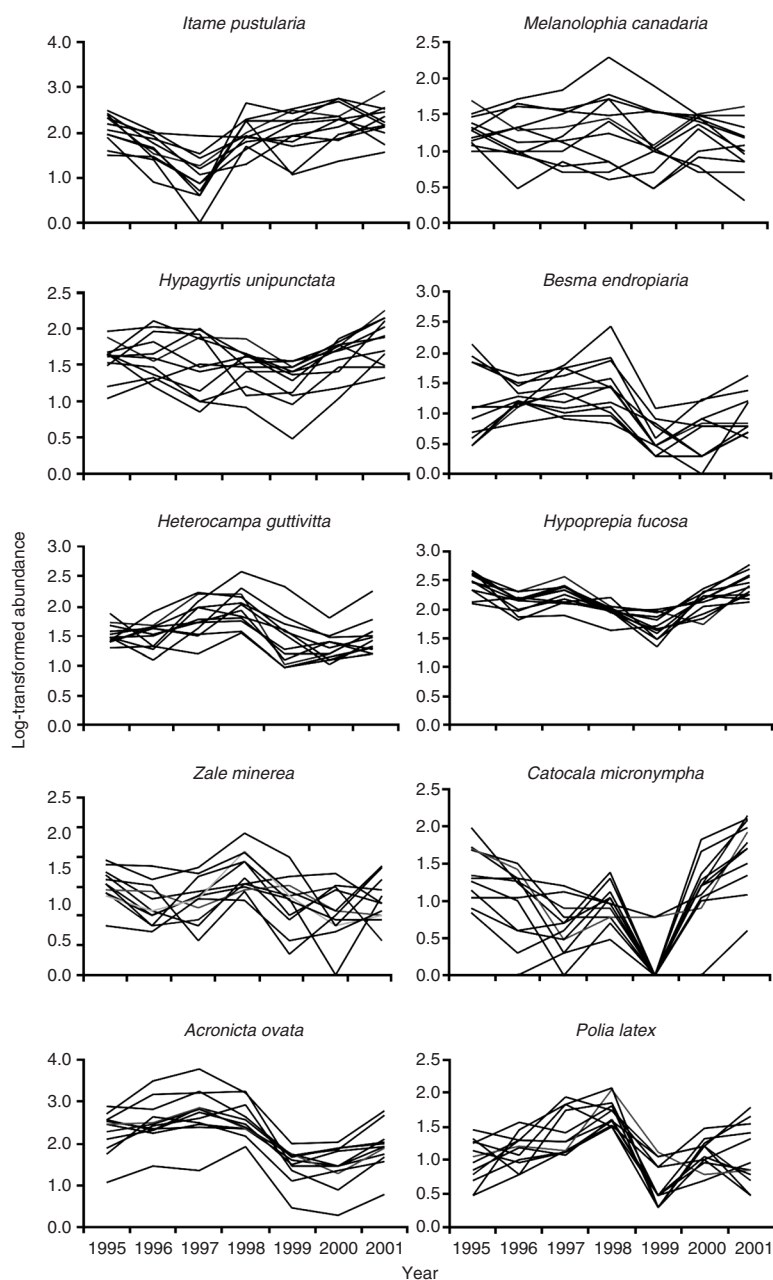
operated simultaneously from dusk to dawn (Butler *et al.*, 2001). The 10 most abundant night-flying Lepidoptera species were selected for analysis. The species selected for this study were those that were collected from every plot in every year to avoid the statistical complications associated with rare species. These species represented four families and diverse life histories (Table 1). Abundance for each species was expressed as the total moths collected throughout each season and log-transformed to generate a 7-year time series for each plot (Fig. 1).

Intraspecific synchrony among local (plot) populations was measured as the region-wide cross-correlation coefficient between time series of log-transformed abundance from the 12 locations (Bjørnstad *et al.*, 1999). Because cross-correlations are not independent due to spatial and temporal autocorrelation in time series, a confidence interval for the mean synchrony was obtained by bootstrapping (1000 iterations) with replacement among the populations with subsequent recalculations of averages (Bjørnstad *et al.*, 1999). The pattern of spatial synchrony was demonstrated using individual correlograms for each species by calculating Pearson correlation coefficients of all local populations and regressing the correlation against the Euclidean distance between pairs of locations (Buonaccorsi *et al.*, 2001).

Weather variables measured weekly at each site were minimum and maximum temperature and precipitation, each of which may directly or indirectly influence the dynamics of forest Lepidoptera. Weather data were collected from stations located next to each light trap and were used to generate 12 annual weather measurements for each site: average monthly minimum and maximum temperature and total monthly rainfall for May through to August. To reduce the number of weather variables in the analysis, a principal components analysis (PCA) was performed separately on minimum temperatures, maximum temperatures, and precipitation measurements. PCAs were performed on each weather variable separately rather than combining all measurements into one analysis because Lepidoptera species differ in their response to environmental variables (Casey, 1995) and this analysis provided a mechanistic approach to associating species abundance and weather variables. From the PCA of each weather

**Table 1.** Selected study species and their respective family, larval season, and larval food preferences. Annual abundance is the average annual abundance from all plots  $\pm$  SD.

Species	Family	Larval season	Larval food plant	Annual abundance
<i>Itame pustularia</i> (Guenée)	Geometridae	Early	Maple	136 $\pm$ 72
<i>Melanolophia canadaria</i> (Guenée)	Geometridae	All	Polyphagous	22 $\pm$ 13
<i>Hypagyrtis unipunctata</i> (Haworth)	Geometridae	All	Polyphagous	46 $\pm$ 18
<i>Besma endropiaria</i> (Grote & Robinson)	Geometridae	Late	Polyphagous	21 $\pm$ 18
<i>Heterocampa guttivitta</i> (Walker)	Notodontidae	Mid-late	Polyphagous	52 $\pm$ 29
<i>Hypoprepia fucosa</i> Hübner	Arctiidae	Early	Lichens/Mosses	173 $\pm$ 59
<i>Zale minerea</i> (Guenée)	Noctuidae	All	Polyphagous	16 $\pm$ 8
<i>Catocala micronympha</i> Guenée	Noctuidae	Early	Oaks	24 $\pm$ 16
<i>Acrionicta ovata</i> Grote	Noctuidae	Mid-late	Oaks	401 $\pm$ 412
<i>Polia latex</i> (Guenée)	Noctuidae	Mid-late	Polyphagous	22 $\pm$ 12



**Fig. 1.** Time series of the 10 study species on each plot within the study area.

variable, the first principal component accounted for the majority of the variation of the monthly measurements and was used as the representative measurement of each variable. The scores of the principal components formed a time series from every plot for each weather variable. Region-wide synchrony and the pattern of spatial synchrony was measured for each weather variable using the same procedure described for intraspecific synchrony.

Since the principal component of each weather variable was representative of all of the measurements taken throughout the season, directly correlating the time series

of each variable to that of each species would have been complicated by the diverse phenologies of the moth species. The spatial synchrony of each Lepidoptera species was therefore related to the synchrony of each weather variable by determining if sites with more synchronous weather conditions had more synchronous moth dynamics. This was performed by fitting the data to a general linear model (SAS proc glm) in which the correlation coefficients of the weather variable calculated for each plot pair were the independent observations and the respective correlation coefficients of species abundance were the dependent

observations. To control for distance, the distance between each plot pair was assigned as the covariate of the analysis. The model tested the hypothesis that the pattern of regional synchrony for a Lepidoptera species was associated with the pattern of regional synchrony of the weather variable. Since this comparison involved a total of 30 separate comparisons (three weather variables  $\times$  10 species), alpha levels were adjusted using a Bonferroni correction factor ( $\alpha = 0.0017$ ).

Interspecific synchrony was calculated as the mean cross-correlation obtained from each site for each pairwise comparison. To score the statistical significance of the average correlation, a bootstrap confidence interval was generated for each comparison by resampling (1000 iterations) and recalculating the average correlation. This method accounted for the autocorrelation among sites. Since measuring interspecific synchrony involved a total of 45 separate comparisons, alpha levels were adjusted using a Bonferroni correction factor. Based on the corrected alpha level, the pairwise 99.9% confidence interval was used to determine the statistical significance of the correlations. Correlations were considered significant if the confidence interval did not include zero.

The extent to which interspecific synchrony differed within and among phylogenetic and phenological (early season/late season/all season larvae) groups was tested. Comparison of taxonomic groups was made using the two-sample Mann–Whitney *U*-test and comparison among larval phenology groups was made using the Kruskal–Wallace rank sum test.

## Results

With the exception of *Melanolophia canadaria* (Guenée), all region-wide cross-correlations between intraspecific populations and between individual weather variables were significant. Region-wide cross-correlations ranged in values from 0.12 to 0.87 (Table 2). Correlograms showed a significant decrease in synchrony with increasing distance for all

**Table 2.** Average region-wide cross-correlation coefficients and 99.9% confidence interval (CI) for intraspecific populations and weather factors.

Species	Correlation	CI
<i>I. pustularia</i>	0.62	(0.48, 0.75)
<i>M. canadaria</i>	0.12	(-0.14, 0.47)
<i>H. unipunctata</i>	0.36	(0.19, 0.53)
<i>B. endropiaria</i>	0.63	(0.53, 0.73)
<i>H. guttivitta</i>	0.56	(0.43, 0.70)
<i>H. fucosa</i>	0.71	(0.63, 0.80)
<i>Z. minerea</i>	0.31	(0.11, 0.47)
<i>C. micronympha</i>	0.72	(0.58, 0.82)
<i>A. ovata</i>	0.87	(0.84, 0.91)
<i>P. latex</i>	0.61	(0.50, 0.74)
Minimum temperature	0.58	(0.47, 0.69)
Maximum temperature	0.64	(0.51, 0.77)
Precipitation	0.90	(0.87, 0.93)

intraspecific populations, which was expected *a priori* from this well-documented pattern of spatial dynamics (Fig. 2).

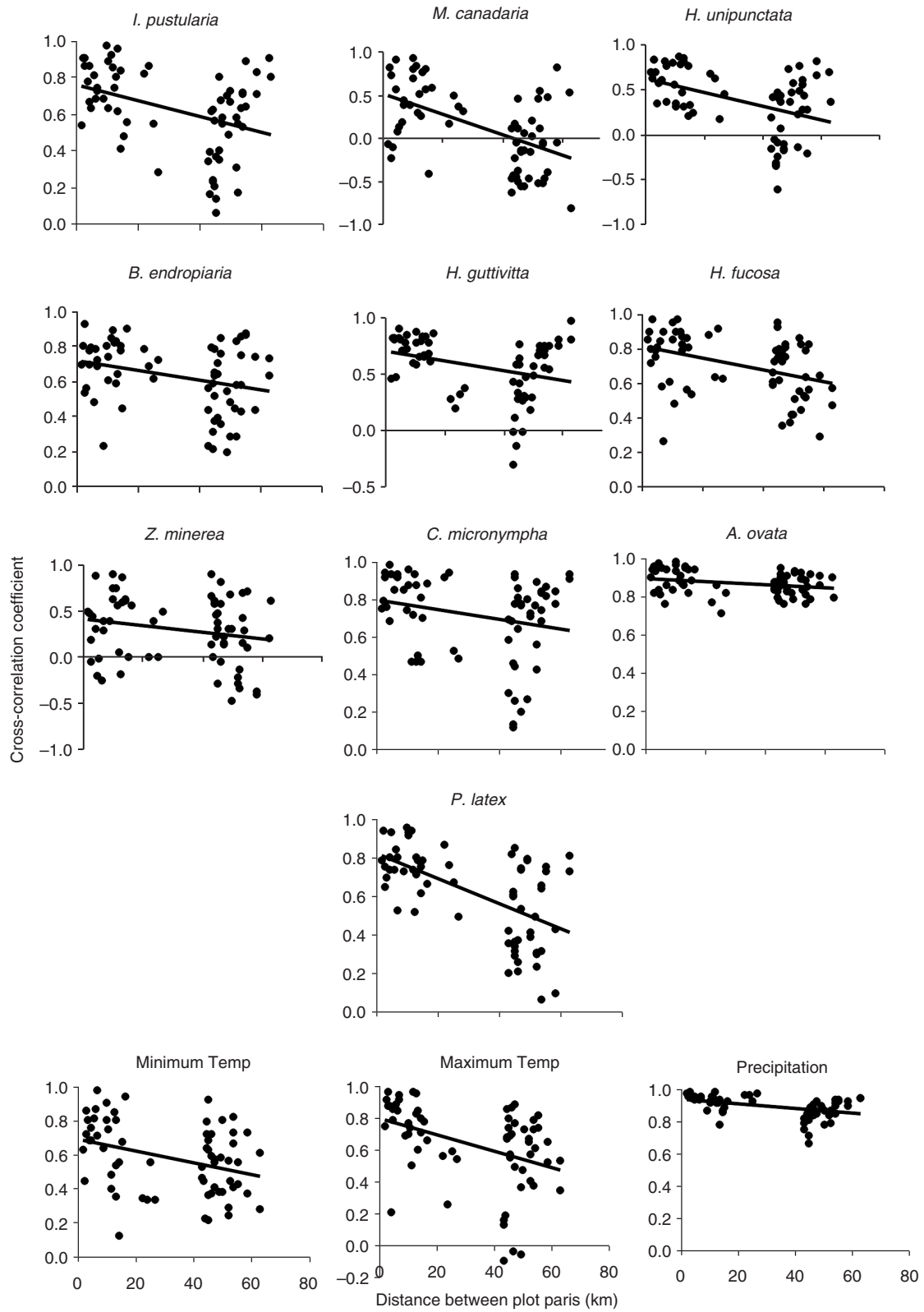
The first principal component generated from minimum temperature, maximum temperature, and precipitation data accounted for 58, 67, and 45% of the variability in their monthly values respectively. Monthly minimum and maximum temperatures were all directly correlated with the first principal component of their respective analysis; however, in the precipitation PCA correlations were variable among months (Table 3). All of the first PCAs of the weather variables had high region-wide correlations (0.58–0.90) (Table 2). Similarly to the pattern of synchrony observed for each species, synchrony of each weather variable decreased with increasing distance between each plot (Fig. 2).

Of the 30 weather–species comparisons, there was a significant positive relationship in nine weather–species pairs (30%) using adjusted alpha levels and in 11 pairs (37%) based on an alpha level of 0.05 (Table 4). Based on the uncorrected alpha level, two weather–species pairs had a significant negative relationship. Only one species (*Zale minerea* (Guenée)) was positively related to minimum temperature, four species [*M. canadaria*, *Besma endropiaria* (Grote & Robinson), *Heterocampa guttivitta* (Walker), and *Hypoprepia fucosa* Hübner] were positively related to maximum temperature, and six species [*Itame pustularia* (Guenée), *Hypagyrtis unipunctata* (Haworth), *B. endropiaria*, *H. guttivitta*, *Catocala micronympha* Guenée, and *Polia latex* (Guenée)] were positively related to precipitation. The two significant negative relationships were the geometrids, *M. canadaria* and *H. unipunctata*, with minimum temperature.

Significant positive interspecific synchrony was found for 17 species pairs (38%) using adjusted alpha levels, and 20 species pairs (44%) using a 95% pairwise confidence interval. Significant negative correlations were found for three species pairs (7%) using adjusted alpha levels and for five pairs (11%) using pairwise alpha values of 0.05 (Table 5). There was not a significant difference in the interspecific cross-correlation of species within vs. among families ( $\chi^2 = 1.85$ , d.f. = 1,  $P = 0.17$ ); however, interspecific correlations were significantly higher among species whose larvae were present during the same season ( $n = 12$ ) than species pairs whose larvae were present during different ( $n = 12$ ) or overlapping ( $n = 21$ ) seasons ( $\chi^2 = 18.66$ , d.f. = 2,  $P = 0.0001$ ) (Fig. 3). Specifically, species whose larvae are present in the latter part of the season were the most highly synchronised species pairs in this study (Fig. 4).

## Discussion

All but one of the Lepidoptera species exhibited significant region-wide intraspecific synchrony, which decreased with increasing distance between local populations. Similar results have been seen for other Lepidoptera (Pollard, 1991; Hanski & Woiwod, 1993; Williams & Liebhold, 2000; Peltonen *et al.*, 2002), as well as for a diversity of



**Fig. 2.** Spatial synchrony (cross-correlation) of conspecific local populations and weather variables. Patterns of synchrony are described by the decay in synchrony against distance for all possible pairs of local populations.

**Table 3.** Specific PCA loadings of the first principal component of each monthly weather measurement. Eigenvalues and the percentage of the variance explained by each component are also presented.

Month	Min. temp.	Max. temp.	Precipitation
May	0.506	0.327	0.178
June	0.529	0.563	0.698
July	0.497	0.557	-0.354
August	0.466	0.515	0.596
Eigenvalue	2.33	2.69	1.78
% variability	58.1	67.2	44.6

other taxa (Ranta *et al.*, 1995a, b; Lindström *et al.*, 1996; Paradis *et al.*, 2000). Interspecific synchrony has received less attention, particularly with regard to numerous species within a feeding guild. In the work reported here, interspecific synchrony was found in 17 out of 45 *Lepidoptera* species pairs and interspecific synchrony was highest among species with larvae present during the same season.

Several mechanisms have been proposed as causes of synchrony within and among species; however, relating synchrony of population fluctuations with specific causes is difficult and often problematic (Ranta *et al.*, 1999). Not only are there statistical complications due to temporal autocorrelation (Koenig, 1999; Buonaccorsi *et al.*, 2001), but multiple synchronising mechanisms may operate simultaneously (Bjørnstad *et al.*, 1999), and differentiating the relative role of dispersal, trophic interaction, and weather is often ambiguous (Ranta *et al.*, 1995a). Relating the pattern of synchrony in environmental factors, such as temperature and rainfall, to the pattern of synchrony in populations may be valuable for understanding the role of weather in synchronising local populations (Moran, 1953; Koenig, 1999); however, this analysis requires that environmental parameters are measured in the same sites as species are collected. Consequently, few studies have been able to

quantify the relationship between the patterns of environmental and population synchrony (Koenig, 1999). Although dispersal rates and the role of trophic interactions were not obtained in this study, these data did provide an opportunity to investigate the potential role of weather in the spatial synchrony of *Lepidoptera* populations.

Reduction of the environmental measurements into one principal component for each weather variable provided a generalised and mechanistic approach to evaluating the relationship of synchrony among weather variables to synchrony among *Lepidoptera* populations. For three variables that could potentially influence *Lepidoptera* dynamics, monthly measurements were combined into one spatio-temporal series accounting for a large portion of the seasonal variation. This approach yielded one seasonal measurement per variable whose own spatial synchrony could be compared with the synchrony of both late and early season species at the same pairs of sites. Since each principal component was a combination of all monthly measurements, the analysis was conservative in detecting mechanistic relationships between weather and species synchrony. Despite this conservative estimate, the analysis showed that the pattern of synchrony of weather was positively related to that of several *Lepidoptera* species. Based on these relationships, it can be concluded that the intraspecific synchrony observed in this study may be caused in part by a Moran effect.

Although temperature and precipitation of the sampling night have a well-known influence on the number of moths collected in light traps (Morton *et al.*, 1981; Holyoak *et al.*, 1997; Yela & Holyoak, 1997; Butler *et al.*, 1999), a previous analysis of the *Lepidoptera* data used in this study showed very high temporal correlations in the total annual abundance of larvae collected from foliage clippings and the corresponding moth generation collected in light traps (Raimondo *et al.*, 2004). Considering the high correlation of annual moth and larval abundances for the species used in this study, the influence of nightly weather condition on

**Table 4.** Results of the general linear model determining significant relationships among the spatial synchrony in weather variables and *Lepidoptera* species abundance. Values of  $R^2$  measure the strength of the relationship and values of  $P$  score the significance of the relationship (\* $\alpha < 0.05$ , \*\* $\alpha < 0.001$ ).

Species	Minimum temp.		Maximum temp.		Precipitation	
	$R^2$	$P$	$R^2$	$P$	$R^2$	$P$
<i>I. pustularia</i>	-0.02		0.03		0.46	**
<i>M. canadaria</i>	-0.23	*	0.26	*	0.17	
<i>H. unipunctata</i>	-0.23	*	-0.14		0.46	**
<i>B. endropiaria</i>	-0.08		0.36	**	0.60	**
<i>H. guttivitta</i>	0.06		0.43	**	0.36	**
<i>H. fucosa</i>	-0.04		0.53	**	-0.07	
<i>Z. minerea</i>	0.40	**	-0.05		-0.08	
<i>C. micronympha</i>	-0.06		0.12		0.59	**
<i>A. ovata</i>	0.02		0.07		0.03	
<i>P. latex</i>	0.03		0.02		0.23	*
Minimum temp.			0.23	*	-0.21	*
Maximum temp.					0.18	*

**Table 5.** Average cross-correlation coefficients for interspecific comparisons are presented in the upper portion of the table. The lower portion of the table contains the 99.9% confidence interval for each species pair. Cross-correlations in bold are significant at the  $\alpha = 0.001$  level and correlations marked by an asterisk (\*) are significant at the  $\alpha = 0.05$  level.

	<i>I. pustularia</i>	<i>M. canadaria</i>	<i>H. unipunctata</i>	<i>B. endropiaria</i>	<i>H. guttivitta</i>	<i>H. fucosa</i>	<i>Z. minerea</i>	<i>C. micronympha</i>	<i>A. ovata</i>	<i>P. latex</i>
<i>I. pustularia</i>										
<i>M. canadaria</i>	<b>0.20</b> (0.01, 0.42)		0.13 0.07	<b>-0.33</b> 0.13 0.10	<b>0.43</b> 0.02 <b>0.54</b>	0.15 -0.06 <b>0.52</b> <b>0.29</b> 0.11	0.03 <b>0.49</b> 0.15 0.23 <b>0.44</b> 0.06	0.30 -0.04 <b>0.40</b> -0.32* -0.29 <b>0.38</b> -0.02	<b>-0.39</b> <b>0.27</b> 0.19 <b>0.71</b> <b>0.67</b> <b>0.31</b> <b>0.25*</b> -0.29*	<b>-0.32</b> <b>0.24*</b> 0.10 <b>0.63</b> <b>0.60</b> <b>0.15*</b> <b>0.40</b> -0.32
<i>H. unipunctata</i>	(-0.27, 0.61)	(-0.38, 0.48)								
<i>B. endropiaria</i>	(-0.61, -0.05)	(-0.22, 0.38)	(-0.19, 0.35)							
<i>H. guttivitta</i>	(-0.51, 0.17)	(0.18, 0.63)	(-0.22, 0.28)	(0.25, 0.78)						
<i>H. fucosa</i>	(-0.12, 0.48)	(-0.55, 0.39)	(0.32, 0.70)	(0.09, 0.50)	(-0.18, 0.43)					
<i>Z. minerea</i>	(-0.29, 0.42)	(0.22, 0.73)	(-0.29, 0.53)	(-0.17, 0.57)	(0.16, 0.70)	(-0.25, 0.38)				
<i>C. micronympha</i>	(-0.38, 0.73)	(-0.47, 0.42)	(0.06, 0.70)	(-0.62, 0.05)	(-0.76, 0.22)	(0.12, 0.66)	(-0.41, 0.27)			
<i>A. ovata</i>	(-0.67, -0.02)	(0.02, 0.54)	(-0.21, 0.50)	(0.61, 0.81)	(0.44, 0.85)	(0.01, 0.58)	(-0.07, 0.58)			
<i>P. latex</i>	(-0.55, -0.02)	(-0.05, 0.44)	(-0.34, 0.49)	(0.40, 0.80)	(0.43, 0.81)	(-0.06, 0.35)	(0.04, 0.65)	(-0.63, 0.18)	(-0.77, 0.29)	(0.46, 0.70)

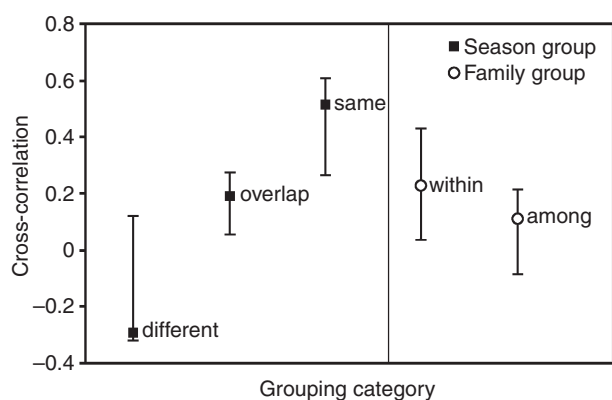
moth behaviour appears to be a negligible influence on the synchrony documented herein.

Weather has been implicated as a synchronising mechanism in several species (Peltonen *et al.*, 2002; Post & Forchhammer, 2002), and there is general agreement on the importance of weather on insect population dynamics. Previous studies examining the role of weather on population synchrony have been either theoretical (Ranta *et al.*, 1995a; Heino *et al.*, 1997; Ranta *et al.*, 1997; Kendall *et al.*, 2000; Ripa, 2000) or utilised weather data from weather stations separated by much larger distances (Lindström *et al.*, 1996; Hawkins & Holyoak, 1998; Peltonen *et al.*, 2002; Post & Forchhammer, 2002). Many of these studies merge on the conclusion that dispersal is an important synchronising agent at local scales, whereas environmental influence, although present at all scales, are a more dominant synchronising agent at landscape scales. In this study, the distance between local populations (<65 km) represents a local scale relative to the spatial scale of previous studies and weather appears to be capable of explaining some of the synchrony of local populations. Despite these findings, dispersal and community processes should not be overlooked as important synchronising mechanisms, nor should the potential interactions among them (Kendall *et al.*, 2000).

Patterns of interspecific synchrony have received far less attention than the spatial synchrony of conspecific populations. Since local populations of different species are not linked by dispersal, synchronous environmental stochasticity (Ranta *et al.*, 1995b; Heino *et al.*, 1997; Hawkins & Holyoak, 1998) and shared trophic effects (Ydenberg, 1987; Marcström *et al.*, 1988; Ims & Steen, 1990; Norrdahl & Korpimäki, 1996) are the mechanisms that have been proposed as causes of synchrony in previous studies. Koenig (2001) expanded the research on interspecific synchrony to include bottom-up factors and found that there was only a weak relationship between interspecific synchrony and the diet of boreal birds throughout North America. In a similar approach, the possible relationship of interspecific synchrony with phylogenetic and phenologic categories is explored here.

The comparison of interspecific synchrony and phylogenetic similarity is based on the assumption that species within a family have more closely related life histories, which are directly related to population dynamics (Price, 1997). Species within a family can also be expected to share more natural enemies than species among families. Since shared natural enemies may synchronise the dynamics of two or more species, a higher synchrony of species within a family than among families could be expected. This study did not detect higher interspecific synchrony within families and was unable to find an association between interspecific synchrony and species taxonomic similarity. This analysis, however, was limited by a small sample of species from large, diverse families and does not rule out synchronisation via shared natural enemies; however, these results do not provide encouraging support for this hypothesis.

This study detected a significant relationship among interspecific synchrony and larval phenology. Based on

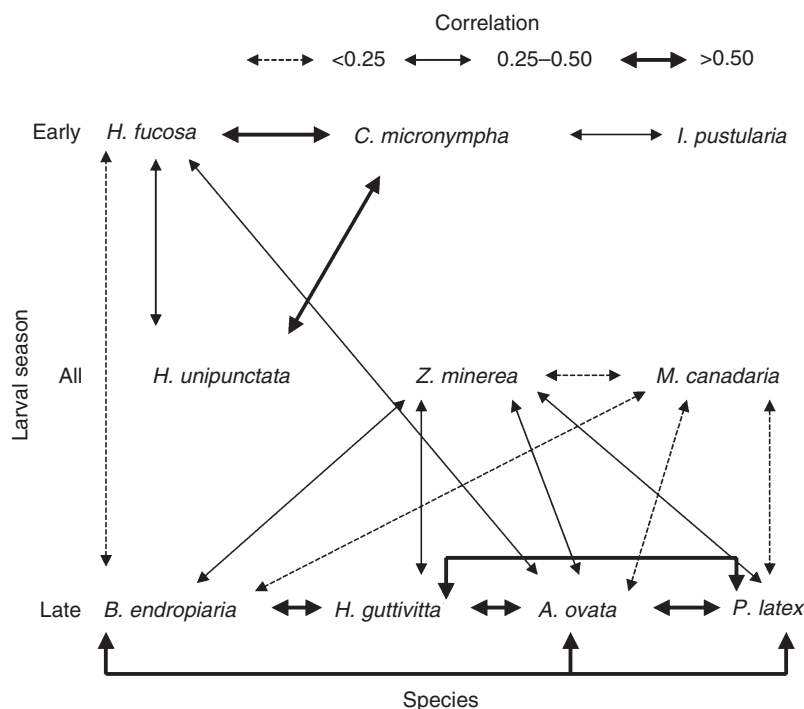


**Fig. 3.** Median correlation of species present as larvae in seasonal and phylogenetic categories. Error bars indicate the inter-quartile range.

the 10 species in this study, species with larvae present during the same season of the year exhibited more highly synchronised fluctuations relative to those with larvae present in different seasons. Species with larvae present during overlapping seasons generally exhibited intermediate levels of interspecific synchrony. High correlations within a phenological group suggest that weather may have a synchronising effect on species whose larvae are present at similar times of the season, and different weather variables may influence caterpillars present during different seasons.

Comparing the observed interspecific synchrony to the relationship of each species with weather yielded mixed results in support of this hypothesis. In six synchronous species pairs, both species were significantly related to the same weather variable (Table 4). Of the three species with spring larvae, *I. pustularia* and *C. micronympha* were related to precipitation while *H. fucosa* was related to maximum temperature. Species whose larvae were present throughout the season were all positively related to different weather variables and *M. canadaria* and *H. unipunctata* were both negatively related to minimum temperature. Species with mid-late season larvae were related to either maximum temperature, precipitation, or both (exception: *Acrionicta ovata* Grote).

Several other environmental variables not measured in this study may also be instrumental in synchronising species within a season. For example, winter temperature and precipitation were not measured on the plots but may have been mechanisms of interspecific synchrony. Host-plant quality also changes throughout the season and influences Lepidoptera dynamics (Price, 1997). Several species pairs that were highly synchronised feed on different plant groups and changes occurring to specific host plants are not a likely candidate to explain the within-season synchrony of the different species in this study. For example, *Hypoprepia fucosa* and *Catocala micronympha* are spring caterpillars with a significant cross-correlation coefficient and feed on different plant groups (*Hypoprepia fucosa*, lichens and mosses; *Catocala micronympha*, oaks). The families of Lepidoptera



**Fig. 4.** Interspecific synchrony of species present as larvae in the early season, late (mid-late) season, and all season. Arrows indicate significant region-wide cross-correlations and the width of the arrow indicates the intensity of the correlation.



studied here are large and diverse, and are composed of species whose larvae are active in several different and overlapping seasons. Therefore, the association of interspecific synchrony with seasonal life history did not appear to be confounded with taxonomic associations in this study.

A complicated step in bridging the gap between theoretical and empirical spatial dynamics is the empirical testing of possible causal mechanisms (Bjørnstad *et al.*, 1999). Identifying cause and effect relationships in highly complex ecosystems such as the eastern deciduous forests realistically may be improbable; however, patterns of spatial covariance among Lepidoptera species abundance, weather, and larval phenology were demonstrated. The species in this study demonstrated spatial patterns that would be expected under the influence of the synchronised climatic effects, although the relative roles of weather, dispersal, and trophic interactions could not definitely be distinguished. Interspecific synchrony may result from the synchrony of both species with weather factors and was related to larval phenology, impressing the potential of weather and seasonality on interspecific synchrony of moth populations.

### Acknowledgements

We are grateful for the work of Vicki Kondo, Deb Blue, Greg Chrislip, graduate students, and numerous summer student workers for their help collecting and processing specimens. Ottar Bjørnstad provided helpful statistical assistance. We thank Todd Petty, James Amrine, Henry Hogmire, and two anonymous reviewers for their comments which greatly improved this manuscript. Financial support was provided by the USDA Forest Service as cooperative agreement 42-793 and 42-98-0006.

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Accepted 1 September 2003